

ECOLOGY & EVOLUTIONARY BIOLOGY  
PRINCETON UNIVERSITY

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SENIOR THESIS ABSTRACTS







## EXPLORING THE SOCIAL AND BIOLOGICAL DIMENSIONS OF INFECTIOUS DISEASE: RUBELLA POPULATION DYNAMICS IN MADAGASCAR

**Introduction:** Rubella is a contagious childhood disease that infects children. Though not fatal, if pregnant women are infected with rubella, their fetus can be infected, resulting in congenital rubella syndrome, a disease with serious, and fatal complications. As Madagascar is on the verge of introducing a rubella-containing vaccine, it is important to explore the population dynamics of rubella and the possible social obstacles that will prevent its success. This study seeks to do so by exploring different biological and social dynamics of rubella in Madagascar. A dataset provided by the Institut Pasteur of Madagascar, where rubella and measles testing is routinely done, consisting of serological and demographic information, will be used.

**Methods:** Statistical tests were performed to measure the significance of predictor variables. We measured the relationship between age and incidence, and age and titers. This was followed by a measurement of the relationship between incidence and titers. We then measured the relationship between population size and incidence, and population size and titers. We measured the relationship between the number of health centers and incidence. Lastly, a descriptive analysis was done using maps to compare poverty levels to incidence.

**Results:** We found that age was a significant predictor of incidence and titers. In addition, we found that incidence, or the number of new cases, had a significant relationship with titers. Population size and the number of health centers were not found to be significant predictors of incidence and/or titers.

**Discussion:** With age and incidence proving to be significant predictor of titers, these two dynamics will be key factors to consider when determining the best mode of implementation. Further testing should be done in order to determine if population size is significant, without the sampling bias that was evident in this study. Lastly, the possibility that the poorer regions would be home to vulnerable populations, is worth exploring as careful implementation is needed for adequate vaccination coverage.

## A SPATIAL AND TEMPORAL SENTIMENT ANALYSIS OF THE HUMAN PAPILOMAVIRUS VACCINE IN THE EUROPEAN UNION AND THE UNITED STATES

The human papillomavirus (HPV) is a sexually transmitted, oncogenic pathogen. High-risk forms of HPV are known to be the foremost cause of cervical cancer worldwide, thus placing a major burden of disease globally in the female population. With the emergence of three separate vaccines (Gardasil, Gardasil-9, and Cervarix) and the introduction of vaccination programs throughout the globe starting in mid-2006, there has been a recent revolution in the treatment and preventative care of HPV. In fact, vaccination has been shown to be the most effective form of protection against HPV infection. However, the relatively novel introduction of the vaccine and the sexual means of transmission have led to a whole new set of problems in terms of vaccine refusal. Specifically, vaccine refusal was observed to have grown stronger in the European Union starting in mid-2013 due to increased concerns that the vaccine was causing side effects, such as Postural Orthostatic Tachycardia Syndrome (POTS) and Complex Regional Pain Syndrome (CRPS). In response to this, at the request of Denmark, the European Medicines Agency (EMA) launched an investigation into the safety profile of the vaccine. Simultaneously, in conjunction with the London School of Hygiene and Tropical Medicine (LSHTM), the EMA conducted a media monitoring project to analyze public HPV vaccine sentiments. On November 5th, 2015, they released a report stating that there was not, in fact, a causal link between the vaccine and POTS or CRPS.

This thesis aims to explore the factors that have inhibited vaccine confidence in both the European Union (EU) and the United States through analyzation of the database produced through the HPV Media Monitoring Project. Through this analysis, I will be able to examine vaccine concerns that have arisen in the EU and the United States in the vaccine's post-authorization phase. My research objective here is three-fold: 1) to determine how European sentiments shifted following release of the EMA review, 2) to examine whether there was any spillover affects from the EMA review in the United States, and 3) to qualitatively examine, compare, and contrast the major concerns that have motivated vaccine refusal in Europe and the United States.

Supported by the Health Grade Challenges, Mount Lake Field Research Fund, Office of the Dean of the College

**TOBI ALADESURU**

ASSOCIATE PROFESSOR ANDREA GRAHAM

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## EFFECTS OF INTESTINAL PARASITE INFECTION ON BLOOD PROTEIN LEVELS IN PEROMYSCUS MANICULATUS AND PEROMYSCUS LEUCOPUS

The global burden of parasite infection is incredibly high, with two billion people being infected with parasitic helminths alone. The ability of an organism to deal with infection is likely one of the most important determinants of the organism's reproductive success and fitness, yet the immunological defenses required to fight infection are costly. This study aims to examine the relationship between parasitic infection, serum protein levels, and body condition in a population of wild *Peromyscus* mice at the Mountain Lake Biological Station in southwestern Virginia. Specifically, I sought to determine how albumin, total protein, and the albumin-total protein ratio relate to body condition and other host traits, to determine the relationship between albumin, total protein, and parasite burden, and to determine how anti-helminthic treatment and the resulting decrease in parasite burden affects albumin and total protein concentrations. *Peromyscus* plasma samples were assayed for albumin and total protein to serum concentrations, *Peromyscus* fecal samples were examined with a fecal egg count, and a scaled body condition index was created for the population. General linear models and general linear mixed models were used to assess the relationships between the factors of interest. It was found that the total protein concentration and the albumin-total protein ratio are significantly related to the change in parasite burden in the host, and the relationship between protein levels and parasite burden is indicative of protein investment in the immune system during immune challenge.

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GENETICS AND ATHLETICS: GENETIC VARIATION IN  
MITOCHONDRIAL DNA COPY NUMBER AND THE RESPONSE  
TO ENDURANCE EXERCISE TRAINING IN DROSOPHILA  
MELANOGASTER

Genetics and Athletics: Genetic Variation in Mitochondrial DNA Copy Number and the Response to Endurance Exercise Training in *Drosophila melanogaster*

Many physical performance-related traits have been shown to exhibit genetic variation. Mitochondrial DNA copy number plays an important role in determining aerobic capacity and therefore overall health and physical performance. However, few studies have identified genetic determinants of interindividual variation in this trait at a baseline level or post-exercise. Some factors controlling the process of mtDNA regulation additionally remain unknown. This project therefore first explores the genetic variability and heritability of baseline mtDNA copy number. By screening the *Drosophila* Genetic Reference Panel (DGRP) for variation in mtDNA content and then performing a GWAS using mtDNA copy number as the trait, I identify 22 highly significant SNPs ( $p < 1E-9$ ) associated with mtDNA content within 7 regions of the nuclear genome. None of the genes within these loci have been associated with mtDNA copy number regulation before. Upon finding that mtDNA content is genetically variable, heritable, and highly associated with these genomic regions, I then investigate how plastic mtDNA copy number is in *Drosophila* in response to endurance exercise training. I also study changes in a number of other phenotypes known to be affected by prolonged exercise, including body size, activity levels, and sleep. Since these traits may be affected differently in *Drosophila* as compared to humans and other vertebrate species, these observations are important in determining the validity of *Drosophila melanogaster* as a model organism for further studies that examine genetic variation in the responses to exercise training. I find that endurance exercise training significantly increases mtDNA copy number, decreases body size and activity levels, and has no significant effect on sleep patterns in *Drosophila*.

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## AGE-DEPENDENT PATTERNS OF ASTHMA SEASONALITY AND ENVIRONMENTAL DRIVERS IN MEXICO

Asthma is one of the most common respiratory diseases, afflicting 300 million people worldwide each year. Despite being a frequent source of hospitalizations in Mexico, little is known about its seasonality. In this thesis, I explore the seasonality of asthma nationwide in Mexico, paying close attention to age-related differences. In addition, I investigate potential relationships between asthma, climatic variables, and respiratory syncytial virus (RSV).

My main findings are that asthma seasonality is age-dependent, evolving from a double-peaked curve to U-shaped with increasing age. The strongest geographic patterns are found for the youngest age group, where the two predominant regions fall mainly along the coast and inland in areas of high elevation. We find that RSV may contribute most significantly to asthma in the purple regions of the youngest age groups, but not to the older age groups or the inland regions of the younger age groups. Humidity appears to be the most influential climatic variable for the two youngest age groups, conceivably indirectly triggering asthma by increasing dust mite populations or other aeroallergens. Relative humidity is the strongest predictor of asthma for age 0-4 and specific humidity is the strongest predictor for age 5-14. Meanwhile, the largest predictor of asthma for the oldest age groups could be minimum temperature, with asthma peaks occurring just after the coldest week in the year for all regions above age 45.

This thesis provides a novel description of asthma seasonality and age-related differences nationwide in Mexico. In it, I employ a novel approach of using EPIPOI data visualization software to form "seasonal regions" rather than geographic regions to crystallize similar patterns could be a useful qualitative strategy for future epidemiologists interested in reducing noise in the preliminary steps of research.

## SOCIOECONOMIC INDICATORS OF DENGUE AND ZIKA IN RIO DE JANEIRO BRAZIL: A BAYESIAN APPROACH

Associating dengue incidence rates with socioeconomic and demographic indicators is vital for anticipating and understanding outbreaks of dengue and other similar arboviruses, like the Zika virus. In this paper, we explore this relationship with a Bayesian model analyzing dengue incidence from the neighborhoods of Rio de Janeiro, Brazil. We aggregate monthly dengue incidence rates into three markers: the first, alpha, characterizes dengue epidemic frequency; the second, beta, shows the average duration of an epidemic; and the third, gamma, is a proxy for maximum dengue epidemic intensity. We demonstrate that though there is a limited relationship between alpha and beta and our indicators, gamma shows a strong positive relationship with the proportion of a neighborhood's heads of household earning less than one minimum wage. This observation adds to the evidence that low socioeconomic status is related to increased dengue incidence in urban environments. Our study's last step is to compare these dengue indices to preliminary Zika data in order to draw early conclusions about this new virus' transmission. Although we found inconclusive relationships between our Zika data and dengue markers, we stress that with dengue data aggregated at a smaller scale and a larger sample size of Zika cases, minor but significant variation between the two viruses will become evident.

THE EFFECT OF OCTOPAMINE BODY SIZE AND OVARIAN  
DEVELOPMENT ON CASTE-CHARACTERISTIC BEHAVIOR IN  
THE FACULTATIVELY EUSOCIAL AND SOLITARY BEES  
MEGALOPTA (HYMENOPTERA: HALICTIDAE)

In eusocial species, workers forfeit their ability to reproduce in order to assist the queen in raising offspring. In the facultatively eusocial and solitary bee, *Megalopta genalis*, queens recruit workers by aggressively dominating their daughters. However, the neurobiological mechanism that underlies this behavior and the emergence of new social phenotypes has not been studied. I observed the effect of the biogenic amine, octopamine (OA), on caste-characteristic aggression in queens, workers, and solitary foundresses, using a circle tube apparatus. Additionally, I compared the effects of body size and ovarian development on behavior in social and solitary females. Although OA did not have a significant effect, I found that in social pairs, a bee's behavior predicted its partner's when these interactions were worker-like. Furthermore, data shows that ovarian development, but not head size, predicted caste-characteristic behavior in workers, while the opposite was true for solitaires; larger head size, but not ovary size, was associated with queen-like behavior. These findings support the hypothesis that queens influence the behavior and physiology of their daughters. Notably, they also suggest that distinct mechanisms determine dominant and submissive interactions in social and solitary females.

**A GOOD LAND IS HARD TO FIND: THE EFFECTS OF LAND  
DEGRADATION ON GIRAFFE SOCIAL STRUCTURE IN CENTRAL  
KENYA**

This research aims to examine the effects of nearby land degradation on the social structure of the Reticulated giraffe (*Giraffa camelopardalis reticulata*) living in the Mpala Research Center, Laikipia County, Kenya. By using photographs to recognize unique individuals, meta-data about group composition and location, lion tracker data, home range and social network analysis, a comprehensive study is created on the differences in how the giraffe in this region are arranging themselves across the various habitats. The results suggest that younger giraffe are more commonly located on the Group Ranches as opposed to the conservancy, as a possible result of their natural predators, lions, not being present at all on the Group Ranches. A second finding supports that tree density is much higher on the conservancy than the Group Ranches, therefore able support a larger population of giraffe. Finally, the social networks created indicate a trend toward closer ties to conspecifics when food abundance is higher. Understanding the effects of lower quality habitats on animal behavior is important for improving future conservation efforts.

AN EVALUATION OF A MITIGATION PROPOSAL FOR THE RED-  
COCKADED WOODPECKERS (*PICOIDES BOREALIS*) OF  
CAINHOY PLANTATION SOUTH CAROLINA

The endangered red-cockaded woodpecker (*Picoides borealis*) has suffered extirpation from the pine forests of the Southeast largely due to loss of suitable habitat to logging and development. In response to these heavy losses, the Endangered Species Act of 1973 mandated that federal and state bodies actively manage the habitat of the bird to encourage population growth and viability. Private landowners are prohibited from harming birds on their property; however, landowners wishing to develop their property may apply for incidental take permits. One such property, with 16 groups of red-cockaded woodpeckers ("RCW"), is the 9,087-acre Cainho Plantation, in South Carolina. In 2013, the owners of Cainho proposed, and received approval for, a master plan to develop the property. Schematics of the master plan show significant portions of the RCW-occupied longleaf pine habitat being developed. This research evaluated the 2013 draft Habitat Conservation Plan off-site mitigation proposal in the context of the literature on RCWs and conservation biology. I came to the conclusion that the following must be included to ensure mitigation for the 11 RCW groups that require incidental take permits prior to development: (i) a 2:1 ratio of established fledglings to impacted groups, (ii) a higher number of average fledglings per group to promote 5 percent population growth, and (iii) articulation plan for long-term population viability of the newly established groups at Cheeha and Hitchcock Woods. I also found that the mitigation proposal overlooks the harm to the RCW population of the adjacent Francis Marion National Forest ("FMNF") and considered the use of buffer zones to mitigate for harm to the neighboring birds. I then considered a "No-Take," on-site mitigation alternative that calls for a revised urban design to eliminate the need for incidental take permits. By examining and weighing the pros and cons of the potential Cainho mitigation mechanisms from a biological perspective, this study discusses two approaches for the mitigation of the Cainho RCWs within the context of the Endangered Species Act, Habitat Conservation Plan, and Recovery Plan.

## JONATHAN CARCIONE

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ASSISTANT PROFESSOR ROBERT PRINGLE

### CAN PREY-NAÏVETÉ EXPLAIN INVASIVE PREDATOR SUCCESS? ANTI-PREDATOR RESPONSES OF NATIVE FLORIDA FISH IN THE PRESENCE OF THE INVASIVE HEMICHROMIS LETOURNEUXI

The African jewelfish (*Hemichromis letourneuxi*) is a freshwater cichlid that has become highly invasive in Southern and Central Florida over the last 50 years. Jewelfish prey on a multitude of native species, though why jewelfish have become so dominant in invaded waters remains largely unknown. To explain jewelfish success, several scholars have invoked the naïve-prey hypothesis (NPH), which attributes invasive species success to native prey species lacking the anti-predator adaptations needed to survive the new threat. However, these studies failed to manipulate prey-naïveté—a necessary requisite for testing the NPH—and are therefore unconvincing. To address this concern, I captured populations of two indigenous prey species, the eastern mosquitofish (*Gambusia holbrooki*) and golden topminnow (*Fundulus chrysotus*), which I then exposed to jewelfish or a native predator, bluegill (*Lepomis macrochirus*). Within these species, I examined the behavioral differences between populations that had previously coexisted with jewelfish (experienced) versus those that had not (naïve) by filming the interaction between a single native fish and a single predator in aquaria. I examined (1) average speed, (2) vertical distribution, (3) predator-prey distance, and (4) proportion of time behind cover. In the presence of jewelfish, only decreased average speed was observed in experienced compared to naïve native fish, lending support to the NPH. However, that I did not observe significant differences between experienced and naïve individuals in (2)- (4) suggests that other, yet-unknown factors beyond the NPH must also account for jewelfish success. To this end, future studies should be intervention-focused, which would not only address the practical issue of jewelfish eradication but also illuminate the underlying scientific principles behind the establishment of jewelfish in Florida.

Supported by the Princeton Environmental Institute, John Bonner Senior Thesis Fund,  
Office of the Dean of the College

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## THE EFFECTS OF URBANIZATION ON THE MAJOR HISTOCOMPATIBILITY COMPLEX IN RED FOX (*VULPES VULPES*)

The red fox (*Vulpes vulpes*) is recognized as being one of the most plastic species in its ability to occupy both cities and their surrounding rural environments. In the city and suburbs of Zurich, Switzerland five fox populations were studied. A previous study by Wandeler et al. (2003) showed that there was genetic differentiation among neutral microsatellite loci. Here, I expanded on their research and explored the hypothesis that varying patterns in genetic structure are due to habitat location. I examined 11 Major Histocompatibility Complex (MHC) loci in 100 foxes from three rural and two urban areas. Non-modeling and modeling approaches were used to estimate spatial clustering and ideal population size and revealed that there was a significant relationship between population loci differentiation and spatial clustering. These results indicate that observed patterns in MHC variation are due to various geographic locations and their respective selection pressures. It would be beneficial for future researchers to explore contemporary studies and further compare the genetic variation among the urban and rural fox populations.

**SCOTT CARPENTER**

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ASSISTANT PROFESSOR CORINA TARNITA

## COMPETITIVE OVERDISPERSAL PATTERNS IN A MULTISPECIES SYSTEM OF MOUND-BUILDING TERMITES

Natural patterns have become increasingly more observable in recent years due to the increase in global satellite images. With these increasing discoveries a debate has formed over the exact mechanisms these patterns form. Recently, models have been proposed that incorporate multiple patterning mechanisms to explain patterns as the result of interactions between these mechanisms at different spatial scales.<sup>1,2</sup> One of these recent models uses interactions between termite mounds and vegetation to explain the presence of gaps and patches in a savannah landscape. Overdispersal patterns resulting from competition between termite mounds have previously been shown to promote vegetation biodiversity and ecosystem resistance to desertification.<sup>3,4</sup> Thus, understanding the details of this overdispersal may provide key insights to interpreting the effects of environmental change in dryland ecosystems. Many studies have shown the formation of competitive overdispersal patterns in systems with a single termite species, but there have been no studies attempting to show the resulting spatial distribution of mounds in a landscape with multiple mound-building species.<sup>5–8</sup> This study uses manual survey techniques to conduct a pattern analysis of multiple plots in Kenya, which contain two genera of mound-building termites (*Macrotermes* and *Odontotermes*).

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SELECTIVE LOGGING IN A SUMATRAN RAINFOREST: AN  
ANALYSIS ON HOW BIRD SPECIES RICHNESS ABUNDANCE  
AND COMMUNITY COMPOSITION RESPOND TO LOGGING  
INTENSITY

Despite decades of study on the impacts of selective logging on forest biodiversity, there continues to be uncertainty on how bird populations respond to this type of habitat disturbance. On the island of Sumatra, Indonesia, a previously heavily logged rainforest, the Harapan Rainforest Ecosystem Restoration Concession, has recently come under environmental protection, opening an opportunity to study how the bird biodiversity in this forest compares to that of an unlogged protected forest. I report on the impact of selective logging intensity on species richness, total abundance, and community composition. I focus my analysis on modeling abundances for 12 focal species, including the critically endangered Helmeted Hornbill. My study suggests that there are limited short-term benefits to some bird species in selectively logged forests but the long-term implications are still not understood.

## HIGH STEAKS: QUANTIFYING THE EFFECTS OF A USER FEE ON ANTIBIOTIC USE IN LIVESTOCK AND IDENTIFYING POLICY IMPLICATIONS

As bacterial resistance to antibiotics rises and poses a threat to human health, efforts to reduce the exorbitant use of antibiotics in livestock are increasingly important. Antibiotic use in livestock has a direct impact on human health. This study used data on retail prices of veterinary antibiotics and trade data to estimate the potential global reduction in use and revenue generated from a tax fee. Calculations estimated large reduction in use with significant revenues generated that could fund research and development of newer, better antibiotics.

## THE GLOBAL EMERGENCE OF COXSACKIEVIRUS-A6 AS A MAJOR CAUSATIVE AGENT OF HAND FOOT AND MOUTH DISEASE

Following the near-complete eradication of polio, non-polio enteroviruses have become responsible for large outbreaks of Hand, Foot, and Mouth Disease (HFMD) and, less frequently, severe and sometimes fatal neurological complications. The predominant enteroviruses responsible for the common childhood illness are Enterovirus-71 (EV-71) and Coxsackievirus-A16 (CV-A16), but Coxsackievirus-A6 (CV-A6) has increasingly been reported as a causative agent in a series of HFMD outbreaks worldwide since 2008. The rise of CV-A6-associated HFMD incidence has presented new challenges in the control and prevention of HFMD not only because CV-A6-associated HFMD has different clinical features from "classic" HFMD caused by EV-71 and CV-A16, but also because of the general lack of understanding of CV-A6 as an etiological agent of HFMD. To address this gap in knowledge, this thesis documents and elucidates the global emergence of CV-A6 as a significant cause of HFMD for the first time through a combination of a systematic review of published studies and public health surveillance reports, epidemiological data analysis, and mathematical modeling. The systematic review revealed that CV-A6's emergence occurred in different regions across the globe over the span of a five-year period (2008-2013) and that it coincided with a change in its genotype. This suggests that a new, more virulent variant of CV-A6, one that has evolved to partially escape from cross-immunity protection from other circulating enteroviruses, is likely responsible for CV-A6's rise as a significant cause of HFMD. As CV-A6 "escaped," its reproductive number ( $R_0$ ) likely increased, and individuals immunologically naive to the strain accumulated until there were enough susceptibles for outbreaks. To test this hypothesis, this thesis adapted a previously published Time-Series Susceptible-Infected-Recovered (TSIR) model and explored the relationship between the transmission rate  $\beta$ , which acts as a proxy for ( $R_0$ ) in this model, and the epidemic patterns through simulations of CV-A6-associated HFMD disease dynamics in Japan. The results ultimately demonstrated that slightly increasing  $\beta$  produces cycles that qualitatively resemble HFMD's biennial patterns in Japan, thereby supporting our hypothesis. However, this study is limited in that it only indirectly investigates the effects of cross-immunity protection, so future models should include multiple enteroviruses to directly test the hypothesis.

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THE GLOBAL EMERGENCE OF COXSACKIEVIRUS-A6 AS A  
MAJOR CAUSATIVE AGENT OF HAND FOOT AND MOUTH  
DISEASE

The Florida Scrub-Jay (*Aphelocoma coerulescens*) lives on a small area of land in central Florida and is dependent on the scrub, a pyrogenic system. It is currently listed as a threatened species due to habitat loss through human development and habitat degradation through fire suppression. Theory surrounding the concept of trade-offs states that an organism's limited reserve of energy requires it to invest in some aspects of life history at the cost of taking investment away from other aspects of life history. Studies have shown that adult Florida Scrub-Jays experience trade-offs in actions as their territory undergoes longer periods of fire suppression. This thesis investigates the effect of Time Since Fire on measurements of fledgling provisioning inequality to determine if fire suppression has an impact on adults' investment in total fledgling provisioning and in preferential provisioning. Furthermore, measurements of fledgling provisioning inequality are investigated to determine if provisioning inequality could potentially affect the ultimate fitness of resulting independent jays. This study shows that the percent of usable land with a TSF of at least ten years has a negative effect on the feeding rate of a territory; the percent of usable land with a TSF of at least ten years has no effect on measurements of feeding rate inequality when unidentified feedings are taken into account; measurements of feeding rate inequality can affect measurements of inequality of body mass at 85 days old. Understanding fire suppression's effect on the Florida Scrub-Jay will allow for better conservation and species management decisions to be made in the future.

**MICROBIAL DYNAMICS OF TROPICAL NITROGEN FIXATION:  
RELAXED SELECTIVITY FOR NODULE SYMBIONTS UNDER  
REDUCED N DEMAND**

Symbiotic nitrogen fixing plants supply tropical forests with much of the nitrogen needed to recover from land use change, respond to disturbance, and to potentially serve as vast carbon sinks under anthropogenic change. However, fixation and the associated rapid plant growth taper off in characteristic ways as forests progress through successional time, relative N supply becomes unproblematic, and active fixation loses its competitive advantage. Although actual N fixation is carried out by microbial symbionts housed inside plants' root nodules, little is known about how the dynamics of the plant-microbe mutualism map onto broad-scale fixation patterns and perhaps contribute to tropical forest growth limitations. In order to investigate potential microbial controls on fixation patterns, this metagenomic study compares partial 16S rRNA data from the bulk soil, the rhizosphere, and the root nodules of a representative N fixing tree at two key successional time points in the tropical forests of Panama—in early succession, when pressure to fix N is high; and in mid-succession, when pressure to fix N is low. Doing so reveals decreased selectivity for nodule community structure under reduced pressure for N fixation, as well as intriguing looks into the give-and-take of this essential mutualism.

**CHAGAS DISEASE ECOLOGY IN TRINIDAD: TRYPANOSOMA  
CRUZI INFECTION STATUS AND BLOODMEAL ANALYSIS OF  
TRITOMINE BUGS ON AN ISLAND CONSIDERED FREE OF  
VECTOR-BORNE TRANSMISSION**

Background: Triatomine bugs, the vectors of Chagas disease, are found throughout several islands in the Caribbean (Petana, 1978), however little is known about the disease in the region despite their presence. This research aims to explore the ecology of Chagas disease in Trinidad through an investigation of triatomine habitat, *T. cruzi* infection status, *T. rangeli* (a common co-infecter (Peterson et al., 2016)) infection status, and bloodmeal source in order to determine if the infected vector is making contact with humans (Eakes, May 2016).

Method: Triatomine bugs were collected across the island of Trinidad using mouse-baited "Noireau traps" (Noireau et al., 2002) and collection cups given to people living near sample sites. Collected bugs were analyzed in lab for the presence of *T. cruzi* DNA, *T. rangeli* DNA, and last mammalian bloodmeal source. Using a Chi-Square Test of Independence, we investigated an association between infection status and 1.) triatomine sex and 2.) bloodmeal source.

Results: In total, 55 triatomine bugs were collected. All bugs were collected in one of five locations, with 46 (83.6%) coming from one location, Coalmine. All successful collection sites were forested areas near the northern and central range mountains, and all bugs were collected in and around human homes. 46 (83.6%) of the bugs were positive for *T. cruzi*, and of these, 20 contained human bloodmeals. We found a significant association between female bugs and positive infection status of bugs from Coalmine ( $p=1.397e-11$ ).

Conclusion: This study suggests that Chagas disease is a health concern in Trinidad, as there is the potential for *T. cruzi* transmission to humans. Much is still unknown about the habitats and seasonal behavior of the triatomine vectors in Trinidad, however this study sets the stage for many promising directions of future research on Chagas disease vector ecology in Trinidad.

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## A MULTIFACTORIAL INVESTIGATION OF THE ROLE OF WATER IN SHAPING STRONGYLE PARASITE BURDEN RISK IN GREVY'S AND PLAINS ZEBRAS

While strongyle parasites infect both Grevy's and Plains zebras, a discrepancy exists in the species' burdens; specifically, Plains zebras typically exhibit higher parasite loads than Grevy's zebras (Rubenstein, 2010). This study sought to understand the underlying interactions that shape this discrepancy in parasite burden by examining how water influences zebra risk of infection on both the host and parasite sides of transmission.

Through field and laboratory work conducted at the Mpala Research Centre in Laikipia, Kenya, this study found a strong inverse relationship between host distance to water and parasite burdens. This relationship is attributed to the greater presence of dung found in close proximity to water sources, which in turn is shaped by the spatial distributions of hosts governed by the water requirements of each species. Plains zebras are more water-restricted, meaning they must remain closer to water, while Grevy's zebras' ability to survive for longer periods of time without water allow them to range farther from shared water sources (Rubenstein, 2010). Given these differences in water use, Plains zebras are more concentrated on landscapes around water and more likely to graze on infected vegetation in these areas of elevated risk. Season was also found to be an influencing but secondary factor for risk of infection. Study of strongyle survival across microclimate conditions corroborated the role of parasite survival in shaping host risk of infection by demonstrating the importance of moisture and grass (as a sheltering mechanism) for maximizing the number of strongyle on the landscape. The study concludes that the availability of water throughout the landscape governs host spatial distributions and strongyle survival, shaping the likelihood of transmission and determining infection risk.

Given the endangered status of Grevy's zebras, understanding the formative role that water plays in determining host risk of infection and subsequent health is essential in crafting effective conservation policies and programs in the face of changing environmental conditions. Finally, the findings of this study can be applied in persuading pastoral herders to cease culling zebras by coupling a non-pharmaceutical parasite reduction strategy found in this study with the facilitative relationship between wildlife and livestock.

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**CAROLINE GRIFFIN**

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ASSOCIATE PROFESSOR PETER ANDOLFATTO

## THE COMMON SKATE: AN ASSESSMENT FOR SUSTAINABLE MANAGEMENT OF A POPULATION ON THE BRINK OF EXTINCTION

World fisheries have been historically plagued by unsustainable fishing practices that result in environmental degradation and population decline due to overexploitation of marine species (Griffin, 2016). Elasmobranch species in particular are among those most severely threatened by the activity of commercial fisheries (Griffin, 2016). Elasmobranchs, which include sharks, skates, and rays, are highly susceptible to by-catch as they get unintentionally caught during efforts to target more commercially valuable fish (Griffin, 2016). Targeted efforts toward skate species are also on the rise in recent years as skates become increasingly valued for their edible wings. With the survivability of such marine species quickly declining, the need for effective management to regulate unsustainable practices in commercial fishing becomes abundantly clear. In this senior thesis we focus in on a particularly threatened elasmobranch species, the common skate. This species is highly susceptible to the threats of commercial exploitation due to its life history characteristics and as a result, has experienced severe declines over the last 40 years, particularly the Northeast Atlantic population of common skate (Dulvy et al., 2006). There is significant evidence for the importance of this skate's ecological function within its marine ecosystem and thus, great motivation for protecting the species from further decline and potential extinction (Link, 2007). This senior thesis will further explore the case study of the Northeast Atlantic population of common skate. After assessing the current status of the common skate based on available scientific literature, the thesis will evaluate the efficacy of the most commonly used management tools for bringing stability to commercial fisheries. Finally, through a synthesis of the first two sections of the thesis, there will be an argument made for the implementation of a management plan to protect and stabilize populations of the common skate in the Northeast Atlantic.

## JUSTINE HAMILTON

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ASSOCIATE PROFESSOR ANDREA GRAHAM

### DIET SELECTION AND PARASITE INFECTION IN PEROMYSCUS LEUCOPUS AND P. MANICULATUS: DO WILD MICE ALTER FORAGING BEHAVIOR TO COMBAT INTESTINAL PARASITES?

The motivation of this study is to explore possible changes in foraging during parasite infection and malnutrition in a population of wild *Peromyscus leucopus* and *P. maniculatus*. Prior literature demonstrates that some animals may alter diet selection during infection to influence immune responses or to self-medicate (Lozano 1991, Lisonbee et al. 2009). This could be a form of resistance as part of the co-evolutionary arms race between parasites and their hosts. Parasites and malnutrition also present a substantial health and economic burden for human populations, particularly in developing nations. The complex interactions between diet, immunity, and infection have been referred to as a negative spiral because malnutrition can be both a consequence and a predisposing factor of infection (Koski 2001). By studying how wild animals mitigate the impacts of parasites through diet modulation, we may learn useful information that can be applied to controlling human infections. Moreover, there are few drugs available to treat parasitic infections and there is a threat of resistant strains emerging in humans, livestock, and poultry. Therefore, addressing compounds that can potentially be used as a springboard for drug development, are valuable. This study uses fecal DNA metabarcoding to characterize diet and explore relationships with body condition and parasite infection. Results indicate that relative read abundance (RRA) of nuts, largely driven by *Quercus* spp. was significantly greater during nematode infection compared to mice that did not have nematodes or had been dewormed ( $p = 0.000154$ ). By contrast, RRA of dry dehiscent fruit, largely driven by legumes, was significantly lower during nematode infection ( $p = 0.00249$ ). Given that acorns tend to have a high fat content, a low fiber content, and contain higher concentrations of condensed tannins, which have been shown to have anthelmintic effects, these results may suggest that nematode-infected mice alter their diet based on nutrient composition and/or presence of anthelmintic compounds. No significant relationships were found between overall diet richness and infection status or body condition. Future research can elucidate the evolutionary significance of these dietary changes, as well as applications for infection control programs and drug development.

Supported by the Health Grade Challenges, Princeton Environmental Institute, Anthony B. Evnin '62 Senior Thesis Fund in Ecology & Evolutionary Biology, Office of the Dean of the College

## TROPICAL FOREST CARBON CYCLES: TWO MODELING CHALLENGES

Carbon storage, particularly above ground biomass (AGB) of tropical forests varies by biogeographic region, with palaeotropical forests in particular having higher AGB than neotropical forests. This regional difference in biomass could be driven by environmental factors, such as rainfall, temperature, soils, or disturbance, or could be driven by regional differences in plant traits, in particular height-diameter allometry. Feldpausch et al. (2010) developed regional allometric equations for African tropical forests that reflect the higher height of African tropical trees compared to Neotropical trees at any given diameter. Current allometric equations in the GFDL LM4-PPA assume pan-tropical height-diameter relationships; if height-diameter allometries indeed vary significantly by biogeographic region, this introduces global bias into tropical biomass estimates. The LM4-PPA has been parametrized in the past for a neotropical forest (Barro Colorado Island, Panama: BCI), but never before for a paleotropical forest. The purpose of this study is to parametrize and test the LM4-PPA for the first time in a palaeotropical forest. To do this, an African-specific plant functional type was created using data from Ankasa, Ghana, and the Feldpausch et al. (2010) regional height-diameter allometries, and simulated in both Ankasa and BCI. The LM4-PPA with African allometry underestimated NPP in Ankasa, yet overestimated biomass. This biomass overestimation was due to the fact that the allometric relationships designed both for the BCI location and the Feldpausch et al. (2010) regional allometry vastly overestimated tree height at every diameter. This work is an indication that there is a need for the LM4 model to be tested in more paleotropical locations, and that more variation in PFT allometry needs to be included in the LM4 PFTs, even beyond the regional level.

## THE EFFECT OF MHC GENES ON VACCINE RESPONSE IN SANTA CATALINA ISLAND FOXES

The island fox (*Urocyon littoralis*), descendant of the mainland gray fox (*Urocyon cinereo argenteus*), has six recognized subspecies, each inhabiting a different Channel Island of California. A combination of factors such as low genetic diversity, lack of previous exposure to common canine viruses, and long history of isolation left the island foxes vulnerable to an epizootic. A canine distemper virus (CDV) outbreak on Santa Catalina Island in 1999 decimated most of the population (Timm et al., 2009).

Intervention by the Catalina Island Conservancy, especially through efficient vaccination protocols, helped to save the population (King et al., 2014). Yet, even though there is a large genetic component to vaccine-induced immune response (Kimman et al., 2007), these fairly genetically monomorphic animals exhibited notable variability in their immune responses. The role that MHC plays in immunity, coupled with the fact that these foxes actually retain considerable variability at MHC loci (Agudo et al., 2011), lead me to believe that MHC genes may be a significant component in vaccine response.

I conducted logistic regressions to see whether or not genotypes at certain MHC genes could predict for high vs low vaccine response, a binary outcome that I denoted as individuals with peaks titer levels of  $\geq 32$  and  $< 32$ , respectively. My tests found associations between genotypes at two MHC Class II genes, CFA12-9 and CFA12-21 ( $p=0.0143$  and  $p=0.020$ ).

## THE DEVELOPMENT AND CHARACTERIZATION OF RECOMBINANT HEV REPORTER GENOMES FOR THE IDENTIFICATION OF POSITIVE AND NEGATIVE REGULATORS OF HEV HOST TROPISM

Hepatitis E virus (HEV) is a quasi-enveloped, positive sense, single stranded RNA virus of the hepeviridae family, with a genome composed of three open reading frames. HEV causes hepatitis E worldwide, leading to 70,000 deaths a year, with a mortality rate among pregnant women as high as 30%. Hepatitis E poses a major public health threat not only in developing countries where it is transmitted fecal-orally, but also in developed nations around the world through food-borne transmissions. As HEV is primarily transmitted to humans from animal reservoirs in developed nations, evaluating the host tropism of the virus can prove useful in a global health campaign. Preliminary work in the Ploss lab shows that replication levels of the virus are 100 to 1000 times lower in murine than human hepatoma cells. I hypothesize that these observations can putatively be explained by dominant negative regulators that hinder HEV replication or absent human specific cofactors for HEV replication in rodent cells. The major aims of this project include the generation of recombinant HEV genomes containing selectable and fluorescent markers that will be useful in the characterization of HEV replication in cell culture. With the use of a novel transcomplementation assay, virally encapsulated recombinant genomes will be developed and used in future loss and gain of function screenings to identify host factors essential for robust HEV infection. Results from this work will lead to an improved understanding of host-virus interactions, contribute to the development of animal models to study HEV, and inform public health efforts to contain HEV spread.

## 1 MOSQUITO 4 VIRUSES: CHARACTERIZATION OF Aedes Aegypti POPULATIONS WITHIN GHANA: CORRELATIONS BETWEEN HABITAT MORPHOLOGY AND BEHAVIOR

The primary vector for transmission of Yellow Fever, Chikungunya, Dengue Fever, and Zika viruses is the *Aedes aegypti* mosquito. This species exists in two forms—*Aedes aegypti formosus* (Aaf), an ecologically variable form found primarily in sub-Saharan Africa, and *Aedes aegypti aegypti* (Aaa), a human specialist found globally in tropical and subtropical regions. The two subspecies show mean differences in morphology, but there is substantial overlap, and they can only reliably be distinguished using genetics. To date, research conducted in Kenya, Senegal, Tanzania, and Cameroon has shed light on *Aedes aegypti* populations based on geography, body coloration, and genetic makeup. However, little is known about the morphology and host preference of *Aedes aegypti* mosquitoes across most of West Africa. The goal of this project was to characterize morphological and behavioral variation among *Aedes aegypti* populations in Ghana that may affect their ability to transmit human disease. Live *Ae. aegypti* eggs were collected in the field and carried back to the McBride lab at Princeton University in the U.S. Morphology and behavior were then examined using a standard dissecting microscope and an olfactometer, respectively. The olfactometer allowed for measurements of preference for human vs. non-human odor. Results of this study suggest that there is significant morphological variation within the subspecies Aaf found in Ghana ( $p < 0.008$ ). On the topic of host preference, each colony preferred the non-human host as opposed to the human host in each trial, suggesting that with increased urbanization and vector density in West Africa, non-human reservoirs can pose a severe threat to humans if effective vector control measures are not prioritized.

**AT LEAST IT'S CLEAN?: A STUDY OF THE EFFECTS OF  
AGRICULTURAL PROXIMITY ON ANTIBIOTIC RESISTANCE IN  
GRAM-NEGATIVE ENTERIC BACTERIA FOUND IN TRIBUTARIES  
OF THE CHESAPEAKE BAY WATERSHED**

As the threat of antibiotic-resistant and multidrug-resistant human pathogens builds, we must take measures to understand what is causing this dangerous trend before our commonly used antibiotics are rendered all but useless. Of special concern to us and our research is the role that agriculture plays in the development of antibiotic resistance in the environment. As such, in this paper we aim to discover a connection between already established reservoirs of drug-resistant Gram-negative enteric bacteria in the waterways of the Chesapeake Bay Watershed and their proximity to farmland. We carry this out via a survey study of the Watershed to ascertain the extent of antibiotic resistance, after which we map the features of the area surrounding the sampling site in order to understand the extent of farmland in the surrounding location. Our results demonstrate that there may be a correlation between resistance to tetracycline, a commonly used antibiotic in animal husbandry, and proximity to farmland, as well as a correlation between general resistance trends and extent of local farmland. As such, we advise that more work be done on this question so that we may gain a clearer understanding and more definitive proof of the factors involved and thus be able to counteract the current trends in antibiotic resistance.

**MARYLIN MO KOUSASSI-BROU**

ASSISTANT PROFESSOR LINDY MCBRIDE

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## THE EFFECTS OF SULCATONE AND LARVAL CROWDING ON OVIPOSITION SITE SELECTION OF *Aedes Aegypti*

The Effects of Sulcatone and Larval Crowding on Oviposition Site Selection of *Aedes aegypti*

The *Aedes aegypti* mosquito is a vector responsible for multiple diseases globally, including Dengue fever and the Zika Virus. Olfactory cues are crucial in both host seeking and oviposition site selection, allowing the species to survive in human habitats and transmit arboviruses from one person to the next. Previous studies have identified that the evolution of the mosquito's human preference may be attributed to an odorant receptor for sulcatone, a compound abundant in human odor. Other works with the malaria vector mosquito suggest that sulcatone may actually repulsive in the context of oviposition. Here, I developed a dual-choice oviposition bioassay in order to analyze the role that sulcatone and larval crowding play in 3 variants of *Ae. aegypti*. Results suggest that sulcatone may be attractive in isolation. Results also imply that gravid females are attracted to low densities of larvae in the water, with attraction increasing to a point and then switching to repulsion at higher densities. Implications for vector control and the role that sulcatone can play in gravid traps are discussed.

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## EFFECTS OF GROUP DISTURBANCES ON AGGRESSION AND AFFILIATION NETWORKS IN DOMESTIC HORSES (EQUUS CABALLUS)

For any group of domestic horses (*Equus caballus*) to live peacefully with each other, there needs to be some sort of hierarchical system to prevent constant turmoil from tearing the group apart. This system places all individuals in a position of dominance or subordination relative to other individuals in the group. These positions affect everything in the individuals' lives, from access to food to reproductive fitness to who they socialize with. Both addition and removal of an individual from the group can lead to changes in behavior as individuals attempt to maximize their fitness in the new hierarchy. Disturbances to the social network can be detrimental to all the individuals in the group, due to increased aggressive behaviors and raised stress levels, sometimes resulting in decreased reproductive capability. It is important for managers and owners of horses to understand this network, and more importantly, disturbances to this social network, in order to best take care of their herd and raise happy, healthy horses. This study investigates the effect of group disturbances on a mixed-gender herd of domestic horses. The removals are designed to explore the intersection between dominance and sociality (in the form of close associations and centrality). For two high centrality horses, the removal of the high-dominant was more disruptive than that of the low-dominant. The removals involving the strongly bonded horse pair showed that each member of the pair serves to tether the other horse to the herd, even in their absence.

## CALLING THE SHOTS: IMPACTS OF MATERNAL KNOWLEDGE AND ATTITUDES ON VACCINATION STATUS AND VACCINE HESITANCY IN INDIA

As of 2013, only 65% of children in India were found to be fully vaccinated in their first year of life. Vaccine hesitancy, defined as “individual delay or refusal of vaccinations despite the availability of vaccines”, may be a large contributor to existing levels of under- or non-vaccination. This is because populations in low- and middle-income countries (LMICs) lack education and knowledge on vaccinations. Social systems, cultural values, and religious beliefs also dominate decision-making, particularly in regards to immunizations<sup>3</sup>. Given this dynamic, it is imperative to understand the drivers of vaccination status and vaccine hesitancy throughout India. This study focuses on vaccine hesitancy behavior in mothers because they are the primary caregivers of young children. Additionally, this study concentrates on maternal knowledge on vaccinations and attitudes because they are complex drivers of vaccination uptake that have been largely unexplored. Overall, this study aims to characterize the impacts of maternal knowledge on vaccinations and confidence in health workers on vaccination status and vaccine hesitancy in India.

The results of this study reveal that maternal knowledge and attitudes are both significant factors that impact the self-reported vaccination status of children in the country. Among mothers that reported incomplete vaccinations, their vaccine hesitancy was largely due to lack of knowledge on vaccination schedules, sessions, and benefits. Further investigation suggests that communication between health workers and mothers on vaccination relevant information should be improved to further expand vaccine uptake. This study also found that vaccine hesitancy can be attributed to a lack of confidence in health workers being available when needed. This suggests that the UIP should continue health infrastructure as improving maternal confidence in the availability and accessibility of health workers may also be critical for expanding vaccine uptake in mothers in India. These findings have many limitations: this study however is a critical first step to understanding the dynamics of vaccine hesitancy in mothers throughout India.

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## RURAL LAND-USE ADAPTIVE CAPACITY AND CONSERVATION: A CASE STUDY OF SMALLHOLDER RUBBER FARMERS IN XISHUANGBANNA CHINA

Throughout the developing world, smallholder farmers are among the populations most vulnerable to climate change and economic instability, and they play an important role in rural land use change. In Xishuangbanna, China, the expansion of smallholder rubber plantations has both driven the rapid displacement of rainforest ecosystems and provided an unprecedented source of income for some rural households. Choices about land use and rubber cultivation among smallholder farmers impact their adaptive capacity and shape the fate of conservation in this exceptionally biodiverse region. This study used 279 household surveys throughout Xishuangbanna to assess smallholders' cultivation decision-making pathways; to quantify farmers' access to context-specific forms of economic, social, and environmental capital; and to identify factors that shape smallholders' perceptions of environmental protection and government-enforced protected areas in Xishuangbanna. I found that smallholders, particularly in the lowlands, are transitioning towards more diversified land uses. Farmers are increasingly cultivating new crops, renting out land, and leaving land to fallow, which indicates that they may be losing confidence in rubber cultivation as a sole source of income. Respondents with lower access to economic capital perceived themselves as more resilient. Although farmers have overall positive attitudes towards environmental conservation in general and protected areas in particular, these positive values did not necessarily translate into conservation-oriented actions. This disconnect likely stems from China's volatile legacy of land tenure policy changes, which has jeopardized farmers' trust in state actors and thus their willingness to support government protected areas. This results of this study show that, to understand smallholder adaptive capacity in the face of economic and climate change and to understand farmers' conservation attitudes and actions in the face of dramatic biodiversity loss, it is essential to consider diverse dimensions of rural change, including social factors, environmental factors, and economic factors beyond income from commodity production.

## PSEUDOPANAX ARBOREUS: AN INVESTIGATION OF ITS NATIVE POLLINATION SYSTEM

*Pseudopanax arboreus* is a winter-flowering, dioecious tree that is native to New Zealand. Despite its common presence in native forests, there is relatively little literature published on it or its pollination system. Using only a pollination syndrome-based examination of its inflorescences, *P. arboreus* appears to fit the generalized, insect pollination system that was initially and indiscriminately proposed for most New Zealand flora. However more recent studies have recognized the wider reach of pollination systems in New Zealand, including some observations of native bird visitors to *P. arboreus* in areas of the country.

Our study investigated the pollination system of *P. arboreus* in Pureora Forest Park, a highly protected area of native New Zealand forest, in an attempt to catalogue its interactions with its evolved pollinators. Here we used both video recording and pollinator-exclusion treatments to quantify the role of vertebrate and invertebrate visitors. Results of the pollinator exclusion treatments indicated significant contribution to *P. arboreus*'s pollination by both insect and vertebrate visitors. Video recordings confirmed the role of insects as pollinators to *P. arboreus*, however no vertebrate visitors were observed in the recordings. Within the video footage, there were significant differences in the duration of insect visitation from different size classes of insect. We found that larger insects spent significantly more time on the inflorescences per visit when compared to medium or small insects. Similarly, the medium insect group spent significantly more time on the inflorescences per visit when compared to the smaller insects. These results highlight the generalized and indiscriminate nature of this plant's pollination system—where a wide variety of insect visitors within each size class were directly observed and the role of larger vertebrate visitors was indirectly confirmed. These finds have implications beyond the pollination system of the tree itself, suggesting that in the context of New Zealand's native ecosystem, *P. arboreus* may be a crucial winter resource to many endemic species.

## RELATIONSHIP BETWEEN CLIMATE AND THE DENGUE FEVER VECTOR Aedes Aegypti in Machala Ecuador

**Background :** Dengue fever is an increasingly widespread disease of which up to one-half of the world's population is at risk. The disease is caused by the dengue virus, which is spread to humans through the bite of the *Aedes aegypti* mosquito. Understanding the climate patterns and socio-ecological factors that may influence this mosquito's feeding and reproductive timing may help inform practices that curb incidence of the disease. Machala, Ecuador is a city with high dengue fever incidence, so finding local trends that may allow epidemiologists to predict when an outbreak may occur in the future would allow for more time to prepare for a potential outbreak and minimize the burden of disease.

**Methods :** Using data collected from 2013-2015, I analyzed three variables collected from households of dengue fever patients that may predict increased rates of dengue fever incidence: mosquito abundance, sex ratio, and proportion of females of the mosquito population. I analyzed these experimentally-collected variables against climate values with a lag of 0, 15, 30, or 45 days, and created a best-fit model of a significant relationship based on past data.

**Results:** Across all of mosquito and climate variables that were analyzed, temperature could not be reliably correlated with any mosquito-related variable. Precipitation with a 15-day lag period, however, had a clear positive correlation total mosquito abundance. A model was created based on this relationship that could predict expected mosquito abundance fifteen days after recording a precipitation value. When tested against the past data, this model had an R-squared value of .192, meaning that the model could successfully predict 19.2% of the data's variance and could be incorporated into a broader system of predictive models for dengue fever in Machala.

**Conclusions:** This model can be incorporated into an Early Warning System (EWS) for public health workers in Machala to help predict when *A. aegypti* abundance will increase. As such, this model would be able to predict when increased incidence of *A. aegypti*-carried diseases, particularly dengue fever, may occur. The significance of precipitation may be because of Machala's inadequate garbage collection system, which leads to more oviposition sites for female mosquitoes. Aiming public efforts towards improving public waste management would likely lower the burden of disease in the area.

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THE EFFECT OF DROUGHT CONDITIONS ON VERTICAL RESIN  
DUCT PRODUCTION IN PINUS PONDEROSA ACROSS AN  
ELEVATIONAL RANGE

Several research studies have investigated changes in ponderosa pine resin duct production after drought, as well as the significant role that investment in resin defense plays in predicting tree mortality in response to drought and insect outbreak. However, there is less existing research on the long-term relationships between climate and resin duct investment of adult ponderosa pine. I investigated the relationship between measures of annual precipitation, temperature and heat moisture index, and characteristics of vertical resin ducts produced by ponderosa pine at different elevations in Colorado from 1985 to 2013. Resin duct observations were performed on tree core samples originally collected for a previous study by Anderegg & Hille Ris Lambers (2015). In accordance with the methods of existing resin duct studies, I collected annual resin duct counts and the area of observed resin ducts (mm<sup>2</sup>). Total duct area per ring (average duct area multiplied by the number of ducts observed in a ring), and relative duct area investment (proportion of total duct area relative to area of an individual ring) were calculated as well. Consistent with existing research, findings demonstrated that duct production, duct area and total duct area tended to decrease in response to drier conditions while relative duct area slightly increased. Additionally, resin duct characteristics followed the same trends in response to decreasing elevation. Despite these relationships, mean ring width was by far the most significant predictor of all resin duct observations, indicating a possible fixed relationship between resin duct production and ring size, which some studies have already suggested. These findings add to the existing literature on drought and resin duct production and have implications for forest conservation efforts, especially at low elevations, in an increasingly arid region of the Western USA.

## CASCADING EFFECTS OF LARGE HERBIVORE LOSS ON LIANA-TREE DYNAMICS IN AN AFRICAN SAVANNA

Large herbivores are crucial regulatory components of global ecosystems, acting to increase community diversity and mitigate ecological disturbances at both micro and macro scales, yet prevailing thought has suggested that, at the individual level, herbivores adversely affect plants via consumption and physical damage. However, recent work highlights various direct and indirect benefits of herbivores on plant species and indicates that herbivore loss may have negative net effects on local flora. One particular ecological threat posed by herbivore loss is the release of rapidly growing, competitively dominant plant species that are normally controlled by herbivory. Using observational surveys and manipulative experiments in a series of herbivore exclosure plots in central Kenya, we monitored the effects of herbivore exclusion on a common opportunistic plant type - lianas (woody vines). Evidence from the neotropics shows that liana infestation negatively affects tree fitness; we therefore measured the relationship between lianas and savanna trees, using *Cynanchum viminale* as a focal liana species. We found that herbivore loss leads to increases in both the incidence of lianas and the severity of liana infestation on trees. The tree fitness surveys showed that increased liana infestation is associated with reduced fruit production among host trees. A mean-field model motivated by this fieldwork reveals that loss of herbivores causes the liana-tree system to shift toward a stable equilibrium at which liana infestation is double its control levels. Together, our empirical and theoretical results demonstrate the importance of herbivores in maintaining stable plant community composition and present a novel mechanism by which large herbivores indirectly benefit savanna trees.

## EVALUATING INDIVIDUAL RESILIENCE TO GROUP PERTURBATION OF THE DOMESTIC HORSE

This study aims to investigate individual responses to group instability based on established character traits. By using various methods of social network analysis, patterns of aggression and sociality were quantified. Instability was induced in a herd of domestic horses through perturbing group membership. Two shortterm removals were performed, followed by a permanent addition of two unknown individuals and the removal of a current group member. The short-term removals revealed dynamics of herd resiliency through changes of individual behavior. When the removed individuals were returned, baseline herd dynamics were conserved. However, the addition resulted in permanent changes in the herd. The character traits of the added individuals were implicated in this group disturbance. This study was able to show that within a functional herd, an individual's ability to cope with a group disturbance is dependent on the character traits of the individual(s) added or removed. For managers of domestic animals, understanding the effects of disturbing a herd's membership is important for promoting group harmony.

### STUDYING THE CORRELATION BETWEEN MHC MICROSATELLITES AND SUSCEPTIBILITY TO MANGE IN THE YELLOWSTONE GRAY WOLF (*CANIS LUPUS*)

Since the reintroduction of the Yellowstone Gray wolf (*Canis lupus*) to Yellowstone National Park some 13 years ago, multiple diseases and parasites have been found to hamper the reintroduction effort. Tightly knit social formation within packs and behavioral patterns allow for parasites like the *Sarcoptes scabiei* to easily sweep through the population. Recently, particular emphasis has been put on discovering the patterns to susceptibility to *Sarcoptes scabiei*, which is the root cause of sarcoptic mange. Current study shows that the population within Yellowstone appears to be highly variable with respect to the risk, severity, and duration of infection (Almberg et al. 2012). A study by Wu (2016) revealed several phenotypic/behavioral categories contribute to patterns of individuals having higher susceptibility to mange infection. This study expands upon previous studies by attempting to find a genetic pattern to susceptibility to mange. This was done by genotyping 163 individuals at 24 MHC loci. Also, the data was used to investigate the level of genetic diversity within YNP. Along with finding an extremely high level of genetic diversity at MHC loci, GLM analysis revealed that the heterozygote allele at ABCF1\_DOWN1 locus may provide the individual that carries it with some type of increased fitness. Statistically, individuals that had the heterozygous form decreased their odds of having mange by 83%. It is suggested that this could display a heterozygote advantage, however, the locus appears to remain in Hardy-Weinberg equilibrium. Possible reasons for the locus remaining in HWE could be due to the fact that selection for the heterozygote isn't as strong because any lowered fitness within homozygotes may be mitigated by social aspects of group living. Other selection factors such as evolutionary time and the possibility that selection doesn't act on the entire population are discussed as possible explanations for this observation.

**HANNAH PRIDDY**

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## AN ANALYSIS OF THE DIFFERENTIAL EFFECTS OF DIETARY PROTEIN ON THE IMMUNOLOGICAL RESPONSE TO INFECTION BY THE HELMINTH PARASITE *TRICHURIS MURIS*

Malnutrition and intestinal helminth infections are chronic conditions that frequently coexist within the same geographic regions. While it is well known that malnutrition increases susceptibility to parasitic helminth infection, many of the immunological mechanisms underlying the relationship between host nutrition and helminth immunity remain largely unknown.

Therefore, this study aimed to experimentally analyze the differential effects of dietary protein on the murine immune response to infection with the helminth parasite, *Trichuris muris*. Importantly, we conducted this experiment in a semi-natural environment in order to ascertain whether outdoor exposure influences the interaction between host protein intake and the immune response. C57BL/6 mice housed in a semi-natural facility were fed either a high protein or low protein diet and infected with a high dose of approximately 200 *T. muris* eggs. Over the course of 3 weeks post infection, blood and fecal samples were collected from each individual and analyzed for the production of Th2 type effectors IgG and mucin 5ac, respectively. At the end of the experiment, final caecum worm burdens were assessed and cytokine production was quantified from mesenteric lymph node cells via flow cytometry. Specifically, we measured the concentrations of Th2 associated cytokines IL-10 and IL-13 as well as the Th1 cytokine IFN $\gamma$ , and the Th17 cytokine, IL-17. Results from these analyses demonstrate that protein deficiency significantly impairs the host Th2 immune response to infection, as evidenced by significant reductions in IL-13 and IgG in mice fed the low protein diet. Interestingly however, diet was not shown to significantly affect final worm burden, which could be a factor of environmentally induced alterations in parasite susceptibility and expulsion. Ultimately, this study provides important insight into the role of host nutrition in the immune response to helminth infection. This research also indicates the importance of studying these immunological interactions in a naturalistic setting that is more generalizable to conditions experienced by wild hosts outside the lab.

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## THE ZIKA VIRUS AND CONGENITAL BIRTH DEFECTS: AN INVESTIGATION INTO THE ROLE OF THE PLACENTA AND THE TIME OF INFECTION

After many years of intermittent individual infections, in the past four years the Zika virus (ZIKV) has spread rapidly. An increase in the frequency of cases of congenital neurological abnormalities, such as microcephaly, has been observed in conjunction with the rise of ZIKV. As of April 21st, 2016, the World Health

Organization (WHO) determined congenital infection with the Zika virus can cause microcephaly.<sup>4</sup> This investigation will look to amalgamate the clinical, laboratory, and morphological information of 33 mothers who were infected with the Zika virus during pregnancy in Rio de Janeiro, Brazil in 2015-2016. First, we explore the influence of time of infection on the presence and severity of malformations in newborns. Second, we evaluate morphological features of the placentas in order to determine if Zika causes structural damage to the placenta, and if so, if these features can be used as a diagnostic tool in the future. To our knowledge, this is the first investigation of its kind which analyzes more than a few placentas. Finally, we compare the morphological features of ZIKV infected placentas to the placental abnormalities produced by TORCH pathogens.

We found the time of infection played a significant role in the incidence of microcephaly and other CNS alterations in fetuses. The majority of children who presented with adverse clinical outcomes were noted during the first trimester (60%), with 6 of 7 (86%) cases in this trimester presenting with microcephaly and/or other CNS alterations. Two cases of second trimester infection resulting in malformations were noted, while no cases of third trimester infection resulted in CNS alterations. While evaluating the placentas, the most common morphological changes were fibrosis of the stroma (97%) and villitis scarring (94%). Several of the placental alterations observed were consistent with structural changes seen in placentas infected with TORCH pathogens. These results provide new cases and information to researchers who are currently working on a vaccine for the Zika virus. In light of our observations, it is likely the placenta could be used as a diagnostic tool in the future, however more research is needed to confirm this. As the placental alterations due to congenital ZIKV infection continue to be investigated, our study will serve as preliminary evidence to suggest that congenital Zika infection can cause morphological abnormalities in the placenta.

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## EFFECTS OF PINE BEETLE EPIDEMIC ON WATER QUALITY IN BOULDER COUNTY CO

Bark Beetle infestation in areas of the Rocky Mountain Range has had a large impact on its surrounding ecosystem, especially as the warmer climate has increased the reproduction cycle of the beetles. Subsequent tree die-out events have been shown to increase water runoff and the concentration of nitrates in soil. This study provides evidence that insect damage in Boulder County, CO has resulted in a significant increase in nitrate levels in localized areas of streams between 5 and 20 years after the initial beetle infestation. Over twelve observed streams, I found that water samples within beetle infestation sites on average had 32% higher nitrates than water samples upstream of the beetle infestation. Total dissolved solids (TDS) showed a strong correlation with nitrate levels. I found no significant difference in downstream nitrate change when stratified by dominant sapling genus, but I found that when grouped by dominant adult, nitrates were higher in aspen-dominated areas than in spruce-dominated areas. Levels of nitrates in beetle sites of 20 years were significantly higher than those in 15-year sites, but no further trend was seen in nitrate levels by latent period. Lastly, I found a significant increase in nitrate levels at sites with greater percentages of dead trees. Elevation of nitrates in streamwater is a public health concern, as toxins from high-concentration streams can cause harm to humans and other animals. Further research would be required to determine whether nitrate values remain elevated downstream, beyond beetle infestation zones. Studies on impacts from bark beetle damage are ever more critical as climate change makes these infestations more prevalent in mountainous areas like Boulder, CO.

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## BLACK AND WHITE AND SPREAD ALL OVER: THE ROLE OF ENVIRONMENTAL VARIATION ON PATTERNS OF SOCIALITY IN PLAINS AND GREVY'S ZEBRAS

It is known that the environment shapes the social system of any species, and mating systems, group size, and spatial dispersion will be influenced as a result of environmental changes. More specifically, bottom-up factors such as resource availability and top-down factors such as predation are known to impact these social systems, but quantitative measurements of change in sociality are necessary to fully comprehend how ecological conditions impact social systems. While plains (*Equus quagga*) and Grevy's zebras (*Equus grevyi*) are two closely related species, they have evolved to exhibit contrasting social structures. The sympatric plains and Grevy's zebras of central Kenya can be used as a case study to attempt to understand and quantify how changes in environmental condition, such as decreased rainfall, vegetation, predation, etc., may drive the changes in a social network. Using past data collected from the summer of 2013 on the same sample of plains and Grevy's zebras, and utilizing social network theory, with its corresponding network metrics, we aimed to quantitatively compare how social networks change as a result of differences in rainfall and resource abundance. Network metrics revealed that in wetter environments, where there is greater vegetation abundance, these two species of zebras are generally more likely to have greater cohesion and connectivity with one another as compared to the networks in a drier environment. In a more arid environment (summer of 2016), plains zebra stallion males are less likely to form herds with other stallions, and will instead break off into their respective harems in search of better vegetation. However, we found that bachelor males will remain preferentially associated to other bachelor males in both years. Territorial Grevy's males in 2016 appeared to occupy the same general regions that were previously observed in 2013, however, the territory boundaries were much less strict than before. It would be expected that because of the pronounced decrease in social connectivity within both species' networks, the rate of disease transmission is lower during drier periods and higher during wetter ones. This has important implications for future studies on the relationship between social networks, environmental change or seasonality, and disease transmission

## WHERE THE GROUNDWATER MEETS THE SEA: ECOLOGICAL IMPACTS OF NUTRIENT-ENRICHED GROUNDWATER DISCHARGE ON BERMUDA'S NEAR-SHORE CORAL REEFS

As climate change increasingly stresses coral reefs globally, it is important to mitigate local factors, including pollution, that can push reefs past their resilience thresholds. In Bermuda, the world's third-most densely populated nation, over 60% of residential sewage enters the groundwater through untreated cesspits. However, the impacts of sewage-enriched groundwater discharge on Bermuda's coral reefs have been little studied.

This project quantified water quality in Bermuda's groundwater, at a coastal groundwater discharge vent, and across three North Shore reefs. Groundwater discharge is characterized by low salinity, elevated nitrate concentrations ( $500\mu\text{M NO}_3^-$ ), and an elevated nitrate  $15\text{N}/14\text{N}$  ratio ( $\delta^{15}\text{N} = 10.9\text{‰}$ ) consistent with human waste. On the most heavily N-enriched site,  $[\text{NO}_3^-]$  averages  $4\mu\text{M}$ , 10x higher than typical on Bermudian reefs without shoreline impacts, with a nitrate  $\delta^{15}\text{N}$  indicating sewage-enriched groundwater is the primary N source. Tissue  $\delta^{15}\text{N}$  in two species of benthic macroalgae collected across the three reefs is correlated with aquatic nitrate  $\delta^{15}\text{N}$ , indicating algae take up groundwater-borne N. We also quantified skeletal growth of *Porites astreoides*, a dominant reef-building coral on Bermuda, across the most heavily N-enriched site, finding a significant decline in calcification rates closer to the shoreline, where  $[\text{NO}_3^-]$  and nitrate  $\delta^{15}\text{N}$  increase.

However, surveys across the three sites found that although overall coral cover is low (~5%) relative to Bermuda's offshore reefs (~20-25%), algal and coral cover are not correlated with N enrichment. Furthermore, in a four-week herbivore exclusion experiment, algal growth and N enrichment were uncorrelated, even in the absence of herbivorous fish. Instead, algae may be phosphate-limited: phosphate is adsorbed onto Bermuda's limestone (Simmons, 1983), and is low ( $[\text{PO}_4^{3-}] < 0.04\mu\text{M}$ ) across these reefs. Further study of the aquifer's potential phosphate saturation limits, and continued management of both  $\text{PO}_4^{3-}$  inputs and herbivore populations, are critical to maintaining coral communities on these N-enriched reefs.

ECOLOGICAL MEMORY IN THE COASTAL REDWOODS:  
INSIGHTS ON EMERGING THREATS IN THE FACE OF A  
CHANGING LANDSCAPE

The Coastal Redwoods range is a unique ecosystem with which spans from mid-California to the Oregon border. This review considers the various disturbance regimes endemic to the Coastal Redwoods within the framework of ecological memory: how the forest builds its information and material legacies allows insight as to how it will respond to changes in the historic disturbance regimes. The relationship between fog and drought stress is analyzed, revealing impacts of drought stress on redwoods and relative vegetation. Spread of Sudden Oak Death and its causal agent *Phytophthora ramorum* throughout the Coastal Redwoods range is considered, as well as its potential future impact on forest fire. This paper reviews the importance of considering the interactions between disturbance regimes to reveal changing dynamics, citing the impact of the simultaneous synchronous spread of Sudden Oak Death and drought stress induced by loss of fog as potential contributors to increased fire severity.

ELUCIDATING *TRYPANOSOMA CRUZI* RESERVOIRS ACROSS  
SOUTH AND CENTRAL AMERICA: A REVIEW OF OVER 70  
YEARS OF SERO-EPIDEMIOLOGICAL EVIDENCE

Chagas disease, or American trypanosomiasis, is the most important neglected tropical disease in terms of Disability-Adjusted Life Years (DALYs) in the Americas. The disease is caused by infection with the protozoan parasite *Trypanosoma cruzi*, which has an incredibly complex transmission cycle that can involve any one of 150 triatomine bug species in addition to more than a hundred mammalian species. Taking into consideration this complexity in combination with the gravity of Chagas disease, it is imperative to understand the vector-host relationships that are key to transmission cycles in a given region or habitat to prevent human infection. While much contemporary scholarship has been done with regards to triatomine vector ecology and domestic animal reservoir potential, the relationship between ecological disturbance and human transmission or the relevance of mammals to *T. cruzi* transmission and maintenance in the wild remain minute. Therefore, we aimed to: 1) briefly summarize the Chagas literature, 2) review and extract prevalence data from the literature on mammal species tested for *T. cruzi* infection in South and Central America and 3) discuss gaps in the literature as well as suggest further research. In this study, 112 articles published between 1940-2016 were reviewed, in which over 120 species were reported to have natural *T. cruzi* infection. Prevalence data from these articles were used to assess whether species identity is an indicator of infection. The ultimate purpose of this study is to highlight what is known with respect to *T. cruzi* transmission and wild mammals in order to better understand where to focus future studies.

## INTRASPECIFIC COMPETITION MEDIATED BY MYCORRHIZAL FUNGI ALTERS PHOTOSYNTHETIC RESPONSE TO HERBIVORY IN SOYBEAN

Application of mycorrhizal fungi in agriculture is becoming increasingly common; the fungi can aid plant nutrient uptake and reduce the negative effects of many abiotic soil stressors. However, little is known about how networks formed by mycorrhizal colonization affect the defense response and resource allocation of plants simultaneously stressed by competition and herbivory. Here, we study the immediate photosynthetic response of herbivore-stressed plants connected to both stressed and unstressed plants via mycorrhizal network. Specifically, we use A/Ci curves to measure maximum photosynthetic capacity ( $A_{max}$ ), maximum Rubisco carboxylation rate ( $V_{cmax}$ ), maximum rate of RuBP regeneration ( $J_{max}$ ), and maximum rate of triose phosphate utilization (TPU). Soybean, *Glycine max* (L.), grown in pairs with mycorrhizal fungi were either separated by an impermeable barrier or by a mesh that only allowed mycorrhizal connection (no root contact). Initially, *Spodoptera exigua* larvae were deposited on one plant in the pair, while the other plants received larvae two days later. Plants which initially received larvae had significantly greater  $A_{max}$  after four days compared to initially unstressed plants, indicative of a compensatory response in stressed plants. In addition, of the plants which initially received larvae, those in pairs separated by mesh had significantly reduced  $A_{max}$ ,  $J_{max}$  and TPU compared to those in pairs separated by a barrier. These findings indicate that intraspecific competition mediated by mycorrhizal networks drastically affects the immediate, plastic responses of soybean to herbivory and, more specifically, negatively affects its compensatory photosynthetic response.

### GECKO POSITION SYSTEM (GPS): AN ANALYSIS OF SPATIAL NAVIGATION ABILITY IN VELVET GECKO (OEDURA LESUEURII)

Spatial navigation is the ability to use cues to effectively transverse one's environment and is vital to the survival of many organisms. Despite the significant behavioral implications of navigation and the of depth studies on spatial navigation in mammals/birds, there are relatively few studies looking into spatial navigation in reptiles, especially in Squamata (lizards and snakes), despite their being the most diverse reptile order. Additionally, among the few studies conducted on Squamata, results of studies conflict, suggesting significantly differing degrees of spatial navigation ability in reptiles. Here, we used a gecko native to Southeastern Australia, *Oedura lesueurii*, to investigate the degree to which these geckos do or do not have the capacity for spatial navigation. Velvet geckos were able to quickly learn to navigate to a contextually relevant stimulus in an initially novel Y Maze improving in terms of the time taken in navigating and the number of mistakes made. Overall, our data suggests that Squamata not only have spatial navigation ability, but also that they can learn unexpectedly quickly, suggesting that in some cases reptiles may have similar cognitive ability to mammals/ birds and highlighting the need for additional studies on spatial navigation and cognitive function in reptiles moving forward.

**MALLIKA VISWANATH**

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WHAT TO INJECT WHEN YOU'RE EXPECTING:  
UNDERSTANDING THE NEWS-VACCINATION RELATIONSHIP  
FOR THE MATERNAL INFLUENZA VACCINE IN ENGLAND

Pregnant women are at increased risk of developing severe influenza infections, which also affect her fetus and her baby. To prevent these cases, many countries recommend pregnant women be vaccinated against the flu. Strong evidence supports the vaccine's effectiveness and safety, and the vaccine also provides protection to her fetus and temporary maternal antibodies to her infant. Despite these benefits, vaccine coverage rates (VCR) among pregnant women in England, where the recommendation was issued in 2010, remain relatively low. This thesis explores the potential of news media to positively influence pregnant women to be vaccinated, hypothesizing that flu- and pregnancy-related media increase VCR.

To analyze this relationship, I collected monthly VCR data, for the six years that the maternal vaccine has been recommended, from Public Health England and news data from NewBank. The news data consisted of the monthly frequencies of five terms related to the maternal flu vaccine. Using the fixed-effects Least Squares Dummy Variable (LSDV) model to absorb month-specific seasonality in the VCR data, I analyzed the relationship between news-VCR for both matched data (i.e. November news and November VCR) and lagged data (i.e. November news and December VCR). I found no significant effect of the news for either of these analyses. In a second analysis in which I switched the direction of my model, I found that VCR influence flu- and vaccine-related news in the following month.

Neither hypothesis is supported, and the absence of a news effect on pregnant women's VCR is surprising. The complexity of health-seeking behaviors during pregnancy may impede this type of analysis. Future research should investigate whether disease incidence plays a role in the VCR effect on news, and future campaigns should continue to strengthen the relationships between pregnant women and health providers.

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THE EFFECTS OF DIGITOXIN ON THE DIFFERENTIAL  
EXPRESSION OF THE SODIUM-POTASSIUM PUMP IN  
ONCOPELTUS FASCIATUS

The widespread adaptations and duplications of the sodium-potassium pump ( $\text{Na}^+, \text{K}^+$ -ATPase), specifically the  $\alpha 1$  subunit, provides a natural platform for examining the effects of cardenolides on the expression of ATPa1 duplicates in insects. *Oncopeltus fasciatus*, or the large milkweed bug, has four copies of ATPa1 with differing amounts of insensitivity to cardenolides depending on the number of mutations they have. To determine if there is a diet specific plasticity in the expression of ATPa1, I conducted a feeding assay using digitoxin, a nonpolar cardenolide. Although I did not find a difference between groups that consumed digitoxin (and methanol) soaked sunflower seeds and groups that did not, my results did show that there is a tissue specific differential expression of ATPa1; more insensitive copies were expressed in the gut while more sensitive copies were expressed in the head. In addition, my differential expression analyses of the *O. fasciatus* genome across the digitoxin (and methanol), methanol, and control groups showed that there were seven genes that were expressed more in the digitoxin group than in the others, notably CG3097, which functions as a metalloproteinase. My results also showed one gene, Gasp, that was under expressed in both digitoxin (and methanol) and methanol groups which indicated that methanol influences the expression of chitin binding. As both important to cancer treatments and to the better understanding of the complex intrinsic genetic interactions with external factors, cardenolides and the adaptations of  $\text{Na}^+, \text{K}^+$ -ATPase to these toxins in insects warrant further study.

## DYNAMICS AND INTERACTIONS: AN ANALYSIS OF CHILDHOOD DISEASES IN LONDON, 1897-1906

**Introduction.** The goal of this thesis is to analyze the disease-induced mortality in London 1897-1906 for measles, smallpox, whooping cough, typhoid fever, diphtheria, and scarlet fever. The questions addressed are: i) what are the patterns of outbreaks exhibited by each of the diseases, ii) how do different diseases interact with measles, and iii) how does the perturbation of a smallpox outbreak affect measles dynamics?

**Methodology.** The dataset used are historical datasets comprised of mortality figures. The statistical analyses conducted to study disease interactions were cross-correlation analysis and wavelet spectral analyses. To model the impact of a smallpox outbreak on regular measles dynamics, a two-strain SIR model was adapted and applied to the dataset.

**Results.** Time series plots reveal annual epidemics for measles, whooping cough, diphtheria, and typhoid fever. There were varying birth rates and thus varying frequency of measles outbreaks, most notably biennial outbreaks in the west. Cross-correlation analysis of measles and whooping cough show that in the west region the diseases are out of phase by 49 weeks. The model depicts a clear disruption of measles dynamics by the smallpox outbreak, resulting in higher and more frequent measles epidemics post-smallpox outbreak, though this is not reflected in the dataset.

**Discussion.** There were significant differences among the different regions in London in regard to measles dynamics. The biennial measles epidemics in the west region may be attributed to its lower birth rate. The out of phase correlations between measles and whooping cough in the west region is consistent with previous analyses of the two diseases. The smallpox outbreak on measles dynamics was successfully modeled. We found the susceptible populations for measles and smallpox during this outbreak were different, explaining why the outcome of the model does not reflect the data. This model has significant implications from both the ecological and public health perspectives as these perturbations in regular dynamics will happen both organically or artificially in nature.





