Graduate Research Plan Statement

The sparse and heterogeneous distribution of water in savanna landscapes largely determines herbivore distributions. Thousands of animals gather at watering holes and riverbanks, which become foci for both competition and predation. Species with relatively low water needs can take advantage of large, naturally occurring gaps ("refugia") between persistent water sources to avoid competition and predation; in fact, these refugia can be critical to maintaining their populations[1]. Kruger National Park ("Kruger"), South Africa, offers a unique long-term experiment of the effects of surface water augmentation on herbivore distributions. Kruger was fenced in the early 1960s, obstructing historic migrations of grazers to dry-season water sources. In response, management installed hundreds of watering holes ("boreholes"), but these fragmented the dry refugia, allowing the ranges of drought-intolerant species (i.e. *Equus quagga, Connochaetes taurinus*) to expand into those of drought-tolerant, locally rare antelope[1,2] (RA) (i.e. *Taurotragus oryx, Hippotragus equinus, H. niger*). This attracted predator attention to refugia and created more competition for forage during the severe droughts of 1981, 1985, and 1992[3]. Surface water also attracts elephants, which can drastically alter the surrounding ecosystem and impact forage biodiversity[4]. This increased predation, competition, and ecosystem engineering all contributed to the alarming population declines in RA in the 1980s[3]. Realizing this, in 1997 Kruger's management scheme was re-examined, and two-thirds of boreholes were closed[4]. The current conditions for Kruger's RA are still fraught, however. Borehole closures have not returned refugia to their original extents[4]; many remain open for their touristic value (e.g. guaranteed presence of diverse species). In addition, climate models project that southern Africa will experience more frequent and intense droughts[5], especially threatening Kruger's drier northern areas, where most of the park's RA refugia are located[6].

Motivation: Water access drives complex savanna dynamics. Lingering hydro-homogeneity in Kruger, along with projections indicating more frequent and intense droughts, make it imperative to understand how this community is structured, how species interactions shape responses to climate change, and how these might change in the future. I will determine (1) how surface water sources and resulting interspecific interactions affect how large herbivores respond to climate variables, and (2) how this changing community structure impacts resilience to extreme environmental events. I will also create a tool for Kruger park managers to infuse sharper knowledge of ecosystem structure into management aims.

Methods: I will analyze herbivores' interactions and responses using GJAMtime, a Bayesian time-series 'generalized joint attribute model' developed by Dr. Jim Clark[7]. GJAMtime models species distributions through environmental and interspecies interactions, improving upon traditional static species distribution models that fail to address interactions between species and temporal dependence on previous conditions. GJAMtime builds species migration, density-independent (DI) growth, and density-dependent (DD) interaction terms into a familiar Lotka-Volterra model and generates a species-interaction coefficient matrix ("α-matrix"), enabling dynamic community structure analysis[8]. In preparation, I have divided a map of the park into 710 30km^2 grid squares, to which I either aggregated (borehole locations, fires, geology, climate variables) or interpolated (rainfall, grass abundance) annual environmental covariates. I determined Bayesian priors for species interactions and responses to covariates through review of savanna literature and personal communication with established savanna scientists. Aerial annual census data are rich; from 1977-98, park rangers counted all animals in parkwide airplane census; from 1998 onwards, 800-m wide transects replaced the expensive full-park census (providing 15-28% coverage instead)[9]. For transects, data on individual animals' distance-from-aircraft were also collected. With knowledge of each species' detection rate (a factor of coloring, preferred habitat, and size), I will derive species detection functions using the R package 'DSim' to estimate true herbivore abundances.

Research Plan: This project extends my exploratory analyses, detailed in my personal statement, to include borehole and fire data, larger temporal extents, narrower hypotheses, and novel statistical tools.

(1) How does surface water affect community structure, and how can this in turn limit RA population density? *Hypothesis: If greater hydro-homogenization permits species invasion of refugia, then negative impacts on RA will be seen through (1) decreased populations and (2) negative α-matrix species interaction coefficients.* Equilibrium population sizes are a function of migration, DI, and DD growth; I will compare equilibrium abundances and α-matrix coefficients from greater and lesser borehole

concentration years to determine whether these boreholes negatively affect RA populations. I will compare pre-1997 data (high borehole density) to post-1997 data, the latter proxying a time with few boreholes. I will extract how much of each species' climate responses are coming from migration, DI, and DD growth using GJAMtime estimates. If results do not support my hypothesis (negative effect of boreholes on RA population density), then this indicates the influence of other sources on RA population decline, including an increase in elephant disturbance after culling was ended in 1992; anthrax outbreaks in roan antelope in the early 1980s; or changes in fire management, extent, and intensity over time.

(2) How does changing community structure affect the savanna ecosystem's resilience to extreme events? *Hypothesis: If these changing community structures reduce ecosystem resilience, then increasing hydro-homogeneity will (1) increase drought recovery time, (2) increase fire recovery time, and (3) increased community instability.* Major droughts occurred in Kruger in 1981-82, 1985-86, 1991-93, 2014-16, and 2018-20. These droughts straddle the borehole closures of the 1990s. Natural and prescribed fires, with varying intensities and times between burns, also occur regularly across the savanna. For intense local fires and parkwide drought events, I will compare each species' population the year before the event to its population in subsequent years to determine population recovery time. I will compare these trends to a stability analysis of the α-matrix (with negative eigenvalues indicating stability) for these periods to see if community structure and species interactions are impairing ecosystem recovery after extreme events. If we do not see evidence for this, then the influence of management decisions (e.g. removal of fencing, end of elephant culling) or climatic interactions (e.g. fires during drought years) played a larger role than species interactions, setting the groundwork for future studies in community stability and resilience.

Resources: The Kruger GIS Lab provided all data, and South Africa National Parks registered my project this fall. In March 2021, I will share my research at Kruger's Savanna Science Network Meeting, discussing my assumptions and findings with other savanna scientists. I will also travel to Kruger in 2021 and 2022 to participate in dry season censuses and attend courses on savanna ecosystems. My math degree and two years' coding experience at IBM prepared me well for the analysis of the complex models proposed in my study. I am advised by statistical and climate-change ecology expert Dr. Jim Clark and Kruger grassland ecologists Dr. Steve Higgins (University of Bayreuth) and Dr. Carla Staver (Yale).

Intellectual Merit: This analysis is crucial to maintaining one of the world's last Pleistocene megafauna savanna ecosystems. My novel statistical analysis will illuminate the relationship between species interactions and community environmental responses, a connection understudied in modern ecological literature. I also propose to determine how a changing community structure affects an ecosystem's resilience to climate change, a pressing issue to today's ecologists. Finally, my analysis of Kruger's extensive, long-term datasets with GJAMtime's Bayesian Gibbs-sampling techniques certainly meet the 2020 GRFP solicitation goal of supporting "computationally intensive research".

Broader Impacts: Adaptive park management requires use of near real-time animal census and climate data. I will provide park managers with a data workflow to feed each year's new census data into my GJAMtime model. I will (1) convert GJAMtime's outputs to be readable by non-statisticians (2) write change detection functions to highlight how herbivore responses vary from previous years, (3) convert the code from steps 1 and 2 into an open-source user interface in RShiny to allow park managers to run code without prior programming skills, (4) solicit regular feedback from park management, and (5) provide iterative, ongoing support and tool improvement through GitHub. These five steps provide a link between the environment-species interactions model and a more user-friendly interface for management decision-making. Additionally, as described in my personal statement, I will use my African savanna conservation research to develop open-source RShiny modules, based on Kruger herbivore and environmental data, to engage high schoolers in Durham Public Schools to boost their skills and confidence in math and coding.

[1] CC Grant *et al.* 2002. *Koedoe* 45. [2] IPJ Smit 2011. *Ecog.* 34. [3] MP Veldhuis *et al* 2019. *Ecol. Lett.* 22. [4] IPJ Smit 2013. *Pachyderm* 15. [5] Working Group II, Fifth Assessment Report of the Inter-governmental Panel on Climate Change, 2014. *In: Impacts, Adaptation, and Vulnerability, Part B: Regional Aspects.* [6] JO Ogutu & N Owen-Smith 2003. *Ecol. Lett.* 6. [7] JS Clark *et al.* 2017. *Ecol. Monogr.* 87. [8] JS Clark, *et al.* 2020. *PNAS*, 117. [9] JM Kruger *et al* 2008. *Wildl. Res.* 35.