LARSEN, ANGELA LYNN, Ph.D. How does Behavior Drive Population and Community Dynamics of Rodents? (2017)
Directed by Dr. Matina Kalcounis-Rueppell. 167 pp

Understanding how population and community dynamics emerge from individual traits is essential to predict responses of animal populations and communities to habitat alterations. Individuals make decisions and are the basic unit of response to changes in the environment. Changes at the individual level can translate to population and community dynamics. Anthropogenic changes to environmental conditions occur frequently and rapidly. One anthropogenic change, biofuel feedstock production, is increasing to reduce dependency on fossil fuels. Switchgrass (*Panicum virgatum*) is a biofuel feedstock being planted between rows of loblolly pine (*Pinus taeda*). I hypothesized that changes in understory vegetation from intercropping switchgrass in pine plantations would alter intraspecific interactions, influencing individual behavioral decisions, which would then drive changes in population and community dynamics. My research aims were to assess effects of three treatments (switchgrass monocrop, switchgrass intercropped in loblolly pine, and control loblolly pine) on rodent: 1) population dynamics and community structure; 2) spatial and foraging behaviors, and patterns of reproduction; and 3) behaviors as predictors of population dynamics and community structure. My model species was the hispid cotton rat (*Sigmodon hispidus*), a common grassland specialist and early successional species. The cotton rat was a suitable model species because it has a relatively large geographic distribution, was easily captured at our site, and was expected to respond to change in grassy understory habitat. I studied the rodent community because they are ecosystem engineers, both prey and predators, and indicators of biodiversity. I used vegetation surveys, live-trapping, radio telemetry, giving-up density surveys, and individual-based modeling (IBM). Monocrop plots were ecological sinks with high adult cotton rat abundance but low juvenile recruitment, and control plots were ecological sources with low adult cotton rat abundance but high juvenile recruitment (Chapter II). Intercrop plots were intermediate for adult cotton rat abundance and juvenile recruitment, likely due to the mixture of cover and food (Chapter II). I also found cotton rats foraged more in monocrop than control plots, with intermediate foraging in intercrop plots (Chapter III). Females in control plots tolerated territory overlap with other females in areas with high amounts of grass (Chapter III). Then, based on an IBM, I found cotton rat populations would persist throughout 10-years of the current management in intercrop plots (Chapter IV). However, if management resulted in reduced non-grass cover, cotton rat populations would decline, whereas if management resulted in additional non-grass cover, cotton rat populations would increase in intercrop plots compared to predicted populations under current management (Chapter IV). Understanding behavioral responses as mechanisms underlying population and community level responses, allowed me to develop and use a functional and predictive IBM. My IBM can be used to predict responses of various prey species to management techniques that affect food and cover resources. My research helped to elucidate properties of populations and communities to better inform, and improve top-down predictive models and management decisions.

# HOW DOES BEHAVIOR DRIVE POPULATION AND COMMUNITY DYNAMICS OF RODENTS?

by

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A Dissertation Submitted to
the Faculty of The Graduate School at
The University of North Carolina at Greensboro
in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

Greensboro
2017

Approved by

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# APPROVAL PAGE

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# ACKNOWLEDGEMENTS

I would like to thank my advisor, Dr. Matina Kalcounis-Rueppell, for her amazing mentorship throughout the past five years. I would also like to thank all of my committee members, Dr. Stanley Faeth, Dr. Jessica Homyack, and Dr. Scott Richter for their support and guidance. Thank you to Dr. Volker Grimm, Dr. Steven Railsback, and Dr. Steven Lytinen for sharing their expertise of individual-based models during a workshop and their continued guidance beyond the workshop. Thank you to Weyerhaeuser Company, Catchlight Energy LLC, National Council for Air and Stream Improvement, Inc., U.S. Environmental Protection Agency (EPA), American Society of Mammalogists, North Carolina Academy of Science, and University of North Carolina at Greensboro for funding. I would also like to thank all of my hard-working technicians; R. Kelble, K. Paolini, E. VanNatta, A. Andrews, D. Bradley, J. Franklin, M. Martin, R. Meyer, K. King, A. Matteson, K. Corson, E. Smerdon, A. Wagoner, A. Culpepper, and G. Mikel. I thank Mississippi State University, Steve Emerson, and the employees of the Scooba Weyerhaeuser office for their help at the field site. I also thank the East Mississippi Sportsman Association and Charlie Studdard with the Kemper County Hunting Club for providing lodging during the field seasons. Thank you to the past and present members of the Bat and Mouse Lab for your feedback, support, and advice. Thank you to all of my family and friends for your unwavering support. Lastly, I would like to thank all of the awesome rodents that were involved in this research.

# TABLE OF CONTENTS

# LIST OF TABLES

Page

# LIST OF FIGURES

# CHAPTER I

# INTRODUCTION

Conservation biology aims to protect biodiversity, especially in areas with anthropogenic changes in land-use. However, conservation biology studies are usually conducted at population and community levels over short time scales. For example, when investigating if land-use changes caused amphibian declines, Houlahan and Findlay (2003) measured species abundance, richness, and community composition over 3 field seasons. Weak, but positive associations were found between amphibian species richness and both wetland area and adjacent forested land (Houlahan and Findlay, 2003). Gordon L. Kirkland (1990) reviewed 21 articles which all showed a general pattern of small mammal populations and communities having a positive response to clear-cutting. More recent studies have pointed out the importance of including behavioral ecology in conservation biology studies (Anthony and Blumstein, 2000; Buchholz, 2007) because behavior underlies changes at the population and community level. Simply observing population and community changes does not provide information about system properties or mechanistic responses to anthropogenic alterations. Management to protect biodiversity is complicated if the underlying mechanisms of populations and communities are not understood. A time lag is possible, or the population and community scales could be too coarse to observe potentially significant changes or lack thereof.

My dissertation includes a collection of field data to assess rodent individual, population, and community responses to habitat modification. Then, using the data collected along with data from previous literature, I, along with my co-authors, developed an individual-based model (IBM). I used life history parameters, rules based on site-specific data and well-documented information (such as required energy intake to reproduce), and submodels (such as territory ownership) to realistically model population and community level changes. My dissertation provides information about population and community responses in Chapter II, behavioral responses in Chapter III, and an IBM to exemplify how short-term field data can be used to forecast rodent behavioral, population, and community responses to different understory habitat characteristics in Chapter IV.

Habitat alterations lead to population and community level changes. For example, rodent populations respond to forest management such as thinning (Suzuki and Hayes, 2003) and clear-cutting (Moses and Boutin, 2001) of forests, prescribed burning (Beck and Vogl, 1972), and the combination of thinning and prescribed burning (Converse et al., 2006). Studies conducted at the population level found species specific responses to disturbance (Beck and Vogl, 1972; Moses and Boutin, 2001). Changes in rodent population and community levels are typically associated with understory habitat changes (Suzuki and Hayes, 2003). More heterogeneous habitats can support more species because they provide a wider diversity of resources. However, habitat alterations may affect the distribution of resource availability and therefore affect the number of species. Community indices decrease in areas with high abundance of one species (Brady and

Slade, 2001; Tuomisto, 2012). Studies have shown *Microtus* spp. have higher recruitment in clear-cut forests than undisturbed forests but *M. gapperi* has higher recruitment in undisturbed forests (Sullivan and Sullivan, 2001). Not all studies found a difference in estimated survival between disturbed and undisturbed areas (Sullivan and Sullivan, 2001). Ecke et al. (2002) found differences in survival of vole species translated into differences in vole species richness. They also showed higher richness in younger forests than older forests (Ecke et al., 2002).

Populations are comprised of individuals that vary in their behavioral decisions. Individuals make decisions based on several factors, such as conspecific density, habitat structure, and resource availability. Other complex factors include environmental cues, microclimate, and innate responses (O'Hara, 1981). Anthropogenic habitat alterations, which occur at an accelerated rate and persist compared to natural habitat succession, have the potential to create ecological traps (Schlaepfer et al., 2002). While sinks are areas where individuals have low reproductive success and survival, an ecological trap is a type of sink where individuals prefer the poor quality habitat over better quality habitat (Gilroy and Sutherland, 2007; Hale and Swearer, 2016; Kristan, 2003). Some behaviors are more plastic than others, and certain behaviors depend on environmental cues which may or may not have changed (Schlaepfer et al., 2002). Individuals may detect and respond to an original environmental cue which still exists in an altered habitat, or a new cue which mimics the original cue and both cases would result in an unexpected outcome (Schlaepfer et al., 2002). Decisions are positive, negative, or neutral and may alter survival and reproduction, which affects population and community levels. A classic example of an ecological trap is grassland birds nesting in what appears to be suitable hayfield that is mowed either before eggs hatch or nestlings fledge (Bollinger et al., 1990). Such ecological traps could be avoided if individual decisions, and the ways they impact populations, are better understood.

There is a mismatch between how land is managed and how wildlife responses are assessed. Although habitat management techniques can be implemented within days or months, their effects can last years. However, most wildlife studies only assess wildlife responses for a few years. Some studies use traditional models to forecast population responses to management techniques. However, traditional models require unrealistic assumptions about individuals, such as assuming all individuals will respond in the same way regardless of behavioral variation and the resources each individual can access (Huston et al., 1988). IBMs are simulation-based models used to predict population and community level changes based on individual decisions (Grimm and Railsback, 2005). Once an IBM is calibrated, the model can be used to simulate several possible scenarios of interest (McLane et al., 2011). IBMs use fitness maximizing decisions, which make the models realistic and able to predict how individuals will respond, even in novel environments (Stillman et al., 2015). Therefore, IBMs can be powerful tools to predict how management techniques will affect species and biodiversity prior to long-term, large-scale management implementation. As an example, an IBM of the spread of rabies infection in foxes (*Vulpes vulpes*) led to effective management decisions that showed there could be a reduction in immunizations needed for a rabies eradication program, which would have economic benefit (Eisinger and Thulke, 2008; Evans et al., 2013).

A current anthropogenic disturbance of conservation interest is the production of biofuels using sustainable methods, which do not negatively impact biodiversity. Biofuel production has been increasing to reduce dependency on fossil fuels and lower greenhouse gas emissions (Cheng and Timilsina, 2011). Conversion of natural habitats to biofuel producing areas may lower local biodiversity (Fletcher et al., 2010). Planting second generation biofuels, such as switchgrass (*Panicum virgatum*), in a monoculture has advantages and disadvantages because converting one feedstock species to liquid biofuel can be easier than converting a mixture of species (Bies, 2006). However, monocultures do not provide diverse wildlife habitat, and when monocultures are harvested, no nearby refugia may remain to provide wildlife habitat (Bies, 2006; Garratt et al., 2012).

Agroforestry researchers have promoted alley cropping or intercropping as an alternative to planting monocultures to sustain diversity and provide other benefits (Cutter and Garrett, 1993; Garrett and Buck, 1997; Palm, 1995). Intercropping switchgrass on lands in use for production of other commodities, such as wood products from pine plantations has occurred throughout the southeastern U.S. on a research scale (Riffell et al., 2012). Intercropping switchgrass between loblolly pine (*Pinus taeda*) rows in plantations avoids competition with food crops and provides landowners with additional potential income (Milder et al., 2008). Intercropping also may provide refugia to wildlife in the pine beds when managers harvest switchgrass. Intercropping switchgrass in pine plantations may increase biodiversity compared to traditional pine plantations by providing both vertical structure from regenerating pines and grassland habitat in the understory (Riffell et al., 2012).

In general, a knowledge gap exists in understanding the mechanisms causing population and community changes associated with habitat heterogeneity (Anholt, 1997). Once mechanisms are better understood, it is possible to make predictions regarding future changes in populations and communities (Evans et al., 2013). For my dissertation, I investigated microhabitat of switchgrass intercropped in pine plantations and associated responses of rodent behavioral, population, and community responses. Furthermore, I developed and implemented an IBM as a new technique in the switchgrass-pine system to simulate responses into future years. I hypothesized differences in understory habitat caused by intercropping switchgrass in pine plantations altered behavioral responses that drove changes in population and community dynamics. I designed 3 aims to test my hypothesis:

Specific Aim I (Chapter II): Assess effects of understory habitat modification (treatment plot [monocrop, intercrop, control]) on population dynamics [abundance, survival, and recruitment] and community structure [diversity, richness, and community assemblages].

Specific Aim II (Chapter III): Assess effects of understory habitat modification (treatment plot [monocrop, intercrop, control]) on spatial and foraging behaviors, and patterns of reproduction [home range size, foraging activity, female home range overlap, and reproductive indices].

Specific Aim III (Chapter IV): Understand how alterations in behavioral responses drive alterations at population and community levels in areas where an understory habitat modification has occurred (treatment plot scale [monocrop, intercrop, control]).

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# CHAPTER II

# EFFECTS OF HABITAT MODIFICATION ON COTTON RAT POPULATION DYNAMICS AND RODENT COMMUNITY STRUCTURE

PUBLISHED AS:
Larsen, Angela L., Jessica A. Homyack, T. Bently Wigley, Darren A. Miller, and Matina C. Kalcounis-Rueppell. (2016) Effects of habitat modification on cotton rat population dynamics and rodent community structure. *Forest Ecology and Management* 376: 238-246.

## Abstract

Concerns over climate change and finite fossil fuels have generated interest in biofuels. Switchgrass (*Panicum virgatum*), a biofuel feedstock, was planted in intensively managed loblolly pine (*Pinus taeda*) stands to investigate sustainability of this system for producing an alternative energy source. We hypothesized that changes in understory habitat conditions caused by intercropping switchgrass in pine stands would affect rodent population and community dynamics within three years. Therefore, we assessed effects of three treatments (control pine, switchgrass intercropped in pine, and switchgrass monocrop) on rodent population (abundance, survival, and recruitment) and community (diversity, richness, evenness, and community assemblages) measures. We conducted vegetation surveys and live-trapping during 2013-2015 summers in Kemper County, Mississippi, USA. We conducted 6 trapping sessions each summer (n=14,112 trap nights per year) and captured 1,733 cotton rats (*Sigmodon hispidus*), 102 *Oryzomys palustris,* 31 *Mus musculus*, 28 *Reithrodontomys fulvescens,* 22 *R. humulis,* 20 *Peromyscus leucopus*, 9 *Microtus pinetorum,* 9 *P. gossypinus*, and 2 *Neotoma floridana*. We found greater cotton rat abundance and lower recruitment in monocrop versus control plots. Rodent diversity was lower in monocrop than control plots. Intercropped plots had intermediate levels of cotton rat abundance and recruitment, and rodent diversity. More dispersal may have occurred in monocrop plots because of high population abundance and limited habitat availability. Cotton rat survival and rodent community assemblage were similar among treatments but differed among years. Although rodents responded negatively to monocrop plots, our results suggested intercropped plots would be an appropriate management practice in pine plantations to produce biofuel feedstocks while maintaining rodent diversity.

**KEY WORDS**: switchgrass, loblolly pine, intercropping, biofuel, *Sigmodon hispidus*, Mississippi

## Introduction

Biofuel production has been increasing to reduce dependency on fossil fuels and lower greenhouse gas emissions (Cheng and Timilsina, 2011). For an alternative fuel to be feasible, it must be cost effective, provide a net energy gain, provide environmental benefits, and be producible without reducing food crops (Hill et al., 2006). Although first generation biofuels do not meet all of these criteria, there have been several technological advances to allow production of second generation biofuels (Cheng and Timilsina, 2011) from lignocellulosic materials such as grasses (Heaton et al., 2008), woody vegetation, and agricultural (Kim and Dale, 2004) and forestry residues. One promising second generation biofuel feedstock, switchgrass (*Panicum virgatum*), mainly has been studied in monocrop settings (Cassida et al., 2005; Fike et al., 2006; Wang et al., 2010). Switchgrass produced on a small farm-scale (3-9.5 ha fields, with an average 6.7 ha field) meets all of the criteria to be an alternative fuel (Schmer et al., 2008).

Planting switchgrass in a monocrop has production advantages and potential sustainability disadvantages. Processing a single species to biofuel is easier than a mixture of species during the conversion process (Bies, 2006). However, monocrops do not provide diverse wildlife habitat structure and when monocrops are harvested, they may not retain refugia for wildlife (Bies, 2006; Garratt et al., 2012). Intercropping, also referred to as alley cropping, is when two crops are planted in alternating rows (Garrett and Buck, 1997). Intercropping is an alternative to planting monocrops that has been promoted by agroforestry researchers to maintain biodiversity and provide other ecological benefits (Cutter and Garrett, 1993; Palm, 1995). Planting trees in agricultural settings potentially increases economic and environmental benefits, such as additional revenue streams to the landowner and wind protection that reduces soil erosion. Intercropping has been used to plant switchgrass on lands already encumbered for production of other crops, such as plantation forestry (Riffell et al., 2012). Planting switchgrass between loblolly pine (*Pinus taeda*) rows in plantations uses land where switchgrass is not competing with food crops and provides landowners with additional potential income (Milder et al., 2008). Wildlife also may find refugia in pine rows, particularly when switchgrass is harvested. Intercropping switchgrass in pine plantations may increase biodiversity compared to traditional pine plantations by providing both young, open pine and grassland habitat structure (Riffell et al., 2012).

In agricultural landscapes, switchgrass monocrops contained a lower diversity of grassland birds than areas planted with a mixture of cool-season grasses, likely because switchgrass is denser and more homogenous (McCoy et al., 2001). In a forestry setting, bird abundances initially declined when switchgrass was planted in an intercropping system, probably due to loss of snags from disturbance during site preparation and when planting switchgrass (Loman et al., 2014, 2013). The bird community changed in monocrop, intercrop, and control treatments between the year switchgrass was planted and the year after planting switchgrass (Loman et al., 2014), but by the third year after planting switchgrass, intercrop and control plots had similar avian community assemblages. However, there is a potential for further change as forest succession continues in the intercrop and control treatment plots (Loman et al., 2014). There is a need for research on effects of planting switchgrass on biodiversity, particularly in intercropped stands (Riffell et al., 2012), because most studies that have examined effects of switchgrass on biodiversity have both compared switchgrass to row crops and native grasslands (Fletcher et al., 2010) and investigated effects on grassland birds and herpetofauna (Homyack et al., 2013; Loman et al., 2014) rather than mammals (but see Briones et al., 2013; Homyack et al., 2014; King et al., 2014; Marshall et al., 2012).

Microhabitat changes due to planting switchgrass are not well understood, but may affect animals that use understory vegetation. Rodents have key ecological roles as seed dispersers, regulators of invertebrate populations, and prey for several species

(Panzacchi et al., 2010). Different rodent species prefer different habitat conditions, so vegetative heterogeneity throughout an area support a more diverse rodent community (Dueser and Shuggart, 1979; Mengak and Guynn Jr., 2003). Abundance of white-footed mice (*Peromyscus leucopus*) has been negatively correlated with grass cover while cotton rat (*Sigmodon hispidus*) captures have been positively correlated with grass cover (Marshall et al., 2012; Mengak and Guynn Jr., 2003). A previous study investigating functional role of white-footed mice in a switchgrass intercropped in a pine system in North Carolina, USA found that there were no differences in carbon or nitrogen isotope signatures between white-footed mice in switchgrass intercropped plots and pine plantation plots, suggesting no change in their functional role (Briones et al., 2013). In established switchgrass intercropped plots, rodent evenness and diversity were lower than in equal aged pine plantation plots (King et al., 2014). Intercropped plots also had greater cotton rat abundances than pine plantation plots, but survival and recruitment did not differ between intensively managed stands that were intercropped and those that were not (King et al., 2014).

To better understand possible effects of intercropping on rodent communities, we investigated microhabitat characteristics of switchgrass intercropped in newly planted pine plantations and associated responses of rodent populations and communities. We hypothesized that change in understory structure caused by intercropping switchgrass in pine plantations would affect rodent population and community dynamics. We assessed effects of three treatments (control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]) on rodent population metrics (abundance, survival, and recruitment) and community structure (diversity, richness, evenness, and community assemblage). We predicted that cotton rats, a grassland specialist species, would have greater abundance, survival, and recruitment in monocrop plots and lower abundance, survival, and recruitment in control pine plots because of predicted resource availability. Further, we predicted monocrop plots would be dominated by populations of cotton rats and therefore would have the lowest rodent diversity, richness, and evenness, whereas intercrop plots would have greatest rodent diversity and richness. Lastly we predicted that community assemblages would differ among treatments. Specifically, we hypothesized that monocrop plots would be dominated by populations of cotton rats but intercrop and control plots would support more species.

## Methods

### *Study area*

‘Alamo’ variety switchgrass, a native biofuel feedstock, was intercropped in loblolly pine plantations in Kemper County, Mississippi, USA, on land owned and managed by Weyerhaeuser Company on experimental plots established and maintained by Weyerhaeuser Company and Catchlight Energy LLC (CLE), a Chevron|Weyerhaeuser joint venture. Each stand received the same site preparation in September 2010 before pines and switchgrass were planted (Loman et al., 2013). One-year-old pine seedlings were planted during January-February 2010. Switchgrass was planted in August-September 2011 and May-June 2012 to ensure full establishment. Switchgrass (intercropped alleys and the entire monocrop plots) received fertilizer (Arborite) and herbicide [banded treatment of triclopyr (Garlon 4 Ultra®), metsulfuron methyl, and chlorsulfuron (Cimmaron Plus®)] in May-June 2014 and fertilizer (Arborite) in May 2015 to promote switchgrass productivity. We used 4 stands (as replicates or blocks) with 4 randomly assigned treatments plots (10ha each) within each stand; two control plots, an intercrop plot, and a monocrop plot (Figure 2.1). Two control plots were studied because of future plans to remove woody biomass between pine beds in one control plot per replicate. We averaged results from control plots within stands to reduce potential bias from increased sampling effort. Our study plots were the same as the pine control, intercropped switchgrass, and switchgrass monocrop plots described by Loman et al. (2014).

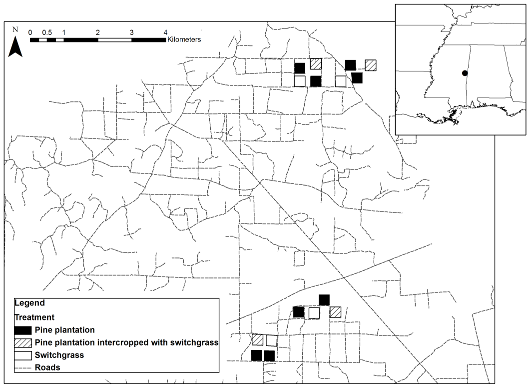

Figure 2.1. Study Site Located in Kemper County, MS, USA (shown in locator map) on Land Owned and Managed by Weyerhaeuser Company. There were 4 replicates, each containing four 10-ha treatment plots; two control loblolly plots (black squares), switchgrass intercropped in loblolly pine (hollow with lines squares), and switchgrass monocrop (hollow squares).

### *Vegetation*

To measure microhabitat characteristics, we used 1.77-$m^2$ hoops centered over each trapping station (see Trapping below) in all plots during May each year. We visually estimated ground cover using the following percent cover classes (absent, 0-1, 1-5, 5-15, 15-25, 25-50, 50-75, 75-95, and 95-100%) for 9 cover types (pine, non-pine woody vegetation, grass, forb, moss, vine, bare ground, other debris [including pine needles and dead vegetation], and woody debris [including downed trees, stumps, and branches]). We converted cover classes recorded at each trapping station to the midpoints of the ranges (e.g., for cover class 15-25 the midpoint value would be 20). We averaged microhabitat variable estimates at all trapping stations within a treatment plot.

We estimated vertical vegetation density using a cover board at the center of each hoop at all trapping stations (Nudds, 1977). We estimated cover of each section of the board while standing 14m away at each of the 4 cardinal directions. The cover board had 6 sections and each section was 30cm high by 18cm wide. We averaged estimates across the 4 observations at each trapping station for each section separately. We then obtained treatment plot averages for each section. We analyzed near-ground (ground up to 90cm) and aboveground (90cm above ground to 180 cm aboveground) sections of the cover board separately to assess cover that may have different functions, particularly relating to ground and aerial predators. We had 2 observers for vegetation surveys each summer (one the lead author) to reduce potential observer bias.

### *Trapping*

We established a 7x7-trapping grid (20 m between traps; 49 trap stations) at the center of each treatment plot that remained in the same location for all three years of our study. We used 42 Sherman 23-cm live traps (H.B. Sherman Traps Inc., 167 Tallahassee, Florida, USA) and 7 Longworth traps (Rogers Manufacturing Co., Peachland, British Columbia, Canada) or 18-cm non-folding Sherman traps per treatment plot (1 smaller trap was randomly placed per trap line) to prevent size bias when trapping (Anthony et al., 2005). We baited traps with crimped oats. We also applied a granular insecticide (Talstar PL, FMC Corporation, Philadelphia, Pennsylvania) around each trap at the beginning of each trapping session to prevent fire ants (*Solenopsis invicta*) from attacking captured rodents. We completed 6 trapping sessions of 3 consecutive nights on each treatment plot from May to August in 2013, 2014, and 2015. We trapped all treatments of a replicate simultaneously. The final trapping session in 2015 was only 2 consecutive nights because of a sudden increase in raccoon (*Procyon lotor*) disturbance to traps. We uniquely marked all captured animals with a numbered ear tag (Model 1005–1, National Band and Tag Company, Newport, Kentucky, USA). We also recorded species, sex, age-class (juvenile, subadult, adult), reproductive condition (scrotal, non-scrotal, perforate, pregnant, lactating, pregnant and lactating, post-lactating), and mass (g). We determined age-class using a combination of mass, pelage, and reproductive status. For cotton rats, we used similar age-classes as previous literature (DeBusk and Kennerly, Jr., 1975), but altered slightly to match our observations of pelage and reproductive status at our site: juveniles (<40g), subadults (40-80g), and adults (>80g). We recorded hind foot, tail, and body lengths (mm) for all mice species to aid in identification. We conducted our work under annual scientific collection permits from the Mississippi Department of Wildlife, Fisheries, and Parks and UNCG IACUC 14-001.0. We followed the American Society of Mammalogists guidelines for use of wild mammals in research (Sikes and Gannon, 2011).

### *Population*

We first completed a population analysis in Program MARK (White and Burnham, 1999) using a Robust design model. However this model produced unrealistic results, potentially because the model did not converge, likely due to low capture and recapture rates in 2014 and 2015. Thus, we used minimum known alive (MNKA) numbers to estimate relative abundance of rodent populations and manually calculated recruitment and survival. Our MNKA numbers were obtained in a way analogous to the Robust design model in Program MARK (White and Burnham, 1999). We considered each trapping session as closed, but we considered time between each trapping session as open. Therefore, we obtained MNKA numbers from each trapping session separately. We then averaged MNKA numbers across trapping sessions to obtain a MNKA number for each year of trapping. We estimated recruitment as number of juveniles captured per adult reproductive female captured per treatment plot and averaged across plots (Long et al., 2015). We were not able to use our trapping data to estimate survival given low number of captures and recaptures, particularly in 2014 and 2015. Instead, we directly measured survival by following fate of 82 different resident, adult, female cotton rats (18 in 2013, 33 in 2014, and 31 in 2015) that were radiomarked (M1450 or M1520 Advanced

Telemetry Systems [ATS], Isanti, MN, U.S.A.) as part of a separate study. Each year we radiomarked new individuals and we followed all radiomarked individuals for a single summer. We located all radiomarked individuals during daylight hours using homing techniques. We initially located each individual via homing 24 hours after being radiomarked to allow the individual to acclimate to the radiotransmitter. We then located individuals via homing using a R4000 or R4500S receiver with a 3 element folding yagi (ATS) at least once a week until either the radiotransmitter was removed or the individual's fate was determined. When we were not locating individuals via homing during the day, we regularly conducted biangulation fixes, which provided information as to whether the individual was still alive or not. If we noticed any indication that an individual was no longer alive (i.e. the individual did not move during an entire night of biangulation fixes), we would use homing to visually locate the individual to determine status. We based all survival data on homing techniques.

### *Community*

We calculated Shannon-Weiner diversity, Simpson's diversity, richness, and Pielou's evenness (Pielou, 1966) using MNKA for each plot in program R (R Core Team, 2014), package Vegan (Oksanen et al., 2013). Simpson's diversity is more dependent on dominant species than Shannon-Weiner diversity, but is recommended for small sample sizes, so we used both diversity indices (Smith and Grassle, 1977).

### *Statistical analyses*

We used non-metric dimensional scaling (NMDS) to compare microhabitat variables within and among treatment plots. We used a two-way permutation multivariate analysis of variance (PerMANOVA) with interaction and stand as a blocking factor to test the null hypothesis that there were no differences in vegetation characteristics among treatments and years. We used a vector-fitting procedure with our vegetation data to find microhabitat characteristics significantly correlated with the ordination (Gallie and Drickamer, 2008; Letnic et al., 2004).

We used repeated measures, randomized block design analysis of variance (ANOVA) with an interaction to test the null hypothesis that there were no differences in treatment plot means of population abundance (calculated as MNKA) and recruitment (calculated as juveniles per reproductive female per plot) among treatments, year, and a possible interaction of treatment and year. We used an overall split-plot model to analyze the repeated measures, randomized block design ANOVA with stand as block, treatment as whole-plot, and year as sub-plot, with degrees of freedom adjusted for non-independence across years. We conducted a Fisher's exact test to assess for effects of treatment and year separately on survival. We only completed population level analyses for cotton rats as this species had sufficient data to estimate abundance, recruitment, and survival.

We used repeated measures, randomized block design ANOVA to test the null hypothesis that there were no differences in treatment plot means of community diversity, richness, and evenness indices among treatment, year, and possible interaction of treatment and year. We used NMDS to compare rodent community assemblage within and among treatment plots. We used a two-way PerMANOVA with interaction and stand as a blocking factor to assess differences in rodent assemblages among treatments and years.

For all NMDS procedures, we used 2-dimensional solutions based on scree plots and the minimal reduction in stress with additional dimensions. For each NMDS, we conducted 50 random starts. For each PerMANOVA, we generated 999 permutations and made post-hoc comparisons using Bonferroni-corrected p-values. For all vector-fitting procedures, we generated 999 random permutations. Given the large number of zeros in the dataset, we used Bray-Curtis dissimilarity matrices for all multivariate tests.

For all repeated measures ANOVAs, we checked normality and sphericity to ensure assumptions were met (D. M. Logan, 2010). We rank transformed data that did not meet the normality assumption as either raw or log transformed data. When the sphericity assumption was violated, we used the Greenhouse-Geisser correction. We investigated pairwise contrasts if the omnibus test was statistically significant using a Tukey HSD. We used Program R (R Core Team, 2014) for all analyses except the PerMANOVA post-hoc tests, which we performed in Paleontological Statistics Software Package for Education and Data Analysis (PAST) (Hammer et al., 2001).

## Results

### *Vegetation*

Within each treatment plot we measured microhabitat characteristics at 49 trap stations resulting in 196 subsamples for intercrop and monocrop plots and 392 subsamples for control plots each year. Microhabitat structure varied by treatment and year based on a NMDS plot and two-way PerMANOVA with interaction (stress=0.13, treatment; $F_{2,27}$=57.66, $R^2$=0.67, p<0.01 and year; $F_{2,27}$=11.15, $R^2$=0.13, p<0.01; Figure 2.2). There was no significant interaction of treatment and year ($F_{4,27}$=1.98, $R^2$=0.05, p=0.10). Monocrop plots had more grass cover and less woody debris, woody vegetation, and other debris compared to control and intercrop plots (based on vectors having r>0.92 and p<0.01; Figure 2.2). All years differed from each other in microhabitat structure (2013 vs. 2014 p=0.01; 2013 vs. 2015 p<0.01; and 2014 vs. 2015 p=0.04). The primary vegetation components each year were woody debris in 2013, woody vegetation in 2014, and other debris in 2015 (Figure 2.2).

We detected a significant interaction of treatment and year ($F_{4,18}$=3.18, p=0.04) for vertical vegetation density near the ground. Overall, control plots had the greatest (mean ± SE; 96.41 ± 0.77), intercrop had intermediate (87.45 ± 1.05), and monocrop had the least vertical vegetation density near the ground (52.37 ± 3.83; Figure 2.3). Vegetation density was less in 2013 in each treatment and remained significantly less in 2014 in both intercrop and monocrop plots compared to 2015. There was also a significant interaction of treatment and year ($F_{4,18}$=5.48, p<0.01; Figure 2.3) for vegetation density in the aboveground section. Similar to the near-ground section, overall, control had the greatest (78.41 ± 4.20), intercrop had intermediate (57.87 ± 3.55), and monocrop had the least vegetation density above the ground (0.85 ± 0.23). However, while control plots increased (63-91%) in vertical density from 2013-2015, intercrop and monocrop plots did not significantly differ across years (46-67% and 0.7-1.5%, respectively). Monocrop plots had the most grass and least vertical vegetation density in both sections throughout our study.

*Population*

Using 14,112 trap nights per year (3,528 per replicate per year), we marked and captured 1,036 unique individuals 2,543 times in 2013; 385 unique individuals 728 times in 2014; and 535 unique individuals 979 times in 2015. Across all years, trapping sessions, and plots, we captured 1,733 cotton rats*,* 102 marsh rice rats (*Oryzomys palustris*), 31 house mice (*Mus musculus*), 28 fulvous harvest mice (*Reithrodontomys fulvescens*)*,* 22 eastern harvest mice (*R. humulis*)*,* 20 white-footed mice, 9 woodland voles (*Microtus pinetorum*)*,* 9 cotton mice (*P. gossypinus*), and 2 eastern woodrats (*Neotoma floridana*).

*Abundance*

The cotton rat was the most abundant species followed by the marsh rice rat (Table 2.1). We also captured 2 juvenile eastern woodrats in a single control plot in 2015. We only conducted population analyses on the cotton rat, the only species with sufficient captures to warrant further analyses. The interaction of year and treatment for relative abundance of adult cotton rats was not significant ($F_{4,18}$=2.56, p=0.07; Figure 2.4). However, relative abundance of adult cotton rats was about 3 times greater in all plots in 2013 than the control and intercrop plots in 2014 and 2015 ($F_{2,18}$=32.51, p<0.01). Monocrop plots also had about 1.5 times greater adult cotton rat relative abundances than control plots ($F_{2,6}$=6.77, p=0.03; Figure 2.4).

*Survival*

In 2013, we radiomarked 18 resident, female cotton rats (6 per treatment; Table 2.2) with no evidence of predation in that summer. In 2014 and 2015, we radiomarked 33 and 31 resident female cotton rats, respectively (minimum of 10 per treatment). Of the 64 individuals radiomarked in 2014 and 2015, 6 of the 33 radiomarked individuals were eaten in 2014 (2 by snakes, 3 by unidentified predators and 1 by possible coyote (*Canis latrans*)), and 3 of the 31 radiomarked individuals were eaten in 2015 (2 by snakes and 1 by an unidentified predator). We radiotracked individuals for an average of 22.51 (± 1.23) days overall (range: 1-50 days). The length of time we radiotracked each individual depended on whether or not (and when) (1) the animal was eaten, (2) the radiomark was lost by the animal, and (3) the animal was easily recaptured for radiomark removal. Survival did not differ among treatments (p=1.00) or years (p=0.15). We calculated survival analyses using known predation events of radiomarked individuals (Table 2.2). We did not detect any other natural sources of mortality during our study.

*Recruitment*

Cotton rat recruitment was 3 times lower in monocrop (0.14 ± 0.05) than control plots (0.46 ± 0.07; $F_{2,6}$=6.42, p=0.03). Recruitment also was 2 times greater in 2013 (0.45 ± 0.08) than 2014 (0.18 ± 0.06; $F_{2,18}$=6.06, p=0.01; Figure 2.5).

*Community*

Richness and evenness did not differ among treatments ($F_{2,6}$=2.94, p=0.13; $F_{2,6}$=3.57, p=0.10, respectively). Rodent assemblages did not vary by treatment, but 2013 was different from 2014 and 2015 based on a NMDS plot and two-way PerMANOVA with interaction (stress=0.10, treatment; $F_{2,27}$=1.47, $R^2$=0.06, p=0.12 and year; $F_{2,27}$=5.80, $R^2$=0.26, $p<0.01$; Figure 2.6). Overall, 2013 had 2.5 times more captures of cotton rats compared to 2014 and 2015. In 2014 and 2015, we captured more woodland voles and fulvous harvest mice than in 2013 (Figure 2.6). There was no significant interaction of treatment and year ($F_{4,27}$=0.93, $R^2$=0.08, p=0.39). Control plots had a greater Shannon and Simpson's diversity than both intercrop and monocrop plots ($F_{2,6}$=7.28, p=0.02 and $F_{2,6}$=7.92, p=0.02, respectively; Table 2.3). There were no significant (p>0.05) interactions of treatment and year, nor were there any year effects for diversity, richness, and evenness indices.

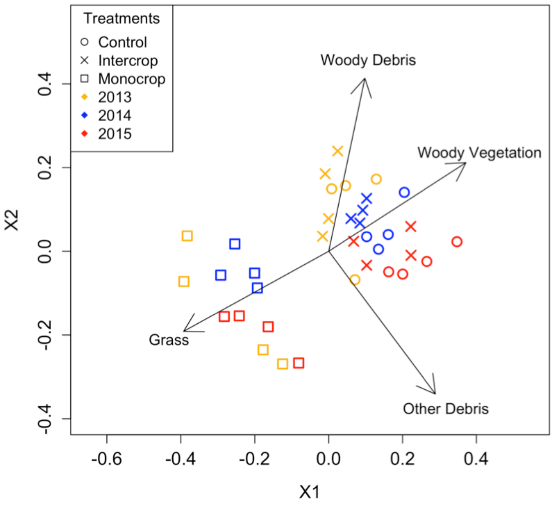

Figure 2.2. Non-metric Dimensional Scaling (NMDS) Plot of Microhabitat Characteristics (ground cover measured at each trapping station and averaged per plot) by Treatment with Vectors (black lines) Fit to Explain Separation. We collected microhabitat data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Based on a two-way permutation multivariate analysis of variance (PerMANOVA), microhabitat characteristics varied by treatment ($F_{2,27}$=57.66, $R^2$=0.67, p<0.01) and year ($F_{2,27}$=11.15, $R^2$=0.13, p<0.01). Stress=0.13.

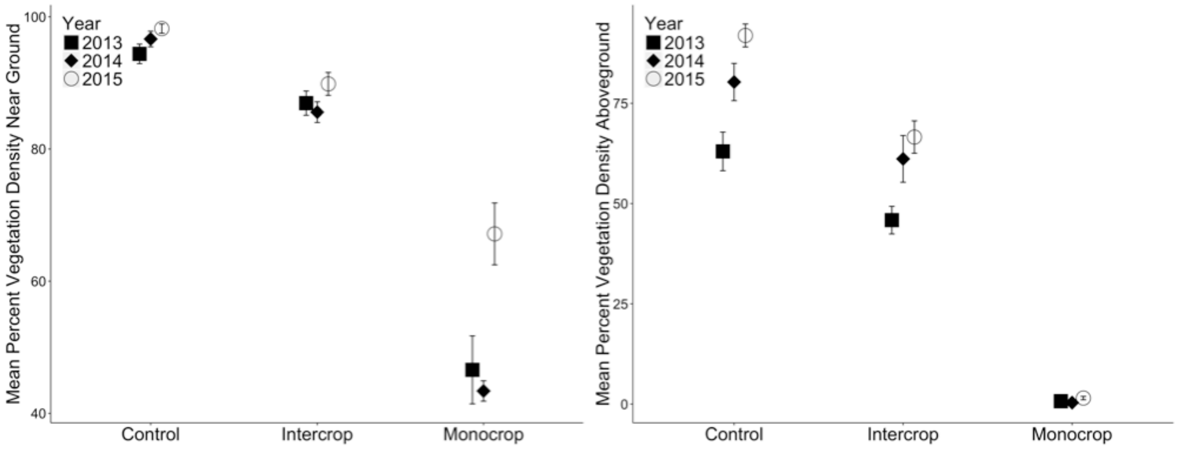

Figure 2.3. Mean (± SE) Percent Vertical Vegetation Density from Both Near Ground (A) and Aboveground (B) Sections of a Cover Board Measured at Each Trapping Station and Averaged per Plot. We collected vertical vegetation estimates in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Overall density was greater for the near ground (A) section when compared to the aboveground (B) section. In both sections, control plots had the greatest, intercrop had intermediate, and monocrop had the lowest density. In the near ground (A) section, density was lower in 2013 and remained lower in 2014 in both intercrop and monocrop plots compared to 2015. In the aboveground (B) section control plots increased in vertical density throughout the years while intercrop and monocrop plots did not differ across years.

Table 2.1. Mean (± SE) Number of Minimum Known Alive (calculated to represent robust design model of population abundance) Averaged Across Trapping Sessions per Plot by Treatment. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Rodent species captured include SIHI: *Sigmodon hispidus;* ORPA: *Oryzomys palustris;* MUMU: *Mus musculus*; REFU: *Reithrodontomys fulvescens;* REHU: *Reithrodontomys humulis*; PELE: *Peromyscus leucopus*; MIPI: *Microtus pinetorum;* PEGO: *Peromyscus gossypinus*.

| | | **SIHI** | **ORPA** | **MUMU** | **REFU** | **REHU** | **PELE** | **MIPI** | **PEGO** |
|---|---|---|---|---|---|---|---|---|---|
| **2013** | **Control** | 17.48 ± 3.45 | 1.48 ± 0.55 | 0.10 ± 0.10 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.08 ± 0.06 | 0.02 ± 0.02 | 0.02 ± 0.02 |
| | **Intercrop** | 17.79 ± 3.21 | 0.25 ± 0.25 | 0.29 ± 0.17 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.88 ± 0.88 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| | **Monocrop** | 17.13 ± 6.91 | 0.33 ± 0.18 | 1.33 ± 0.98 | 0.00 ± 0.00 | 0.08 ± 0.05 | 0.21 ± 0.21 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| **2014** | **Control** | 4.19 ± 2.42 | 0.56 ± 0.15 | 0.00 ± 0.00 | 0.06 ± 0.04 | 0.04 ± 0.04 | 0.02 ± 0.02 | 0.04 ± 0.02 | 0.00 ± 0.00 |
| | **Intercrop** | 5.46 ± 1.76 | 0.13 ± 0.08 | 0.00 ± 0.00 | 0.17 ± 0.07 | 0.04 ± 0.04 | 0.08 ± 0.08 | 0.04 ± 0.04 | 0.00 ± 0.00 |
| | **Monocrop** | 8.88 ± 2.99 | 0.17 ± 0.10 | 0.08 ± 0.05 | 0.00 ± 0.00 | 0.21 ± 0.10 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |
| **2015** | **Control** | 6.46 ± 1.73 | 0.46 ± 0.18 | 0.00 ± 0.00 | 0.46 ± 0.20 | 0.02 ± 0.02 | 0.00 ± 0.00 | 0.06 ± 0.04 | 0.08 ± 0.08 |
| | **Intercrop** | 5.29 ± 2.13 | 0.21 ± 0.13 | 0.00 ± 0.00 | 0.25 ± 0.08 | 0.13 ± 0.08 | 0.17 ± 0.17 | 0.25 ± 0.25 | 0.08 ± 0.05 |
| | **Monocrop** | 11.04 ± 2.10 | 0.38 ± 0.24 | 0.00 ± 0.00 | 0.08 ± 0.08 | 0.42 ± 0.20 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 |

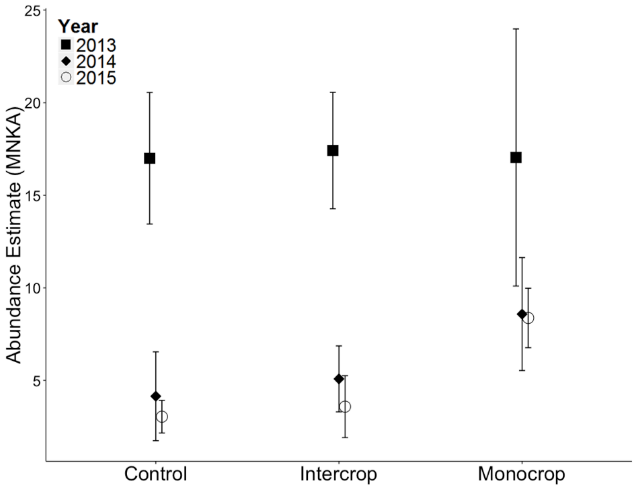

Figure 2.4. Adult *Sigmodon hispidus* Mean Population Abundance Estimates (± SE) Based on Minimum Known Alive (MNKA) Averaged Across Replicates and Plotted by Treatment per Year. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop

[monocrop]. Both treatment ($F_{2,6}$=6.77, p=0.03) and year ($F_{2,18}$=32.51, p<0.01; 2013 significantly greater than 2014 and 2015) effects were significant. Letters denote significant treatment pairwise comparisons.

Table 2.2. Adult, Female *Sigmodon hispidus* Depredation Data Based on Fate of Radiomarked Individuals. We collected radiotelemetry data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Numbers to the left of brackets are the number of individuals that were eaten out of all radiomarked adult, females within each year and treatment (the number in brackets). We did not detect any other natural sources of mortality during our study.

| | **2013** | **2014** | **2015** |
|---|---|---|---|
| **Control** | 0 [6] | 3 [10] | 0 [10] |
| **Intercrop** | 0 [6] | 1 [11] | 2 [11] |
| **Monocrop** | 0 [6] | 2 [12] | 1 [10] |

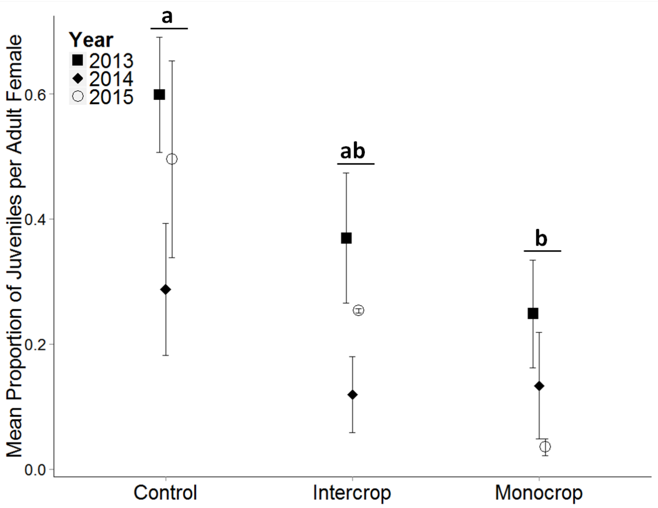

Figure 2.5. Mean Recruitment Estimates (± SE) of *Sigmodon hispidus* (juveniles per reproductive female captured) Plotted by Treatment per Year. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Both treatment ($F_{2,6}$=6.42, p=0.03) and year ($F_{2,18}$=6.06, p=0.01; 2013 significantly greater than 2014) were significant. Letters denote significant treatment pairwise comparisons.

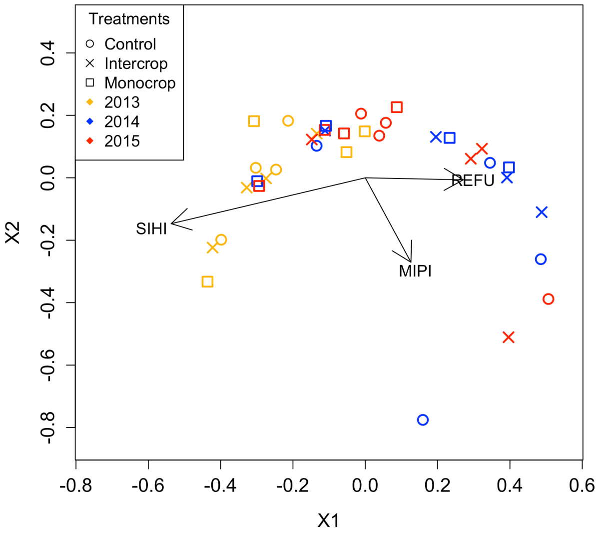

Figure 2.6. Non-metric Dimensional Scaling (NMDS) Plot of Rodent Assemblages by Treatment with Vectors (black lines) Fit to Explain Separation. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Based on a permutation multivariate analysis of variance (PerMANOVA), rodent assemblages did not vary by treatment ($F_{2,27}$=1.47, $R^2$=0.06, p=0.12), but they did vary by year ($F_{2,27}$=5.80, $R^2$=0.26, p<0.01); 2013 was different from 2014 and 2015. Stress=0.10. Vector codes are SIHI: *Sigmodon hispidus;* REFU: *Reithrodontomys fulvescens;* and MIPI: *Microtus pinetorum*.

Table 2.3. Mean Diversity Indices (±SE) Averaged Across Replicates and Years. We collected trapping data in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Treatments were control loblolly pine [control], switchgrass intercropped in loblolly pine [intercrop], and switchgrass monocrop [monocrop]. Richness and evenness indices did not significantly differ among treatments. Shannon and Simpson’s indices of diversity were significantly greater in control than monocrop plots (different letters indicate significant differences among treatments).

| | **Shannon** | **Simpson's** | **Richness** | **Evenness** |
|---|---|---|---|---|
| **Control** | 0.54 ± 0.09 **a** | 0.28 ± 0.05 **a** | 3.58 ± 0.29 | 0.42 ± 0.07 |
| **Intercrop** | 0.44 ± 0.12 **ab** | 0.21 ± 0.06 **ab** | 3.00 ± 0.39 | 0.35 ± 0.07 |
| **Monocrop** | 0.34 ± 0.08 **b** | 0.17 ± 0.04 **b** | 2.75 ± 0.28 | 0.29 ± 0.06 |
| | $F_{2,6}$=7.28, **p=0.02** | $F_{2,6}$=7.92, **p=0.02** | $F_{2,6}$=2.94, p=0.13 | $F_{2,6}$=3.57, p=0.10 |

## Discussion

Our results suggest that intercropping switchgrass in pine plantations can both produce biofuel feedstocks and maintain similar rodent population metrics and community structure to traditional pine plantations. Thus, switchgrass could be considered a feasible alternative fuel that can be planted on land not used for food crops while maintaining a diverse rodent community, which provides environmental benefits such as a food source for predators and effective seed and spore dispersal. Although we hypothesized that intercropping would change the understory and therefore would affect rodent populations and communities, we found intercrop plots were consistently intermediate and not significantly different from control and monocrop plots. Further, our predictions regarding cotton rat populations were not supported consistently as abundance was greater in monocrop than control plots, but the opposite result was found for recruitment. Lastly, our predictions of community responses were partially supported as diversity was found to be least in monocrop plots, but richness and evenness did not differ among treatments.

Treatments varied in vegetation heterogeneity, and vegetation composition changed over time. Monocrop plots were the most homogeneous as switchgrass and other grasses were dominant cover types. Woody debris remained from site preparation in intercrop and control plots and decomposed during our study, whereas it was removed from all monocrop plots during site preparation in 2013. Leaving woody debris provides additional structure for wildlife (Loeb, 1999), which is an additional benefit of the intercropping system compared to monocrops when producing a biofuel feedstock. Other debris was greater in percent cover by 2015 because vegetation from previous years died and pine trees continuously lost needles. Vertical vegetation density was least in monocrop plots and increased throughout the years as switchgrass established. However, it is important to note that vertical vegetation density also increased throughout each summer, especially in intercrop and monocrop plots as switchgrass and other vegetation grew.

Switchgrass is not only a biofuel feedstock, but is a cover and potential food resource for cotton rats so, in areas where it was planted, it was expected that cotton rat population abundance and recruitment would be high (Kincaid and Cameron, 1982a; Rehmeier et al., 2005). Interestingly, planting switchgrass in a monocrop setting resulted in high cotton rat abundance, but low recruitment in comparison to control pine plots. One explanation is cotton rat dispersal could have occurred at younger ages than normal in monocrop plots because of high population abundance and limited habitat availability. Cotton rats have been shown to readily disperse and are able to easily move through landscapes (Bowne et al., 1999). If juvenile cotton rats dispersed as soon as they were capable, abundance of juveniles, and therefore recruitment, would decrease. Detection in our study may also have been particularly low given we had relatively low captures and recapture rates, particularly in 2014 and 2015. Because young cotton rats are less likely to enter traps that have been used by older, more dominant cotton rats, it is possible our results are simply due to known trap bias (Summerlin and Wolfe, 1973).

Alternatively, monocrop plots could be sinks, and control plots along with older surrounding pine stands could be sources. Cotton rats are grassland specialists and may perceive monocrop plots as quality habitat (Cameron and Spencer, 1981). However, the homogeneous habitat structure may reduce survival of adults, offspring, or both. In fact, one study found that female cotton rats preferred a mixture of monocot and dicot vegetation (Cameron and Spencer, 1985) as was present in our control pine and intercrop plots. However, we cannot make that conclusion based on our data. Even with detailed population data, it is difficult to account for temporal variation that could change areas previously described as sinks to sources (Kreuzer and Huntly, 2003). Additionally, well documented social dominance of cotton rats affects population abundance and recruitment, particularly in preferred habitat conditions (Cameron and Spencer, 1985; Doonan and Slade, 1995; Fleharty and Mares, 1973). Dominant cotton rat individuals may be less tolerant of home range overlap with other individuals and have more offspring, leading to low adult abundance yet high recruitment on a plot level.

Our estimates of cotton rat survival for females may be an overrepresentation of true survival given that rodents are common prey species for many predators. In Barrett et al. (2001), 5 of 72 cotton rats (4 male and 1 female) were preyed upon in one summer (Barrett et al., 2001). Comparing these results to our own, and considering we only radiomarked females, it is possible that we detected low levels compared to actual levels of predation. To reduce predation risk, cotton rats use habitat structure with dense, tall understory vegetation and low overstory canopy cover (Bowne et al., 1999; Fleharty and Mares, 1973). Although vegetation was relatively dense in all of our treatments, homogeneity of vegetation type in monocrop plots may have provided fewer refugia to rodents seeking protection from predators. Further, vegetation density would be most relevant to decreasing success of predators that use visual cues. Some predators of rodents, however, do not strictly rely on visual cues. Snakes, including black rat snakes (*Pantherophis obsoletus*) and timber rattlesnakes (*Crotalus horridus*), which were both common on our plots, mainly use vibrations as cues (Friedel et al., 2008; Young, 2003) and use vegetation cover themselves to ambush prey while being protected from their own predators (Kotler et al., 1992). In cases where predators are using different cues, dense vegetation may be detrimental as it would give prey less time to visually detect a predator (Schooley et al., 1996). Future research should evaluate differences in survival and dispersal in cotton rats among age classes and compare to the potential predator community.

Rodent community diversity was affected by planting switchgrass, particularly in monocrop plots. Switchgrass monocrops have been shown to have greater diversity of herpetofauna species when compared to pine and intercrop plots (Homyack et al., 2013). However, this greater diversity was likely due to a decrease in abundance of a common species, the southern toad (*Anaxyrus terrestris*) (Homyack et al., 2013). In our study, monocrop plots contained high abundances of the dominant species (the cotton rat), leading to low diversity (Brady and Slade, 2001; Tuomisto, 2012). The cotton rat is an ecologically dominant species, particularly at high densities. Therefore, high cotton rat abundances lead to reduced abundances of smaller species, such as western harvest mice (*R. megalotis*) and deer mice (*P. maniculatus*) (Brady and Slade, 2001). Similarly in our study, it was not until cotton rat abundances decreased in 2014 and 2015 that we captured greater abundances of smaller species such as fulvous harvest mice and woodland voles.

The marsh rice rat was the second most commonly captured species in our study and had a particularly high abundance in control plots in 2013, but their abundance declined from 2013 to 2014. Marsh rice rats and cotton rats do not highly overlap in diet (16.7% overlap), which may explain why both populations could have had relatively high abundances in 2013 (Kincaid and Cameron, 1982b). However, marsh rice rats and fulvous harvest mice have an average of 97.8% overlap in diet (Kincaid and Cameron, 1982b). Therefore, as fulvous harvest mice abundance increased, marsh rice rats may have experienced increasing competition for food resources. Heterogeneous habitat conditions provide a variety of resources and therefore are capable of supporting more species (MacArthur and MacArthur, 1961). Throughout the years our control and intercrop plots became more heterogeneous and were therefore able to support more of the rare species. The increase in rare species may have caused a decrease in common species abundances.

Previous studies of switchgrass intercropping suggested a possible association between switchgrass and non-native, invasive house mice (Homyack et al., 2014; Marshall et al., 2012). Although our study detected house mice in initial years in plots where switchgrass was planted, by year three, we no longer detected house mice in any plots. House mice are associated with humans and disturbance and by year three there was limited disturbance in our plots. There were also native species in the area that may have competed for resources. However, one study that investigated interspecific competition with house mice and old field mice (*P. polionotus*) found that house mice were more aggressive (King, 1957). Furthermore, house mice are seminomadic and may have simply immigrated to an area of newly disturbed land given the landscape is a matrix of actively managed pine plantations (Caldwelll and Gentry, 1965). Therefore, house mice are more likely associated with initial disturbance of planting switchgrass and with agricultural fields that surrounded plots in a previous study than with switchgrass directly (Homyack et al., 2014; Marshall et al., 2012).

### *Conclusions*

In conclusion, planting switchgrass as a monocrop within a managed pine plantation landscape reduced rodent diversity. However, it is unlikely that this management regime would be implemented in managed pine plantation landscapes and results may differ in agricultural or other forested landscape settings. Intercropping systems, however, are well suited for managed pine plantation landscapes and, as our study shows, appear capable of providing heterogeneous habitat conditions to support a diverse community of rodents. Therefore, intercrop plots would be recommended as a management practice in pine plantations to increase biofuel feedstock production while maintaining rodent diversity.

## Acknowledgments

We thank Weyerhaeuser Company, Catchlight Energy LLC, National Council for Air and Stream Improvement, Inc., U.S. Environmental Protection Agency (EPA), American Society of Mammalogists, North Carolina Academy of Science, and University of North Carolina at Greensboro for funding. This publication was developed under STAR Fellowship Assistance Agreement no. FP-91763501-0 awarded by the U.S. EPA. It has not been formally reviewed by EPA. The views expressed in this publication are

solely those of the authors, and EPA does not endorse any products or commercial services mentioned in this publication. Weyerhaeuser Company employees operated under a Statement of Work with CLE during this study. We thank R. Kelble, K. Paolini, E. VanNatta, A. Andrews, D. Bradley, J. Franklin, M. Martin, R. Meyer, K. King, A. Matteson, K. Corson, E. Smerdon, A. Wagoner, A. Culpepper, and G. Mikel for their hard work in the field as technicians. We thank Mississippi State University, Steve Emerson, and the employees of the Scooba Weyerhaeuser office for their help at the field site. Lastly, we thank the East Mississippi Sportsman Association and Charlie Studdard with the Kemper County Hunting Club for providing lodging during the field season.

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# CHAPTER III

# HOW DO ALTERED UNDERSTORY CHARACTERISTICS AFFECT SPATIAL AND FORAGING BEHAVIORS AND PATTERNS OF REPRODUCTION?

This chapter is coauthored by Angela L. Larsen, Jessica A. Homyack, T. Bently Wigley, Darren A. Miller, and Matina C. Kalcounis-Rueppell.

## Abstract

Understanding how changes to habitat characteristics affect behaviors is important when integrating biodiversity goals with land management. Managed forests are a significant landscape component in the southern United States providing opportunities for conservation alongside wood products. We investigated behavioral responses of rodents to differences in understory habitat characteristics from intercropping of switchgrass (*Panicum virgatum*), a native biofuel feedstock, in intensively managed loblolly pine (*Pinus taeda*) stands. Previous research indicated that planting switchgrass increased rodent population abundance but reduced recruitment and community diversity. To understand potential mechanisms underlying our previous results, we measured behaviors of individual cotton rats (*Sigmodon hispidus*), a grassland specialist, to planted switchgrass. We hypothesized that female territory size, foraging activity, overlap with other adult females, and reproduction indices would differ among treatments (switchgrass monocrop, intercropped switchgrass, and control plots) due to variation in grass and vertical vegetation cover. We conducted live-trapping, radio telemetry, and foraging activity surveys on cotton rats during summers of 2013-2015. We found no treatment effect on territory size, but foraging activity was 2 times higher in monocrop than control plots. We also found a positive relationship between female territory overlap and percentage of grass in control plots and evidence for higher reproductive indices in control than monocrop plots. Our results suggest that cotton rats in monocrop plots exhibited unexpected behaviors, causing monocrop plots to serve as population sinks with low rodent diversity. Overall, results from this replicated experiment suggested that intercropping provides adequate food and cover to maintain rodent communities and produce forest products.

**Keywords:** Biodiversity; Conservation Behavior; Forest Management; Intercropping; *Panicum virgatum*; *Sigmodon hispidus*

## Introduction

Conservation behavior, a relatively new interdisciplinary field, includes three domains that influence fitness and therefore can inform management decisions to conserve biodiversity: 1) movement and space use, 2) foraging and vigilance, and 3) social behavior and reproductive output (Berger-Tal et al., 2011). Individuals base behavioral decisions on several factors related to habitat, such as food availability and predator avoidance (Wasko and Sasa, 2012) and respond to changes in habitat by altering behaviors to increase fitness. However, anthropogenic habitat alterations may create ecological traps where individuals make faulty behavioral decisions due to altered resource availability and environmental cues (Schlaepfer et al., 2002). Faulty decisions are a result of individuals not recognizing a change in resources because they are responding to an unchanged cue (Schlaepfer et al., 2002). Thus, studying population abundance alone can produce misleading results and lead to poor management decisions (Van Horne, 1983), especially if there is a time lag between behavioral decisions and population level changes. Behaviors provide a direct and immediate assessment as to whether or not individuals are responding to their environment to maximize fitness and can indicate future population dynamics.

Individual decisions about movement and space use differ with vegetation structure. As juveniles, individuals may disperse and then make decisions that determine location and size of their home ranges or territories (Grant, 1993; Mabry et al., 2008; Mabry and Stamps, 2008). For example, individual brush mice (*Peromyscus boylii*) prefer to disperse to areas that are similar to their natal habitat (Mabry et al., 2008; Mabry and Stamps, 2008). Another study of female striped mice (*Rhabdomys pumilio*) documented that a combination of season (breeding versus nonbreeding), percent cover, percent food plants, number of neighbors, and relative body mass influenced home range size (Schradin et al., 2010). Other factors, such as predation risk, interspecific competition, and individual variation in explorative behavior, also influenced home range size of striped mice (Bell, 2007; Schradin et al., 2010). Assuming resources are abundant and all other factors are equal, an individual should require a relatively small area to obtain all required resources. At high densities, there is also a higher probability that individuals will have a smaller territory, as there will be more conspecifics defending their territories. However, there could also be a density threshold where defending a territory no longer outweighs costs, and that point may vary among individuals (Grant, 1993). Individual rodents who have smaller territories, and likely move less to obtain necessary resources, would be predicted to have higher survival compared to individuals with larger territories due to less exposure to predators (Lima and Dill, 1990).

Individuals evaluate costs and benefits to determine when and where to forage. Altered habitat can affect how individuals perceive predation risk when foraging. An individual may cease foraging when perceived costs (e.g. predation risk) become greater than perceived benefits (e.g. energy intake) (Brown, 1988). Predation risk is influenced by the amount and structure of vegetative cover individuals can access to avoid predators, although ambush predators, such as snakes, have an opportunity to hide in dense cover (Abu Baker and Brown, 2010). Perceived benefits also depend on the quality of the individual's environment, including resources in areas of competition (Abu Baker and Brown, 2010). For example, in areas of low food availability and high competition, an individual will perceive a food patch as having higher benefits than if that same food patch was in an area with high food availability and low competition, given there are likely several food patches available (Abu Baker and Brown, 2010).

Lastly, social behavior and reproductive output can be behavioral indicators of individual responses to altered habitat. Female territoriality in small mammals is hypothesized to be driven by protecting resources (Ostfeld, 1985) or protecting offspring from infanticide (Wolff, 1993). Ostfeld (1985), based on the resource-defense hypothesis, predicted that female territoriality would exist in areas where food is limited, patchy, and slowly renewable and there is low to moderate population density. Further, territoriality increases during the breeding season because energetic demand of females is higher in an area with limited resources, but the cost of defense is lower in areas where there are few conspecifics (Ostfeld, 1985). Infanticide, which can occur in small mammal species (Wolff, 1993), has been found to increase with increasing density of conspecifics (Korpela et al., 2010) and vary with heterogeneous resources (Rémy et al. 2013). Thus, reproductive output depends on survival, availability of resources (especially food and nesting sites), and ability to locate a mate, all of which vary in heterogeneous environments (Wellington and Victor, 1988).

As habitat loss for some species continues with spreading human development, managed lands will be increasingly important to consider when planning for biodiversity conservation (Chapin et al., 1998; O'Bryan et al., 2016). In the southern US, 19% of forests are intensively managed for high productivity of wood products, but while also contributing to conservation of biodiversity (Wear et al., 2012). Yet effectiveness of some management techniques for biodiversity conservation in intensively managed forests are not fully understood (Greene et al., 2016). The drive for renewable fuels (Cheng and Timilsina, 2011) has caused some landowners to consider using intercropping, where two crops are planted in alternating rows (Garrett and Buck 1997). In one form of intercropping, switchgrass (*Panicum virgatum*) is planted between loblolly pine (*Pinus taeda*) rows. This method allows managers to plant a biofuel feedstock crop, switchgrass, in planted pine stands where it is not competing with food crops and can provide an additional income source (Milder et al. 2008). Intercropping may provide suitable habitat conditions for some wildlife species by the combination of pine trees with a large amount of grassy cover between pine rows (Riffell et al., 2012).

Previous research indicates that switchgrass increases grass cover, reduces vertical vegetation cover, increases rodent population abundance, and reduces rodent population recruitment and community diversity compared to control pine plots (Larsen et al., 2016). Behaviors of individuals responding to planted switchgrass may elucidate the mechanism underlying these results. For our current study, we investigated understory microhabitat structure of switchgrass intercropped in pine plantations and associated changes in hispid cotton rat (*Sigmodon hispidus*; hereafter, cotton rat) behavior. The cotton rat, a common, wide-ranging, grassland specialist species, was a useful model species in this system because cotton rats are associated with grassy understory. Furthermore, rodents provide trophic linkages in an ecosystem and are indicators of biodiversity (Dickman, 1999).

We hypothesized that differences in grass and vertical vegetation cover due to planting switchgrass would affect cotton rat behavior (Figure 3.1). Our aims were to assess effects of grass and vertical vegetation cover among three treatments (switchgrass monocrop, intercropped switchgrass, and control plots) on cotton rat behaviors. To address these, we studied movement and space use, foraging activity, and social behavior and reproductive output. Specifically, we measured territory size, giving-up densities, overlap with other adult and subadult females captured within each female's territory, and estimated two reproductive indices: number of juveniles weaned per female and number of litters per female. We predicted that territory size would be smaller, whereas overlap and reproduction indices would be higher, in plots where managers planted switchgrass (monocrop and intercrop), because of increased food availability. We predicted that foraging activity would be lower in monocrop and intercrop plots compared to control plots because of increased predation risk in areas of decreased vertical vegetation cover where switchgrass was present. Even if cotton rats were moving less in monocrop plots due to smaller territories, reduced vertical cover should decrease the amount of time a cotton rat would spend foraging in a patch.

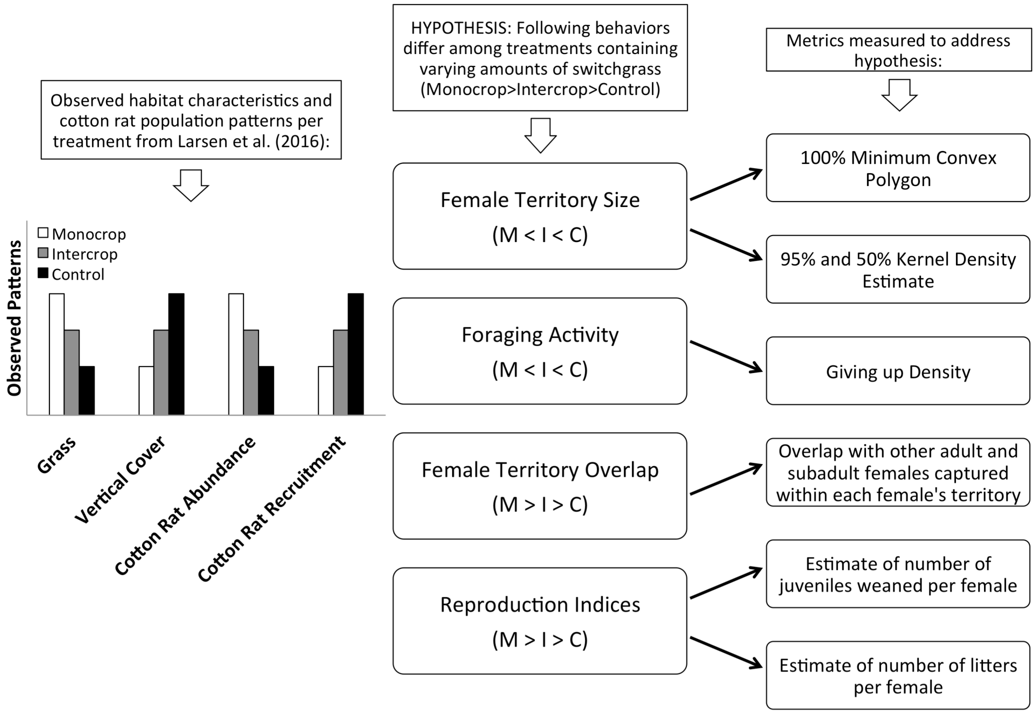

Figure 3.1. Descriptive Figure of Habitat and Cotton Rat Population Patterns Observed in Larsen et al. (2016) with the Current Study's Hypothesis and Measurements. Predictions of treatment pattern for each cotton rat behavior are listed in parentheses (M = Monocrop, I = Intercrop, C = Control). We based predictions on the amount of switchgrass in each treatment and whether switchgrass is providing adequate food and cover resources per behavior. We measured behavior to understand cotton rat responses.

## Methods

### *Study area*

Our study was conducted in Kemper County, Mississippi, USA, on land owned and managed by Weyerhaeuser Company on experimental plots established and maintained by Weyerhaeuser Company and Catchlight Energy LLC (CLE), a Chevron|Weyerhaeuser joint venture. We used 4 forest stands as replicates, and within each replicate, there were 4, 10-ha treatment plots (2 control loblolly pine plots, 1 switchgrass intercropped in loblolly pine plot, and 1 switchgrass monocrop plot; Figure 3.2). In 2010, managers planted one-year-old loblolly pine seedlings in pine beds. Between pine beds were rows where either switchgrass (intercrop plots) or naturally occurring woody and herbaceous vegetation grew (control plots). Switchgrass in monocrop and intercrop plots was mowed but not baled in spring 2013 and mowed and baled in fall 2014 and 2015. Therefore, switchgrass was short in late spring and grew throughout the summer months. Switchgrass grew dense in areas, but growth was not consistent. For details of study area, site preparation, and treatment maintenance see (Larsen et al., 2016; Loman et al., 2014)

### *Trapping*

We live-trapped rodents using a 7x7 trapping grid (20 m spacing, 49 trap stations, Figure 3.2) at the center of each plot. We trapped all treatment plots in a replicate simultaneously for 3 consecutive nights per trapping session and conducted 6 trapping sessions each summer 2013-2015. We identified all captured rodents to species, marked them with a uniquely numbered ear tag (Model 1005–1, National Band and Tag

Company, Newport, Kentucky, USA) and weighed them (g). We also determined sex, age-class (juvenile, subadult, adult), and reproductive status (scrotal, non-scrotal, non-perforate, perforate, pregnant, lactating, pregnant and lactating, post-lactating), after which we immediately released each individual. Additional trapping details can be found in (Larsen et al., 2016). We followed regulations of annual scientific collection permits from the Mississippi Department of Wildlife, Fisheries, and Parks and UNCG IACUC 14-001.0 and the American Society of Mammalogists guidelines (Sikes and Gannon, 2011).

### *Space use*

To determine territory area, we radio-collared (M1450 or M1520 Advanced Telemetry Systems [ATS], Isanti, MN, U.S.A) 18, 30, and 30 different resident female cotton rats in 2013, 2014, and 2015, respectively. Some studies have presented evidence that female cotton rats may be territorial (Doonan and Slade, 1995; Howell, 1954), while other studies suggest cotton rats utilize home ranges (Fleharty and Mares, 1973; Slade and Swihart, 1983). We considered our space use measurement to be of territories. We studied female cotton rats during peak breeding season, which is when female rodents tend to defend an area (Fortier and Tamarin, 1998). We defined resident female cotton rats as reproductive (perforate, pregnant, lactating, pregnant and lactating, or post-lactating) adults weighing >95 grams. We radio-collared 6 individuals/treatment in 2013 and 10 individuals/treatment in 2014 and 2015. To ensure they returned to normal behavior before measuring biangulation fixes, we located all radio-collared individuals via homing using a R4000 or R4500S receiver with a 3 element folding yagi antennae

(ATS) 24 hours after they were radio-collared. We also homed on individuals at least once per week during daylight. Lastly, for each radio-collared individual, we obtained 6 biangulation fixes between 18:00 and 09:00 for 4 to 6 nights. To reduce autocorrelation of fixes, we obtained fixes for each individual at intervals of at least one hour apart. We located individuals until either their radiotransmitter was removed or their fate was determined. We radio-tracked individuals for 7-52 days (mean=23.18 days).

We calculated biangulation errors for each observer by taking bearings of radiotransmitters at known locations in a plot of each treatment type. We trained all observers until biangulation errors were ≤5°. Furthermore, we used trapping locations and location points from daytime homing to ground truth biangulation fix locations and to increase locations when needed to calculate territories. We removed any biangulation fix locations that were unrealistic before calculating territories. We considered locations from biangulation fixes to be unrealistic when they were ≥60 meters from the nearest neighboring location. We chose to use 60 m as our threshold because of the observed clustering of most points in each female's territory. Furthermore, we found that most recaptured adult female cotton rats were captured in traps <60 m from each other. Our unrealistic locations were likely due to human error during biangulation fixes and explorative bouts by cotton rats. Finally, for all individuals with more than 25 locations, we randomly selected a subset of locations to balance number of locations per individual (set to 25). However, we had some individuals with fewer than 25 locations (12-24 locations) because of logistical reasons. Territory areas tend to be under-, but not over-estimated with fewer locations, particularly when using minimum convex polygon

(MCP) (Blundell et al., 2001; Girard et al., 2002; Swihart and Slade, 1985). Therefore, we kept all individuals in our analyses to maintain our sample size.

We calculated 100% MCP territory areas, 95% kernel density estimates (KDE), and 50% KDE core estimates using Home Range Tools (HRT) for ArcGIS (Rodgers et al., 2015) and ArcMap 10.2.2 (*ArcGIS*, 2014). We calculated both MCP and KDE to ensure both resulted in the same pattern and for comparison to previous studies (Farmer and Ault, 2014; Morris et al., 2011). To calculate 95% and 50% KDEs, we rescaled our locations in HRT because our data set had high variance. We had completed rescaling before we calculated the smoothing parameter. We used both fixed and adaptive kernel methods to see if either caused oversmoothing. Both kernel methods provided similar results, but we used the adaptive method because it fit our data better based on the territory boundaries and density of locations. We also calculated each individual's reference bandwidth ($h_{ref}$) in HRT, and used each $h_{ref}$ to calculate each territory.

### *Foraging*

We measured foraging behavior with giving-up density (GUD), which is a behavioral assay that quantifies remaining amount of food in a patch for comparison across treatments (Brown, 1988; Jacob and Brown, 2000; Jones and Dayan, 2000; Morris and Davidson, 2000; Orrock et al., 2004). We hypothesized that increased cover decreased predation risk (Lima and Dill, 1990) and food availability and intra- and inter-specific competition affected perceived foraging benefits (Mitchell et al., 1990).

We collected GUD data in each treatment in August 2015 using foraging trays. We used 13x9x2 inch aluminum foil, oblong cake pans with clear plastic lids as GUD foraging trays and cut two squares approximately 2x2 inches cut into two adjacent sides. We only used 1 control per replicate, which was the control plot with the higher rodent captures in 2015 (12 treatment plots in 4 replicates; Figure 3.2). We randomly selected 10 of the 49 trapping stations per treatment plot and placed 2 foraging trays at each selected trapping station, one in the pine bed and one in the row in control and intercrop plots. We also placed 2 foraging trays at each selected station in monocrop plots. At each trap station, we placed the 2 trays 1-2 m apart in all treatments. We placed foraging trays with 1 liter of sand, but no seed, at their selected stations at least 3 nights before data collection to allow animals to acclimate to foraging trays and substrate. On day 4, we added 5 g of crimped oats to each. We applied approximately 0.5 ounces of Talstar PL granular insecticide (0.2% bifenthrin, FMC Corporation, Philadelphia, Pennsylvania) around each foraging tray and within 0.25 m of the edge of each tray to prevent fire ants (*Solenopsis invicta*) from infesting the trays. We checked each tray every 24 hours for 3 days. If we observed any animal sign (tracks, feces, and seed hulls) in the sand, we sieved and collected remaining seeds and hulls. We only detected signs of rodents entering our trays. We replenished each tray that had animal sign during our 24-hour checks with a new 5 g of seed to reset the tray for the next 24-hour period. We did not dry seeds in a drying oven to ensure consistency in moisture obtained from humidity during initial and final weighing.

We calculated GUD as proportion of seeds (in weight) remaining from a 24-hour period. We transformed GUD into foraging activity by first subtracting the GUD mass from the starting mass (5 g). We averaged GUD across nights and plots but separately for trays in pine beds and those in rows. In an exploratory analysis, we found foraging activity significantly increased with increasing total rodent minimum number known alive (MNKA) per plot (foraging activity~0.20*Total (MNKA) + 0.19; $F_{1,22}=28.38$, $p<0.01$, $R^2_{adj}=0.54$). Therefore, we divided each average GUD by the estimate of total rodents per plot because we did not know which species entered trays. To account for rodent abundance per plot, our estimate of total rodents per plot was average MNKA of captured rodents over the summer trapping sessions in 2015 from the same plot in which we placed the tray. We used the adjustment to standardize foraging activity by rodent abundance.

Figure 3.2. Modified Study Area Map from Larsen et al. (2016) of Kemper County, Mississippi, USA. Map depicts which trapping plots we used to collect giving-up density (GUD) data. The inset map is one of our treatment plots showing the trapping grid of 49 trapping stations (circles). The 10 trapping stations with squares around them are the 10 randomly picked trapping stations used to collect GUD data on that plot. At each of the 10 GUD stations there were 2 foraging trays; 1 placed in the pine bed (a) and 1 placed in the row (b).

### *Social behavior and reproductive output*

We measured of social behavior with female overlap. We overlaid MCP territories (see methods above) on trapping station grids. We projected both MCP territories and trapping station grids in ArcMap 10.2.2 (*ArcGIS*, 2014), and used the Spatial Join tool to determine which trap stations each territory contained. To measure female overlap, we used the MNKA of all adult and subadult female cotton rats within a collared female's territory and divided that by number of trap stations within the territory. We used the same summer's trapping data as the telemetry data to calculate MNKA. We analyzed both adult only and the combination of adult and subadult female cotton rats.

We estimated number of juveniles weaned per female and number of litters per female as measures of reproductive output. We used trapping data to identify clusters of juveniles that likely were from the same litter. Our trapping data contained age class (juvenile, subadult, or adult) information and we trapped at a high spatial and temporal intensity, so we were not likely to miss major juvenile foraging bouts. From our trapping data, we determined maximum juvenile movement using recaptures. We also determined, from our trapping data, the range of days juveniles remained on the same treatment plot and the range of days we classified them as juveniles when recaptured. We then clustered individual juveniles into a litter using our determined thresholds of maximum movement distance of 44.7 m and 1-19 days between recapture. We mapped all litters and used the Minimum Boundary Geometry tool in ArcMap to assess if we appropriately assigned juveniles to litters based on determined maxima. We based our indices on number of juveniles per cluster (number juveniles weaned) and number of clusters (number of litters). Lastly, as with our calculations of overlap, we divided our reproductive indices by mean MNKA over the respective summer of adult female cotton rats to account for number of potential reproductive cotton rats on each plot. Our final measure of reproductive output was juvenile recruitment. We calculated proportion of juveniles per treatment plot as number of juveniles trapped per plot divided by total number of juveniles trapped in our entire study area per year.

### *Statistical analyses*

We used two-way analyses of variance (ANOVAs) to test for effects of treatment, year, and the interaction of treatment and year on 100% MCP territory area, 95% KDE area, and 50% KDE core area. Although our plots were set up in a randomized block design, we did not use a blocking factor in our ANOVA models. We opportunistically radio-collared individuals, so we were unable to balance individuals among stands. For this analysis, therefore, we assume no variability among our blocks because each block had similar habitat conditions and was within close proximity to other replicates. However, each year, unique radio-collared individuals were balanced among treatments.

Also, we assessed whether space use was affected by grass and vertical vegetation cover changes at the territory scale. We conducted regression analyses to investigate relationships between each of our dependent variables (territory size, foraging activity, overlap with other adult and subadult females captured within each female's territory, number of juveniles weaned per female, and number of litters per female) and grass and vertical vegetation cover data. We obtained vegetation data from (Larsen et al., 2016). We developed a linear regression model with grass or vertical vegetation cover nested within treatment and without the intercept. For any significant relationship (slope ≠ 0), we subset data by treatment and developed a linear regression model for that relationship alone to obtain the final model values. We used diagnostic plots to ensure our models met assumptions of normality, constant variance, linearity, and independence.

We used a one-way randomized block design ANOVA to evaluate whether foraging activity differed among treatments. We used stand as a random factor. We analyzed foraging activity from intercrop and control plots separately to test if, within plots, cotton rats were foraging differently in switchgrass rows than in pine beds. We used a paired t-test to assess mean foraging activity per plot in switchgrass rows versus pine beds for both intercrop and control plots. We also conducted regression analyses as described above to further investigate possible relationships between foraging activity and grass and vertical vegetation cover.

We conducted repeated measures, randomized block design ANOVAs to test effects of treatment, year, and the interaction of treatment and year on number of litters per adult female cotton rat, average litter size per plot, and juvenile proportions per plot. We also conducted regression analyses as described above to further investigate possible relationships between our social behavior and reproductive output dependent variables and grass and vertical vegetation cover.

We examined normality and homogeneity of variance to ensure all data met assumptions for ANOVAs (M. Logan, 2010). We used rank transformations of raw data if data did not meet assumptions as either raw or log-transformed. We investigated pairwise contrasts using a Tukey HSD if the omnibus test was statistically significant. We used Program R (R Core Team, 2014) for all analyses.

## Results

*Space use*

We used 25 locations for 82% of radio-collared individuals for our territory analysis. However, we did not have 25 locations for some individuals (10 in 2013; 2 in 2014; 2 in 2015) but we included them in analyses. We found 100% MCP and 95% KDE territory sizes (n=78) did not differ among treatments, but territories were about 2 times larger in 2013 than both 2014 and 2015 ($F_{2,69}=8.05$, $p<0.01$ and $F_{2,69}=12.74$, $p<0.01$; respectively, Figure 3.3). Similarly, we found 50% KDE core area sizes did not differ among treatments but were slightly more than 2 times larger in 2013 ($F_{2,69}=16.90$, $p<0.01$) than in 2014 and 2015. We also completed all space use analyses without individuals that had fewer than 25 locations (n=64). For each analysis, year was the only significant effect and consistently, 2013 was significantly greater than 2014 and 2015 (year effect: 100% MCP $F_{2,55}=4.41$, $p=0.02$; 95% KDE $F_{2,55}=4.22$, $p=0.02$; 50% KDE core $F_{2,55}=5.95$, $p<0.01$).

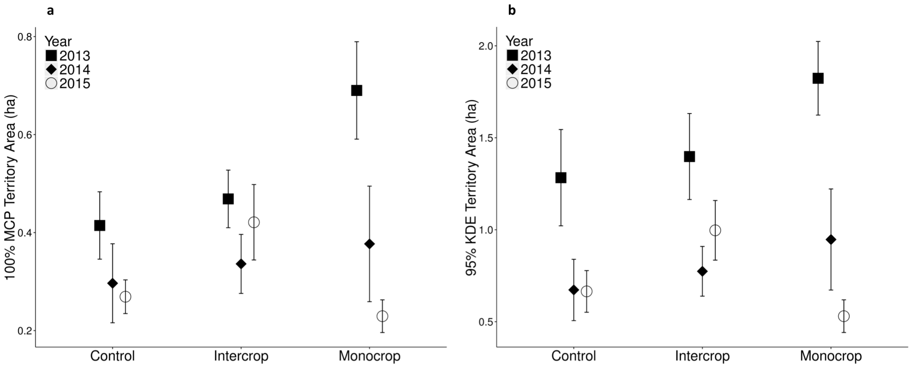

Figure 3.3. Mean (±SE) Female Cotton Rat Territory Areas Based on 100% Minimum Convex Polygon (MCP) [a] and 95% Kernel Density Estimate (KDE) [b] Plotted by Treatment per Year. We collected all locations necessary to calculate territory areas in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Both MCP and KDE territory areas were larger overall in 2013 but did not differ among treatments.

### *Foraging*

Foraging activity was nearly 2 times greater in monocrop than control plots ($F_{2,6}$=5.29, p<0.05; Figure 3.4). Foraging activity was intermediate in intercrop plots and did not significantly differ from foraging activity in either control or monocrop plots. Foraging activity did not differ between rows and pine beds in either intercrop (t=-2.05, df=3, p=0.13) or control plots (t=-0.98, df=3, p=0.40).

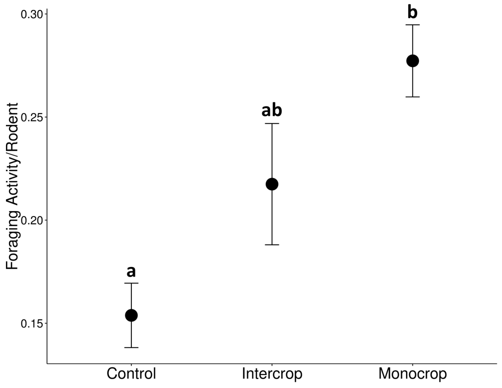

Figure 3.4. Mean (±SE) Foraging Activity per Minimum Known Alive Number (averaged across trapping sessions) of Rodents on Each Plot by Treatment. We measured foraging activity using giving up density trays in Kemper County, Mississippi, USA in summer of 2015. Foraging activity significantly differed among treatments. Letters denote significant treatment pairwise comparisons.

*Social behavior and reproductive output*

Territory size was not significantly correlated with female overlap ($r$=-0.05, df=75, p=0.67). We found significantly higher adult female overlap in 2013 than in 2014 and 2015, but adult female territory overlap did not significantly vary among treatments ($F_{2,66}$=3.85, p=0.03 and $F_{2,66}$=1.84, p=0.17, respectively; Figure 3.5a). When we combined subadult and adult females, territories in monocrop plots in 2014 had twice the overlap of intercrop and control plots ($F_{4,66}$=6.22, p<0.01; Figure 3.5b). Across all years, adult female overlap was positively related to percent grass in the reference female's territory in control (adult female overlap~0.02*Grass (%) + 0.15; $F_{1,21}$=9.17, p=0.01, $R^2_{adj}$=0.27; Figure 3.6a) but not intercrop or monocrop plots ($F_{1,24}$=1.75, p=0.20 and $F_{1,24}$=0.39, p=0.54; respectively). Similarly, when considering both adults and subadults across all years, only overlap in territories in control plots had a significantly positive relationship with grass cover (subadult and adult female overlap~0.04*Grass (%) - 0.24;

$F_{1,21}$=26.53, $p<0.01$, $R^2_{adj}$=0.54; Figure 3.6b). We did remove potential outlier points from both regressions, but our overall results did not change so we only report on the full dataset. One adult female cotton rat's territory that contained an area of overlap exemplified this pattern. We captured both the territory holder and an additional adult female at 2 different trap stations with 62.5% grass cover at each trap station. However, within the same territory, no additional females were captured at trap stations with 37.5% and 3% grass cover. Female overlap in control plots was the only dependent variable to have a significantly linear relationship with grass cover. None of our dependent variables (territory size, foraging activity, female overlap, number of juveniles weaned per female, and number of litter per female) had a significant linear relationship with vertical vegetation cover.

Females in control plots weaned 2 times higher number of juveniles per female than in monocrop plots ($F_{2,6}$=14.22, $p<0.01$; Figure 3.7a). Number of juveniles weaned per female was intermediate in intercrop plots and was not significantly different from control and monocrop plots. We also found a significant interaction of treatment and year for the number of litters per female ($F_{4,18}$=3.97, p=0.02; Figure 3.7b) with adult females on control plots having 5 times more litters than adult female cotton rats on monocrop plots in 2015. In 2015, number of litters per female was intermediate in intercrop plots and did not significantly differ from control and monocrop plots. Control plots also had higher proportions of juveniles when compared to monocrop plots ($F_{2,6}$=6.02, p=0.04; Figure 3.8). Intercrop plots had an intermediate proportion of juveniles that did not significantly differ from control and monocrop plots' proportions of juveniles.

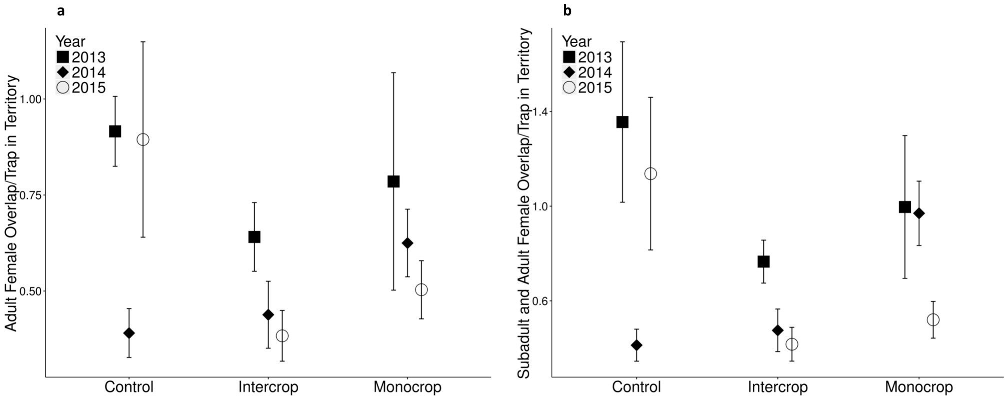

Figure 3.5. Mean (±SE) Minimum Known Alive Number of Adult Only (a) and Adult and Subadult (b) Female Cotton Rats in Territories of Radio-collared Female Cotton Rats Plotted by Treatment per Year. We radio-collared and followed adult female cotton rats to determine territory areas and live-trapped rodents to determine number of other adult female cotton rats in the same territory areas throughout the summers of 2013, 2014, and 2015 in Kemper County, Mississippi, USA. We found significantly more adult female overlap in 2013 than in 2014 and 2015. In 2014, we also found subadult and adult female overlap was highest in monocrop plots.

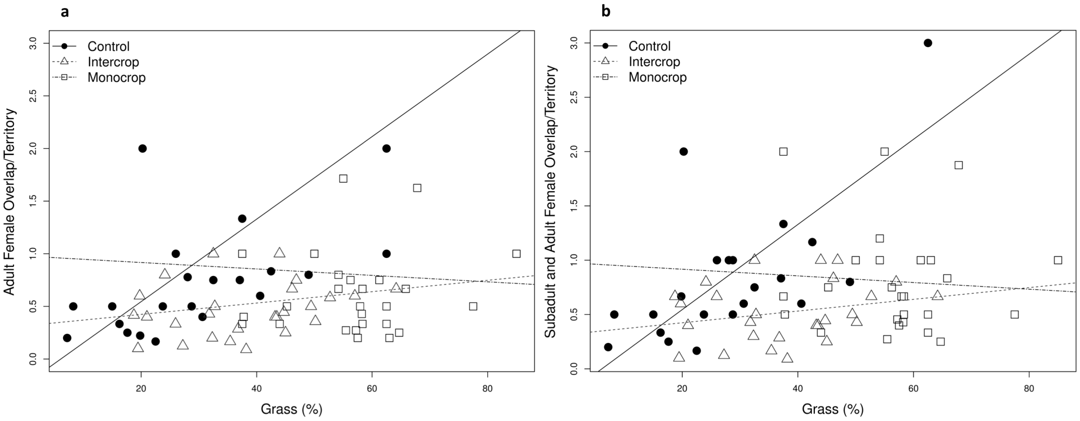

Figure 3.6. Scatterplot of the Minimum Number Known Alive of Adult (a) and Subadult and Adult (b) Female Cotton Rats Trapped in Radio-collared Female Cotton Rat Territories Over the Average Percentage of Grass Measured at Trap Stations Within Each Territory. Shapes denote the treatment each territory was in, and we overlaid the regression lines for each treatment to show relationships between the two variables. We collected trapping and vegetation data in the summers of 2013, 2014, and 2015 in Kemper County, Mississippi, USA. Only control plots had a significant positive relationship between female cotton rat overlap and percentage of grass.

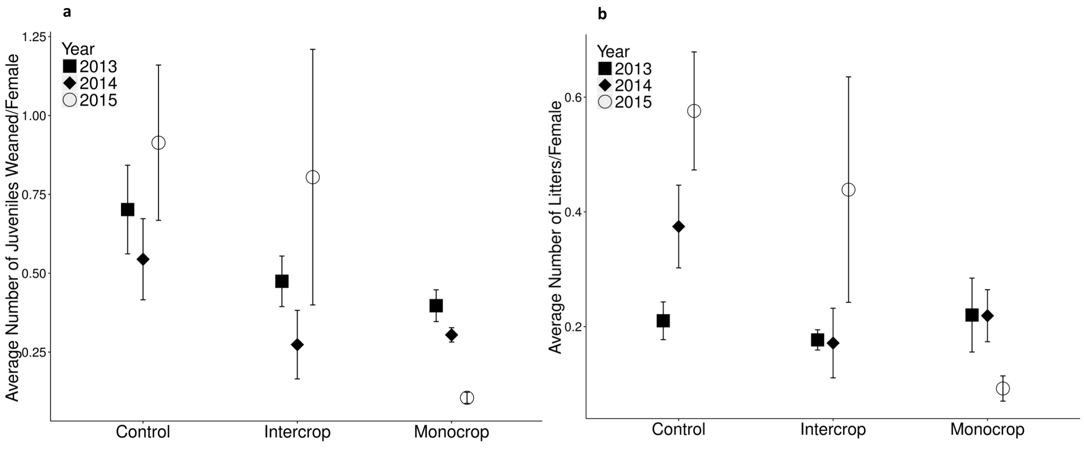

Figure 3.7. Average Number of Juveniles Weaned per Adult Female Cotton Rat (a) and Average Number of Litters per Adult Female Cotton Rat (b). We based averages on trapping data of cotton rats. We live-trapped rodents to determine the number of juvenile and adult cotton rats throughout the summers of 2013, 2014, and 2015 in Kemper County, Mississippi, USA. Our estimate of number of juveniles weaned per female cotton rat was higher in control than in monocrop plots (a). We also found our estimate of number of litters per female was higher in control than monocrop plots in 2015 (b).

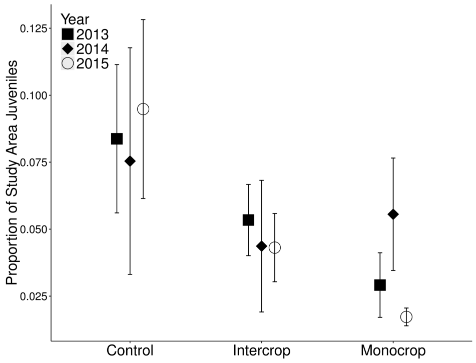

Figure 3.8. Proportion of Study Area's Juveniles Captured per Year and per Treatment. We live-trapped rodents to determine the number of juvenile throughout the summers of 2013, 2014, and 2015 in Kemper County, Mississippi, USA. We found control plots contained higher proportions of our study area's juveniles compared to monocrop plots.

## Discussion

We hypothesized that cotton rats would exhibit different behaviors because of different habitat characteristics associated with producing biofuel feedstocks. Female territory size did not differ among treatments, but foraging activity, female territory overlap, and reproduction indices did differ among treatments, yet not as predicted (Figure 3.1). There was more female overlap in control plots, particularly in areas of high grass cover, than monocrop and intercrop plots. Our reproductive indices were higher in control than monocrop plots and rodents foraged more in monocrop than control plots.

Results from our population abundances, reproductive indices, and foraging activity suggest that monocrop plots act as population sinks and possibly even ecological traps for cotton rats (Larsen et al., 2016). We found foraging activity was high and reproductive indices were low in monocrop plots where predation risk for cotton rats likely was high because of limited vertical vegetation cover. However, intercrop plots were intermediate in both foraging activity and reproductive indices, which follows the pattern of intermediate amounts of food and cover resources measured in intercrop plots. Female overlap in intercrop plots was similar to the pattern of monocrop rather than control plots, suggesting grass was not limiting in intercrop plots.

Although other studies have reported a negative correlation between cotton rat density and territory sizes (Cameron and Spencer, 1985), we found cotton rats had larger territory sizes when population density was high. Our study was conducted during a natural boom (2013) and bust (2014 and 2015) rodent population cycle (Larsen et al., 2016). Cotton rat population densities in 2013 may have been too high for individuals to maintain territories and instead we may have been measuring home ranges (areas used, but not defended by individuals) (Grant, 1993; Maher and Lott, 2000). Being territorial in an area of high cotton rat density could be costly to a female cotton rat because of the increased risk of predation and injury (Wingfield et al., 2001). Thus, female cotton rats may have devoted less energy to territorial defense. In 2013, the understory may not have been established enough due to recent switchgrass establishment to provide adequate food sources and therefore required more expansive foraging bouts, particularly during a time of high competition (Boutin, 1990; Jacob, 2008). However, once the understory established fully, cotton rats may have had enough food resources in defendable, smaller areas. Switchgrass and overall graminoid biomass increased in our intercrop plots, and white-tailed deer (*Odocoileus virginianus*) carrying capacity at a 6% crude protein threshold increased in our intercrop and control plots from 2012 to 2015 (Loman et al., 2017). Further, managers mowed switchgrass in monocrop and intercrop plots each year. The switchgrass regrowth may have been more nutritious, which would also allow cotton rats to obtain required nutrients in smaller areas (De Cauwer et al., 2006).

According to our GUD data, cotton rats were risk averse in control plots, which may have increased fitness. Control plots had a higher proportion of our study area's juveniles each year, more juveniles weaned per female and, by 2015, more litters per female when compared to monocrop plots. Although other studies (Boyle and Smith, 2009) have reported low juvenile recruitment in areas where densities are high and/or resources are low, our results were not due to females being non-reproductive. In monocrop plots, however, adults were risk prone and foraged more. Our site had several rodent predators including raptors (e.g. *Strix varia*, *Accipiter cooperii*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and snakes (e.g. *Pantherophis obsoletus*, *Crotalus horridus*), and a rodent's predation risk increases with increased movement. Thus, their risky behavior may have led to inadequate protection of their young. If a predator would find an unprotected nest, the entire litter would likely be consumed, which would lower juvenile recruitment. Additionally, infanticide risk may have been higher in monocrop plots because of high population density (Korpela et al., 2010).

Additionally, foraging activity provides us with further evidence that the monocrop plots may have acted as a sink (Larsen et al., 2016). More specifically, monocrop plots may be an attractive sink (Delibes et al., 2001) or an ecological trap (Battin, 2004). Monocrop plots had higher adult cotton rat abundance, lower juvenile recruitment, but higher foraging activity compared to control plots. If predation risk was high and was perceived correctly in monocrop plots, cotton rats should have foraged less and limited reproductive efforts (Lima and Dill, 1990). We do not have any evidence that the number or type of predators differed among our treatments, but the complexity of understory habitat could affect predation risk. On the other hand, rodents may have been foraging more in our artificial foraging trays because there was less food available on monocrop plots. Monocrop plots may have had limited food due to reduced diversity of food resources and high competition on plots with high densities of cotton rats. To further disentangle if high foraging activity in monocrop plots was due to mismatched cues of predation risk or lack of food, future work should artificially cover a foraging tray per station (Mattos and Orrock, 2010).

The location of grass in control plots limited cotton rats. Grass grew in clusters, potentially making territory availability smaller and causing cotton rat territories to overlap. Cotton rats were condensed into areas with high grass cover, making space available for other rodent species to use (Brady and Slade, 2001), particularly some of the rare species in our study area such as woodland voles (*Microtus pinetorum*; (Goertz, 1971). Available habitat likely led to higher rodent diversity in our control plots, which contained the most heterogeneous conditions (Larsen et al., 2016). Grass was a limiting factor in control plots, leading to female cotton rat overlap whereas intercrop plots had less overlap because there was more grass throughout the plots. Intercrop plots also provided suitable habitat conditions in the pine beds for other rodent species and therefore had higher rodent diversity compared to monocrop plots (Larsen et al., 2016).

Our study included behaviors from each of the three key behavior domains, but there may have been other relevant behaviors, within or separate from the three key domains, that we did not measure (Berger-Tal and Saltz, 2016). We did not find differences in fitness-related behaviors between intercrop and control plots, so cotton rats may have enough behavioral plasticity to maintain constant levels of fitness (O'Bryan et al., 2016). On the other hand, our results could provide evidence that cotton rat behavior is instead very rigid, which can be detrimental in the long term (Berger-Tal and Saltz, 2016). We limited radio-collaring to females >95 grams and may have collared more dominant females (higher body mass) than subordinate females (lower body mass).

Additionally, determining reproductive output of all females via genotyping of all surviving juveniles would have been a better method to measure female reproductive output, but this was not logistically feasible. However, our reproductive indices were consistent among treatments and years and were adequate comparisons. Our trapping data provided evidence to justify our use of reproductive indices. We were able to unequivocally match juveniles to their respective mother for 6 cases throughout our summers. For these 6 cases, we only captured one female in each area where we were identifying a cluster of juveniles and in each case there were 1 to 3 juveniles weaned from each female. Furthermore, during our trapping, 12 female cotton rats (10 in 2013 and 2 in 2014) gave birth in a trap. From these, we know that cotton rats had litter sizes of 4 to 7 pups (average=5.67 pups/female) at our site. From reproductive status we observed during trapping, adult female cotton rats were pregnant from 0 to 3 times throughout each summer (average=1.05 litters/female).

Here, we present evidence that considering population abundance alone can be deceiving and lead to poor management decisions. Our previous study (Larsen et al., 2016) reported that monocrop plots had the highest cotton rat abundance. However, our current study shows that cotton rat behaviors in monocrop plots will not lead to stable populations over time. Overall, cotton rats did not respond to the reduction in cover in our monocrop plots. Our results suggest that cotton rats are attracted to the grass in monocrop and intercrop plots, but require a certain amount of vertical cover to have high reproductive indices. However, it is important to note that previous experiments suggest there is variation in cotton rat response depending on size and age of treatment areas. For example, in 1.11-ha plots, cotton rat abundance, survival, and recruitment only differed among years not among treatments (Homyack et al., 2014). Yet, in 7-year old stands, cotton rat abundance was higher and rodent diversity was lower in intercrop compared to control plots (King et al., 2014). Furthermore, our study showed that some behaviors are more plastic (foraging activity, female tolerance, and reproduction indices) than others (territory size) in response to different amounts of food and vertical cover. Based on our results, managed intercrop plots have an adequate mixture of grass and vertical cover for cotton rats to have fitness-enhancing behaviors that will lead to a stable population. Our next step is to incorporate behavioral decision rules into a predictive model to assess if the observed individual behaviors and population trends will persist (Owen et al., 2017).

## Acknowledgements

We thank our funding sources; Weyerhaeuser Company, Catchlight Energy LLC, National Council for Air and Stream Improvement, Inc., U.S. Environmental Protection Agency (EPA), American Society of Mammalogists, North Carolina Academy of Science, and University of North Carolina at Greensboro. Weyerhaeuser Company employees operated under a Statement of Work with CLE during this study. This publication was developed under STAR Fellowship Assistance Agreement no. FP-91763501-0 awarded by the U.S. EPA. It has not been formally reviewed by EPA. The views expressed in this publication are solely those of the authors, and EPA does not endorse any products or commercial services mentioned in this publication. We thank all of our hard-working field technicians; R. Kelble, K. Paolini, E. VanNatta, A. Andrews, D. Bradley, J. Franklin, M. Martin, R. Meyer, K. King, A. Matteson, K. Corson, E. Smerdon, A. Wagoner, A. Culpepper, and G. Mikel. We would like to thank the people who helped us with logistics at our field site; Mississippi State University, Steve

Emerson, and the employees of the Scooba Weyerhaeuser office. Lastly, we thank; the East Mississippi Sportsman Association and Charlie Studdard with the Kemper County Hunting Club for lodging.

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## CHAPTER IV

# AN INDIVIDUAL-BASED MODEL OF HISPID COTTON RAT RESPONSE TO HABITAT VARIABLES IN A BIOFUEL FEEDSTOCK PRODUCTION SYSTEM

This chapter is coauthored by Angela L. Larsen, Volker Grimm, Jessica A. Homyack, T. Bently Wigley, Darren A. Miller, and Matina C. Kalcounis-Rueppell.

## Abstract

Assessing effects of forest management practices on wildlife primarily focuses on monitoring responses of populations or communities. However, populations are composed of individuals making decisions. Therefore, modeling behaviors that drive population dynamics while accounting for individual variation may improve predictions of population responses in managed systems. One current forest management practice involves producing biofuel feedstock by planting switchgrass (*Panicum virgatum*) between rows of planted loblolly pine (*Pinus taeda*) in the southeastern United States. We used an individual-based model (IBM) to test the hypothesis that different amounts of grass and non-grass cover in switchgrass-pine plots alters behavioral decisions that produce changes in population and community dynamics. We used the hispid cotton rat (*Sigmodon hispidus*), which is a dominant grassland specialist, as a focal species. We expected cotton rats to respond positively with increases in grass and non-grass cover because they need grass as a food source and non-grass cover to reduce predation risk. Our previous research using a replicated experiment indicated cotton rat home range size,

foraging activity, reproduction indices, and population dynamics in switchgrass-pine plots were intermediate to switchgrass monocrop and pine only (control) plots during the first three years of biofuels production. Our first objective was to simulate future cotton rat population dynamics (adult and juvenile abundance as a recruitment index) in switchgrass-pine plots with predicted grass versus non-grass vegetation cover for 10 years after treatment implementation. Our second objective was to simulate different levels of vegetation cover (grass and non-grass) to determine effects on cotton rat populations. Using our IBM, we set habitat variables to realistically represent vegetation succession but allowed behaviors (territoriality, reproduction, and survival) to emerge from our model based on individuals' decisions. We calibrated the model with field data on vegetation and behaviors from manipulations of habitat across a replicated and randomized experiment. We found that predicted vegetation cover at the level observed in our study would lead to cotton rat populations increasing approximately 3 times overall until year 8, with a population decline to year 10 of our simulations. If the landscape contained more grass and less non-grass cover across the 10 years, adult cotton rat abundance would be about 0.5 times lower than our observed scenario. If the landscape contained less grass and more non-grass cover, adult cotton rat abundance would be about 1.5 times higher than our observed scenario. Some level of cotton rat abundance decline was expected for all of our scenarios because previous research has shown rodent abundances decrease with pine stand succession and canopy closure in our study forest type. Our results suggest cotton rats are more tolerant of decreases in grass cover than decreases in non-grass cover. With minor adjustments, our model could be used to investigate effects of various habitat management settings on rodents and other prey species, with similar behaviors.

## Introduction

Wildlife management focuses on monitoring populations and communities to assess impacts of habitat management practices to support commodity production. Rodents are often chosen as appropriate study species for monitoring programs due to their ecological roles and relatively cost and time efficient methods to sample populations (Dickman, 1999). For example, researchers study rodent response to forestry (Converse et al., 2006), agricultural (Heroldová et al., 2007), and agroforestry practices (Homyack et al., 2014; King et al., 2014; Larsen et al., 2016). However, population monitoring alone may not elucidate all impacts or mechanistic effects of habitat change on species. A time lag of population responses is possible between when an individual alters its behavior to accommodate for differences in their environment, and when population and community levels present measurable differences. Previous studies provide evidence that individual behaviors affect populations and communities, and individual decisions are especially important to consider when assessing habitat management practices (Owen et al., 2017). For example, models including availability of food resources best explained rodent population dynamics (Previtali et al., 2009). *Peromyscus leucopus* populations were also best modeled in altered habitat (clear-cutting and prescribed burning) with individual demographic and movement information (Burns and Grear, 2008).

Individual-based models (IBMs) simulate individual responses under different scenarios and into the future using prior knowledge about individual and population responses (Berger-Tal et al., 2011; Grimm, 1999; Grimm and Railsback, 2005; Huston et al., 1988). Although strength of inferences from models is validated with observed results from field experiments, IBM simulations can identify detrimental habitat management actions. Therefore, researchers can focus on realistic and environmentally beneficial habitat management techniques. IBMs are relatively common in forestry (Botkin et al., 1972) and fishery science (Clark et al., 2001; Penaluna et al., 2015; Railsback et al., 2009) and more recently have been used for wildlife management research (Carter et al., 2015; Liu et al., 2013; Wang and Grimm, 2007). In contrast to traditional mathematical models, IBMs allow for adaptive behavior, local interactions, and variability via unique interactions with an individual's neighbors and environment and can also include dynamic and spatially heterogeneous habitat characteristics (Huston et al., 1988, Stillman et al., 2015). Further, behaviors modeled in IBMs emerge from fitness-seeking decisions and have more predictive power than traditional models (Stillman et al., 2015). As modeling progresses, even more complexity will be added, including microevolution (Grimm and Berger, 2016), which is not possible with traditional models.

IBMs can provide useful insight into wildlife management decisions because of lasting effects of habitat management actions on populations that may be difficult to ameliorate. Furthermore, managed lands are becoming increasingly important to protect biodiversity particularly in light of limited terrestrial lands under protection (Hansen et al., 1991; Noss et al., 2012). However, most studies only investigate short-term effects on wildlife populations due to financial and logistical limitations. IBMs can predict possible future scenarios with a significantly smaller investment and flexibility to incorporate scenarios that are not yet realized on the ground (Stillman et al., 2015).

Planting switchgrass (*Panicum virgatum*) in regenerating pine plantations is a potentially efficient sustainable land management technique to increase production of biofuel feedstocks while conserving biodiversity. Currently, switchgrass-pine management includes harvesting switchgrass annually in fall through spring after senescence for approximately 7-10 years. By about 7-10 years, canopy closure occurs and switchgrass productivity decreases (Jose et al., 2009). Hispid cotton rat (*Sigmodon hispidus*) population and rodent community responses differed among 3 experimentally applied treatments of a switchgrass-pine system (control: typical pine plantation management; intercrop: switchgrass intercropped with planted pines; and monocrop: switchgrass only; Larsen et al., 2016). Control plots had low adult cotton rat abundance, but high juvenile recruitment (Larsen et al., 2016). Switchgrass-pine plots were intermediate for both adult abundance and juvenile recruitment (Larsen et al., 2016). Monocrop plots had high adult cotton rat abundance, yet low juvenile recruitment (Larsen et al., 2016). We also measured female cotton rat territory behavior and reproductive indices, and rodent foraging behavior in all 3 treatments of the switchgrass-pine system (Larsen et al., In prep). Further, cotton rat territory size was affected by density of conspecifics but not treatment, and territory overlap only occurred in control plots where percent grass was high (Larsen et al., In prep). Rodents foraged more in monocrop than control plots and was intermediate in switchgrass-pine plots. Lastly, female cotton rats in control plots had higher reproductive indices than cotton rats in monocrop plots while cotton rats in switchgrass-pine plots had intermediate reproductive indices (Larsen et al., In prep).

This previous research developed an understanding of cotton rat responses to habitat alteration for 3 years following switchgrass-pine establishment. However, cotton rat responses to variations in habitat characteristics, or through the 10 years of effective switchgrass-pine management is unknown. For example, if switchgrass-pine plots would have limited grass with abundant non-grass cover through time, cotton rat behaviors and populations may resemble populations in control plots. If switchgrass-pine plots would have abundant grass with limited non-grass cover through time, cotton rat behaviors and populations may resemble populations in monocrop plots. For cotton rats to maintain a stable population, they likely require grass for food and more complex non-grass vegetation for cover from predators. As shown by King et al. (2014), cotton rat abundance was low in control versus switchgrass-pine plots 7 years after stand establishment. King et al. (2014) conducted their research at the same study site on older pine stands that had been established before our experiment. Although previous studies have investigated how vegetation (Loman et al., 2017), herpetofauna (Homyack et al., 2013), birds (Loman et al., 2014), and rodents (Homyack et al., 2014; King et al., 2014; Larsen et al., 2016; Marshall et al., 2012) are impacted in switchgrass-pine systems, all previous studies have only investigated responses for 1-3 years at reduced spatial scales compared to standard pine management stands.

Our study modeled how a rodent, the cotton rat, responded to understory habitat characteristics of switchgrass, a biofuel feedstock, in intensively managed loblolly pine

(*Pinus taeda*) plantations. The cotton rat is a useful model species because it is a grassland specialist and the dominant rodent in our study area with a key ecosystem role. Our model was designed to be able to assess how various potential habitat management techniques impact prey species. We used an IBM to test the hypothesis that different amounts of grass and non-grass cover in switchgrass-pine plots would alter behavioral decisions that drive changes in population and community dynamics. Our previous research indicated cotton rat behaviors and population dynamics were intermediate in switchgrass-pine plots compared to switchgrass monocrop and pine only (control) plots during the first three years of switchgrass-pine management. Our first objective was to simulate future cotton rat population dynamics (adult abundance and juvenile abundance as a recruitment index) in switchgrass-pine plots with predicted grass versus non-grass vegetation cover for 10 years after pine stand establishment. Our second objective was to simulate different levels of vegetation cover (grass and non-grass) to determine effects on cotton rat populations. Although we used a general change in understory habitat characteristics, future work could alter our model for several potential habitat management techniques, such as changes in herbicide application or switchgrass harvesting. Future work could also explore how other prey species would respond to switchgrass-pine systems.

## Methods

### *Model background*

In general in our model, switchgrass was food, and non-grass vegetation was cover, for cotton rats. Naturally occurring woody and herbaceous vegetation grew between pine trees and switchgrass at our study site and was referred to as edge. Habitat patches designated as pine, edge, and switchgrass all provided some amount of both cover food (Table 4.1). All habitat types had a combination of grass and non-grass cover. Pine habitat patches contained the lowest grass and most non-grass cover, grass habitat patches contained the most grass and lowest non-grass cover, and edge habitat patches contained intermediate amounts of both grass and non-grass cover. We included territory size, reproduction, and survival as submodels because our previous work showed the importance of each individual behavior to cotton rat population response (Larsen et al., In prep). Each submodel was composed of parameters. Parameter values were determined based on our previous field data (Larsen et al., 2016, In prep), previous literature as cited, or inversely via calibration. We adapted the Habitat-Based Models Building Block: Territory Emergence submodel from Zakrzewski (2016) and the reproduction submodels from Liu et al. (2013) to obtain realistic estimates of cotton rat populations (adult abundance and juvenile abundance as a recruitment index). Some IBMs include territory behavior, but little consistency exists among models. Some models impose territories (Liu et al., 2013) whereas others have attempted to allow territories to emerge from the models based on resource availability (Wang and Grimm, 2007). Zakrzewski (2016) developed a new Habitat-Based Models Building Block: Territory Emergence submodel to allow territories to emerge and may become a new standard building block for models implementing territories. Models have been used for more singular applications and usually do not build on previous models. Our study developed a more general IBM that is built from previous programs to aid in the advancement of IBMs.

Through scenario simulations, we determined how cotton rat populations would respond to different amounts of grass and non-grass cover. We included natural vegetation succession as increased cover on pine and edge patches through 10 years. We also modeled annual switchgrass harvest as decreased cover through winter with increasing cover on grass patches throughout the summer months. Furthermore, we included an overall reduction in grass after year 7 when the pine trees were estimated to provide too much shade for switchgrass growth (Blair and Enghardt, 1976). All field data (Larsen et al., 2016, In prep) were collected in Kemper County, Mississippi, USA, on land owned and managed by Weyerhaeuser Company on experimental plots established and maintained by Weyerhaeuser Company and Catchlight Energy LLC (CLE), a Chevron|Weyerhaeuser joint venture. At our site, we had 4 forest stands as replicates, each with 4, 10-ha treatment plots (2 control loblolly pine plots, 1 switchgrass-pine plot, and 1 switchgrass monocrop plot). For more details about our study site, please see Larsen et al. (2016).

### *Model description*

We followed the ODD (Overview, Design concepts, Details) protocol to describe our model below (Grimm et al. 2006, 2010). See Figure 4.1 for a broad overview of the model. We implemented the model in NetLogo 6.0.1 (Wilensky 1999; program code in Appendix A).

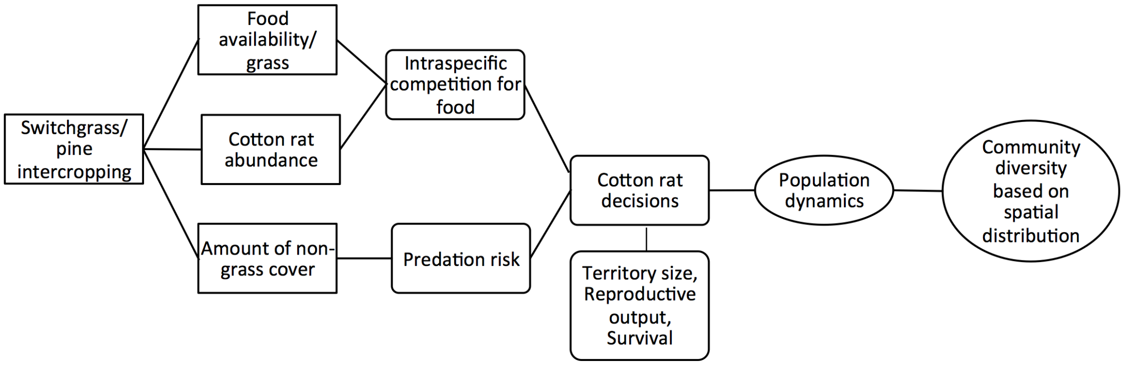

Figure 4.1. Broad Overview of the Conceptual Model. We set components in the left hard-edged rectangles as initial parameters. Both grass and non-grass cover were updated throughout our 10-year simulation to represent natural succession and annual switchgrass mowing. Components in the middle soft edged rectangles were parts of our model to allow cotton rat decisions to emerge. Components in the right circles were direct (population dynamics) and indirect (community diversity based on spatial distribution) outputs from our model.

### *Purpose*

The purpose of our model is to simulate cotton rat population abundance and spatial distribution in switchgrass-pine plots based on field data and data from previous literature, for habitat management technique assessment. Our model is used to predict how cotton rat populations respond in future switchgrass-pine management years and under different switchgrass-pine management scenarios.

### *Entities, state variables, and scales*

Our model entities are habitat patches to make up the landscape, and female cotton rats (Table 4.1). Each habitat patch is 1.5 m x 1.5 m and defined as pine, edge (mix of woody and herbaceous vegetation), or grass. Our model world is 300 m x 300 m for a total of 9 ha, which is large enough to buffer cotton rat movement around the 1.96 ha trapping grid area (Larsen et al., 2016). Our model does not allow simulated individuals to leave one boundary and enter back into the landscape from the opposite boundary. We contain our simulated rats to the interior 1.96 ha area of our world to best represent our sampled trapping grid area. We only consider female cotton rats in our model because: 1) cotton rats are promiscuous, so reproduction is mainly limited by the number of females (Liu et al., 2013) and 2) our previous studies only obtained female behavior data, not male behavior (Larsen et al., 2016). Each time step in our model is one day.

Table 4.1. State Variables for Habitat Patches and Cotton Rats. A brief explanation of each variable, possible values, and units where necessary are included.

|  | **Variables** | **Explanation** | **Possible Values** | **Units** |
|---|---|---|---|---|
| **Habitat Cell** | location | x and y coordinate |  |  |
|  | habitat type | pine, edge/mixed, grass |  |  |
|  | habitat quality | amount of cover | (pine>edge>grass) | % |
|  | resource | amount of food | (pine<edge<grass) | % |
|  | owner | rat(s) that own patch as part of territory |  |  |
| **Rat** | ID | # |  |  |
|  | age | juveniles – not sexually mature and remains at nest | juveniles - 1-21 (Meyer and Meyer, 1944) | days |
|  |  | subadults – dispersing/establishing a territory | subadults - 22-80 (Clark, 1972) |  |
|  |  | adults – reproductive and established territory | adults - 81-360 (max lifespan is 360) (Clark, 1972; Larsen et al., 2016) |  |
|  | territory | set of habitat cells | Range of patches will be based on our territory data (Larsen et al., In prep) |  |

|  |  |  |  |
|---|---|---|---|
|  | enforcement | Territory program from Zakrzewski (2016) |  |
| reproductive traits | Breeding season | February-October |  |
|  | pregnant or not | gestation - 27<br>Needs 1.5 times amount of base energy in territory to reproduce<br>(Clark, 1972; Randolph et al., 1977) | days |
|  | lactating or not | lactating - 21<br>(Meyer and Meyer, 1944) | days |
|  | litter size | random number in range of 1-3; only modeling females so halved 1-7<br>(Cameron, 1977; Larsen et al., In prep; Meyer and Meyer, 1944) |  |
|  | litters per year | random number in range of 1-3<br>(Cameron, 1977; Larsen et al., In prep; Meyer and Meyer, 1944) |  |
| survival | malnutrition | Driven by energy needed vs. energy obtained in territory (Inversely calibrated) |  |
|  | predation | Driven by cover needed vs. cover obtained in territory (Inversely calibrated) |  |
|  | juvenile and subadult | Minimum 0.80 probability (based on adult survival in control plots of |  |

| | |
|---|---|
| | Conner et al. (2011); and inversely calibrated) |

*Process overview and scheduling*

Every time step goes through the process outlined in Figure 4.2 and in the following. Each submodel is underlined in the description below. State variables update immediately after each action and entities perform actions in a randomized sequence each time step.

Update Patches and Update Breeding Season: Habitat patches and time steps are updated first to allow subsequent submodels to respond to updated settings. Habitat quality (cover) is updated to represent cut grass from fall to spring with growing grass throughout summer months. Furthermore, habitat quality (cover) increases throughout the years in pine patches to represent pine trees continuously growing and shading out grass, reducing resources (food; Jose et al., 2009). Furthermore, for each habitat patch, habitat quality and resources vary randomly within a range of observed and expected percentage patterns to create a dynamic and heterogeneous landscape.

Maturation: Cotton rats age by one day for each time step that our model progresses and changes life stages as cotton rats reach maturation ages. When a juvenile is born, its age is set to 1 day. Once a juvenile becomes a subadult, that individual is no longer dependent on their mother because our classification is based on weaning age (Meyer and Meyer, 1944). Once a subadult becomes an adult (Table 4.1), that individual establishes a territory.

Establish Territory: In our model, cotton rats establish territories based on food, cover, and competitive interactions with other females. Once an individual becomes an adult it begins to establish its territory based on the sum of food and sum of cover within its territory. If the sum of food or cover is below the malnutrition or risk avoidance parameter values respectively, the individual continues to add patches to grow its territory. The individual cannot grow its territory if the number of patches have already reached the maximum number, which is based on our field data (Larsen et al., In prep). The individual removes patches if the sum of food or cover within its territory is more than double what it needs to survive. If a territory has a detached cluster of patches, the detached cluster of patches is also removed. The edge patches with the lowest sum of food and cover combined are removed when an individual is shrinking its territory. If 2 individuals compete for the same patch, first the original owner receives a 0.5 probability of winning to provide the owner of the patch with home advantage. Second, the randomly assigned competitive value is compared between the 2 individuals and the individual with the higher competitive outcome takes ownership of the patch. Our territory submodel is an adaptation of Zakrzewski's (2016) Habitat-Based Models Building Block: Territory Emergence with the addition of the predation component. For details of the base submodel refer to Zakrzewski (2016).

<u>Reproduce</u>: Reproduction is possible if adults have more energy (food resources) than the malnutrition threshold times 1.5 in their territory (Randolph et al., 1977). Our model updates number of litters, days of pregnancy, birth, and days of lactation per adult within each breeding season.

Survive: Survival in our model depends on age. For juveniles and subadults, predation is considered random. For adults, survival is based on cover within their territory to reduce predation risk and food within their territory to reduce malnutrition risk. Furthermore, juveniles die if their mother dies. Lastly, adults die if individuals age to the maximum lifespan of 360 days.

Plot Cotton Rat Adult, Subadult, and Juvenile Abundance over Time: Cotton rat abundance per age group is measured and plotted over time.

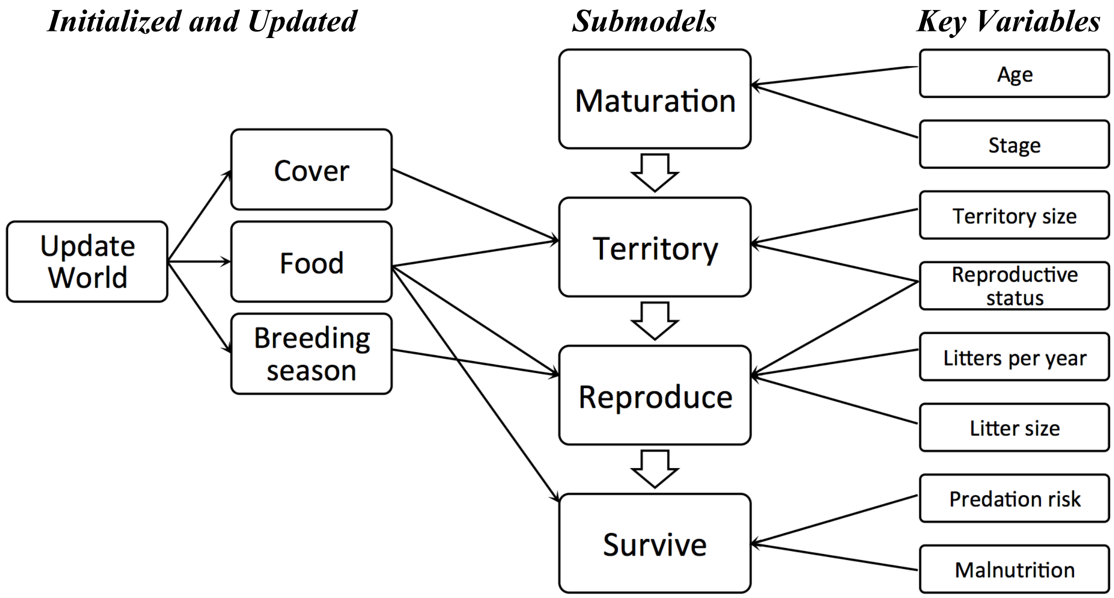

Figure 4.2. Overview of Model Processes with Landscape Factors on the Left and Key Variables on the Right of the List of Submodels (maturation, territory, reproduce, and survive). At each time step, our model processed the submodels in the same order.

*Design concepts*

*Basic principles*. Key processes are cotton rat territory establishment, reproduction, and survival. All processes are affected by cover and food availability and lead to population dynamic changes. Concepts in our model are influenced by earlier models; territory (Zakrzewski 2016, Van Moorter et al., 2009), reproduction (Liu et al., 2013), and survival in terms of obtaining enough energy to avoid malnutrition while finding enough cover to avoid predation (Roese et al., 1991).

*Emergence*. Population dynamics and spatial distribution of territories emerge from individuals' behaviors and interactions with other rats and their environment. When different grass and cover amounts are introduced, individuals' behavior (movement and reproduction) impact population dynamics and spatial distribution of territories.

*Adaptation*. Adaptation is based on reducing predation risk by obtaining enough cover in an individual's territory. However, individuals are still required to obtain food so individuals may add habitat patches with low cover but high food to their territories. Our previous results suggested cotton rats had to forage in monocrop plots even though cover is poor ((Larsen et al., In prep).

*Prediction*. Our model includes an indirect prediction that cover is negatively correlated with predation risk (mortality rate).

*Sensing*. In our model, cotton rats sense 1) habitat quality, defined as food and cover amounts, of environment within their territory, 2) presence of other rats in their local environment.

*Interaction*. Cotton rats compete for habitat patches to add to their territories.

*Stochasticity*. Litter size is randomly determined within a range of 1-3 pups. We based the 1 on our field data of captured juveniles (Larsen et al., In prep). We used 3 as half of 7, which is the number of pups observed when cotton rats gave birth in our traps

(4-7 pups; average=5.67 pups/female; (Larsen et al., In prep)) and previous literature (Cameron, 1977; Meyer and Meyer, 1944). We halved the maximum because we are only modeling female cotton rats and assume a 1:1 sex ratio. Number of litters per female is also randomly determined within a range of 0-3 per breeding season because our trapping data showed females were pregnant 0-3 times each breeding season (average=1.05 litters/female; (Larsen et al., In prep)). Maximum lifespan, gestation, and lactation duration are all constants in the model. Environmental fluctuations (weather and climate) are not included to keep our model as general and simple as possible.

*Collectives*. Each territory is defined as a collection of all patches each individual decides to own.

*Observation*. Population abundance as number of adults, subadults, and juveniles is output and displayed from the model. Population abundance provides information about the population dynamics and how individual behavior impacts the population level. Territory shapes and spatial distribution is observed and used to assess spatial availability for other rodent species.

### *Initialization*

Our model is initialized with a set number of adult cotton rats randomly distributed throughout the trapping grid area. Our starting number of adults is 10, based on our field data (Larsen et al., 2016). The model starts on January 1st. The landscape starts with the switchgrass-pine system and the number of patches of edge and grass can be changed to conduct different simulations to test responses. The initial landscape is a row of pine (1 patch wide), a row of edge (1 patch wide), a row of grass (2 patches wide), a row of edge (1 patch wide), and this habitat patch pattern is repeated for the entire ‘length’/x-axis of the world to represent switchgrass-pine plots. Pine trees are set in rows as would be in a traditional pine plantation. Then grass is set in the middle of the space between the pine trees (in the interbed or row). Finally, we define the naturally occurring vegetation that grows between the pine beds and grass rows as edge.

*Input data*

Our model does not use any input data.

*Submodels*

*Maturation*. In our model, cotton rats age by 1 day at each time step. Cotton rats are juveniles from 1 to 21 days, subadults from 22 to 80 days, and adults from 81 to 360 days (Clark, 1972; Meyer and Meyer, 1944). Average cotton rat lifespan is 6 months (Clark, 1972), but maximum lifespan is set to 360 days (1 model year) because we recaptured individuals 1 year after initial capture, but never more than 1 year.

*Territory*. Our model includes an adapted version of Zakrzewski’s Habitat-Based Models Building Block: Territory Emergence. Only adult cotton rats establish territories. Adults grow their territories if cover and food are lower than needed for survival. If an individual’s territory is near a neighboring cotton rat, the two individuals need to compete if both individuals want to add the same patch to their own territory. Adults will shrink their territories if their territory has grown beyond the maximum allowed number of patches (based on observed field data; (Larsen et al., In prep).

*Reproduce*. An adult reproduces if it is breeding season and the individual has 1.5 times the amount of baseline energy within its territory (Randolph et al., 1977). After a gestation period of 27 days (Clark, 1972), an individual gives birth to a litter of 1-3 pups (half of 1-7 range given we are only modeling females). Lactation then occurs for 21 days, unless all pups die. Once 21 days is over, or all pups die, the female is fertile again.

*Survive*. If a female cotton rat survives to 360 days, that individual dies because maximum lifespan is 360 days. If a female cotton rat dies in the model and has juveniles, all juveniles die too because they are not weaned and therefore depend on their mother. Malnutrition and predation are the risks for adults in our model. Juveniles and subadults are susceptible to random predation events, but their 'death' could also be considered emigration. Probability of death from predation increases when an adult does not have the baseline amount of cover in their territory. Similarly, probability of death from malnutrition increases when an adult does not have the baseline amount of food in their territory.

*Plotting*. Our model is set to plot population size as number of adults, subadults, and juveniles and is updated each time step.

We included a TRACE document ("TRAnsparent and Comprehensive model Evaludation"; Schmolke et al. 2010; Grimm et al. 2014; Augusiak et al. 2014) containing evidence that our model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose (Appendix B). Below we provided a summary of model testing, calibration, sensitivity, and validation that we conducted.

*Model testing and calibration*

To test our model, we visually inspected the ‘world’ during simulations and performed stress tests. We also tested each submodel independently. An example error we found with visual inspection was that juveniles were not always dying when their respective mothers would die. We corrected the juvenile death issue in the code. Stress tests included using extreme parameters expected to affect individuals’ survival. We addressed any issues in the code if the population did not either grow quickly or go extinct.

For calibration, we used the observed patterns from our field data. Specifically, we used female adult and juvenile minimum known alive (MNKA) numbers, or the minimum number of unique individuals known to be alive during a sampling period. We also used territory size and spatial distribution patterns (Larsen et al., In prep) to allow for calibration of our unknown survival parameters. We compared patterns with the first 3 years of simulation because all field data were from the first 3 years of switchgrass-pine establishment. First, we determined a range of parameters that fit our overall observed patterns. We then used the BehaviorSpace tool in NetLogo to run 15 replicates of various sets of parameters to determine which set most closely matched our observed patterns. We averaged simulated data from June and July because both months were our main trapping months in each of the 3 years of our fieldwork. Our model does not include environmental data, so we were not trying to match yearly variation in our observed data.

### *Sensitivity*

We altered our model's energy (housekeeping-demand) and non-grass cover (predation-avoidance) requirement parameters independently by values of 1. From our calibrated parameter values, we varied each by ±2.

### *Validation*

We used a similar study conducted at the same study site in older pine stands to validate our model at year 7 (King et al., 2014). Although we knew the results of King et al. (2014) before calibrating our model, we did not use our knowledge to influence our calibration. King et al. (2014) reported on cotton rat population and rodent community responses to planting switchgrass in pine plantations during the 7th year after managers had planted the pine trees. We then compared our 7th year model output to data reported by King et al. (2014), without further calibration.

### *Applied simulations*

We implemented changes in the understory habitat characteristics that could occur under different switchgrass-pine management techniques to show the effectiveness of our model and how our model could be used to investigate the impacts of different scenarios. Habitat management techniques could alter the amount of food and cover for various prey species. In our study, high amounts of food and low amounts of cover were expected to cause population dynamics to be similar to observed patterns in monocrop plots (Larsen et al., 2016). On the other hand, low amounts of food and high amounts of cover were expected to cause population dynamics similar to observed patterns in control plots (Larsen et al., 2016). To explore potential outcomes of such habitat changes, we implemented 3 scenarios; 1) less grass, more non-grass cover as 12.5% more edge patches, 12.5% fewer grass patches than scenario 2, 2) baseline with habitat patches set as observed in the field, and 3) more grass, less non-grass cover as 12.5% fewer edge patches, 12.5% more grass patches than scenario 2 (Table 4.2). Hereafter, we only referred to scenarios by their respective number. Each scenario was simulated for 10 years and 15 replicates. We used scenario 2 to run and plot the averages of adult abundances for odd number years to determine that 15 replicates would reduce variation and therefore provide an adequate sample size for our simulations (Figure 4.3).

We also ran a repeated measures analysis of variance (ANOVA) to test if simulated cotton rat adult and juvenile abundances were different among our landscape scenarios, year, or an interaction of scenario and year. We rank transformed data because data were non-normal. We investigated pairwise contrasts using a Tukey HSD. We used Program R (R Core Team, 2014) for all analyses. Although we used a general change in understory habitat characteristics for our study, future work could alter our model for several potential habitat management techniques or to explore how other model prey species would respond to changes in understory habitat characteristics.

Table 4.2. Details of Each Landscape Simulation Scenario Used in our Individual-based Model. A brief description and possible reasons for the differences in habitat patches are provided for each scenario.

| **Scenario** | **Description** | **# of Grass Patches** | **# of Edge Patches** | **# of Pine Patches** | **Possible Reasons** |
|---|---|---|---|---|---|
| 1 | Less grass, more non-grass cover | 70 | 90 | 40 | Natural succession at a faster rate than expected, less herbicide treatments, poor switchgrass establishment and growth |
| 2 | Baseline | 80 | 80 | 40 | Current switchgrass-pine management |
| 3 | More grass, less non-grass cover | 90 | 70 | 40 | Natural succession at a slower rate than expected, more herbicide treatments, good switchgrass establishment and growth |

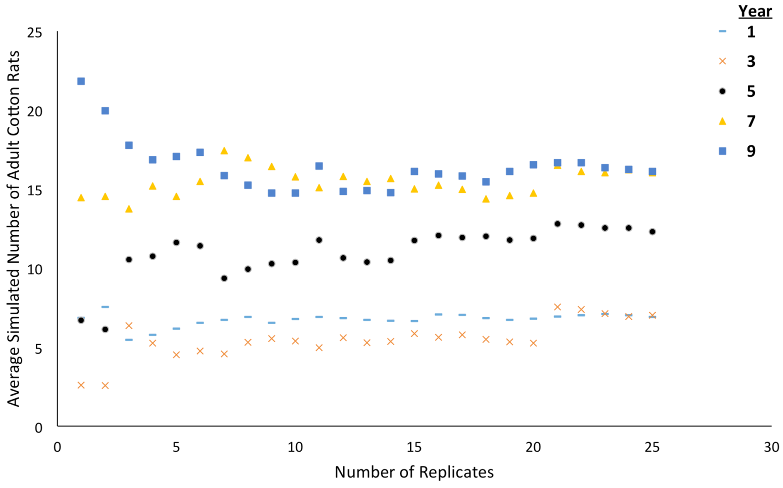

Figure 4.3. Average Number of Adult Cotton Rats Across an Increasing Number of Replicates. We only plotted odd simulated years to simplify the plot. We detected a plateau in points at 15 replicates, providing evidence that 15 replicates are sufficient to use for our model simulations.

## Results

*Calibration*

We compared the relative size and spatial distribution of 100% minimum convex polygon (MCP) from one of our field plots to one of our simulations (Figure 4.4). Overall, the model underestimated the MCP area but represented the shape and spatial distribution of the territories well. We found our field data did not match our simulated results exactly, but the overall patterns were similar (as seen in Figure 4.5; years 1-3).

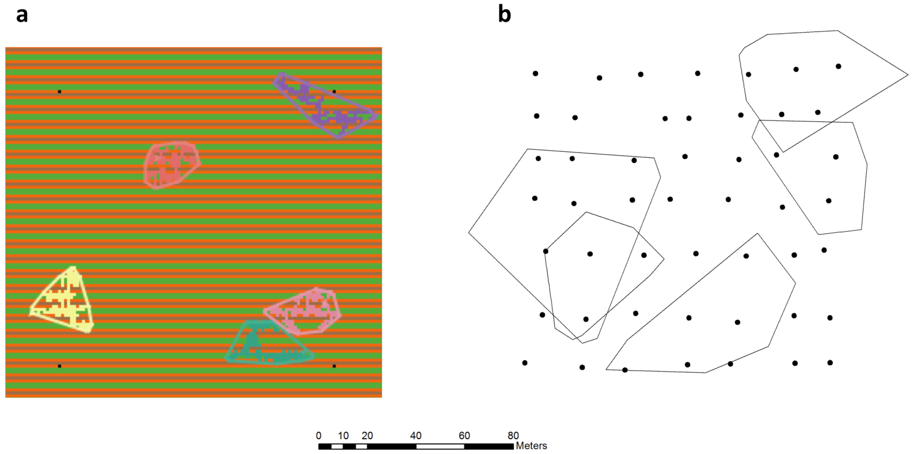

Figure 4.4. Comparison of Simulated (a) and Field Observed (b) Cotton Rat 100% Minimum Convex Polygon Territories. Simulated world from NetLogo was scaled to reflect trapping grid of field plot. Simulated world (a) shows edge of trapping grid with 4 black dots and the field data (b) shows the entire 7x7 trapping grid as black dots with 20m spacing between each trap (Larsen et al., In prep). The simulated world also shows where the pine (orange), edge (brown), and grass patches (green) are located and the trapping grid for the field observed plot was positioned to match switchgrass-pine orientation.

*Validation*

We observed increased adult population abundance by year 7 (Figure 4.5a; baseline), similar to what was observed in field data (King et al., 2014). Assuming sex ratio was 1:1, our model slightly overestimated the number of adult females. King et al. (2014) reported population estimates from Program MARK (White and Burnham, 1999), while our model was calibrated based on MNKA. Our model also did not incorporate yearly variation due to weather, and King et al. (2014) may have been conducted during a poor weather year.

### *Sensitivity*

We found our model output to be more sensitive to changes in the cover (predation avoidance) than the energy (housekeeping demand) parameter (Table A2).

### *Landscape simulations*

Overall, we found both adult and juvenile abundance to increase from year 2 to year 8 with a decline from year 8 to year 10 when simulated with our scenario 2 of observed habitat characteristics. We also found a significant interaction of scenario and year for both adult and juvenile simulated abundances ($F_{18,378} = 8.83$, $p<0.01$ and $F_{18,378} = 8.31$, $p<0.01$; respectively). We were only interested in differences between scenarios 1 and 2, and 2 and 3. Specifically, for adult abundance, we found our scenario 3 had significantly lower abundance compared to our scenario 2 during years 3-10. For scenario 1 we found adult abundance was significantly higher than our scenario 2 during years 4 and 6 (Figure 4.5a). For juvenile abundance, we found our scenario 3 had significantly lower juvenile abundance compared to scenario 2 during years 3-9. We found scenario 1 had significantly higher juvenile abundance compared to scenario 2 in years 3 and 4 (Figure 4.5b).

Given the relatively low overall predicted population abundances for all of our scenarios and the general territory spatial distribution observed, other rodent species would be able to use habitat in switchgrass-pine plots. Therefore, based on our model simulations, rodent diversity would likely be maintained in switchgrass-pine plots throughout 10 years. Our scenario 3 could be detrimental to all rodent species because rodents need cover to avoid predation. Therefore, even though cotton rats did not dominate simulated plots under scenario 3, rodent diversity was predicted to be low.

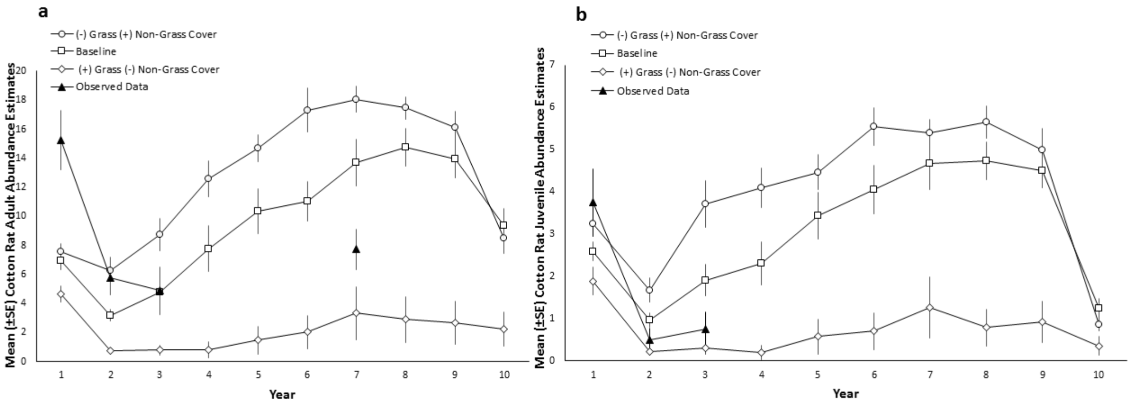

Figure 4.5. Mean (±SE) Female Adult (a) and Juvenile (b) Cotton Rat Abundances under Different Scenarios with 15 Simulations Across 10 Years and 3 Years of Field Data. All simulated means were averaged between June and July data to match our field data. Scenarios included: scenario 1 (decreases grass and increases cover compared to scenario 2), scenario 2 (the baseline landscape we calibrated the model with to represent how managers are currently treating the study area), and scenario 3 (increases grass and decreases non-grass cover compared to scenario 2).

## Discussion

Our model allowed assessment of switchgrass-pine management over a longer temporal scale than was feasible to measure in the field. Overall, given our model's simplicity, we found our model fit well with observed field data (Figure 4.5). The amount of grass and non-grass cover in our switchgrass-pine plots appears to be sufficient to ensure persistence of cotton rats populations for the first 10 years of pine stand establishment. Furthermore, rodent communities are expected to be relatively diverse because cotton rat populations gradually increased in our simulations but did not reach levels at which they would completely dominate an area. All yearly variation that resulted from our model was due to switchgrass-pine management and vegetation succession because we did not include any weather data. The abundance decline from years 8 to 10 probably occurred because as pine stands continue through natural succession, cotton rat abundances tend to decrease (King et al., 2014). Cotton rats prefer grasslands to forests (Cameron and Spencer, 1981).

Our model underestimated abundances in 2013 (year 1). However, we know cotton rat population abundances were exceptionally high in 2013, independent of treatment (Larsen et al., 2016). Given that our model did not account for environmental variation, we expected our model would underestimate 2013. Furthermore, our model overestimated adult and juvenile population abundances for 2014 (year 2) and 2015 (year 3). Overestimation is not surprising given our model would better capture all individuals on the simulated plot whereas we were not able to trap all individuals on our plots. We found discrepancies between our simulated and field data when we looked only at June abundances. Simulated data were consistently higher in June than field data in June. The difference was likely due to the animals acclimating to the traps. Trapability is particularly low for juveniles and small rats in general because of sensitivity of traps (Davis and Emlen, 1956), but particularly in cotton rats because of social dominance

(Summerlin and Wolfe, 1973). Furthermore, juveniles do not leave the nest the first few days after birth, but our model would have counted all juveniles beginning at age 1 day.

Our scenario 1 represented how switchgrass-pine plots would be if they were more similar to our control plots. However, our simulations did not fully represent our previous results in control plots. Instead of low adult abundance as in our control plots, our simulation resulted in high adult abundance. Grass was more uniformly distributed in our simulated landscape than in our control plots. Uniformly distributed resources in our model would reduce competition for clumped resources, possibly increasing survival and reproduction (Nonaka and Holme, 2007; Rémy et al., 2013). We do not think adult cotton rat abundances would be detrimentally high if an area represented scenario 1, because we found low adult abundances in our field control plots. Juveniles born in control plots likely emigrated to other areas, but our model did not directly include emigration.

Similarly, our scenario 3 represented how switchgrass-pine plots would be if they were more similar to our monocrop plots. Yet, our simulations resulted in low adult abundance rather than high adult abundance, which we observed in our field data. Our simulated landscape had pine patches and therefore had more non-grass cover compared to monocrop plots. Furthermore, our model did not include immigration. If monocrop plots were acting as ecological traps (Battin, 2004; Kristan, 2003) as our previous data suggested, then high population abundance would have been due to immigration (Pulliam and Danielson, 1991). Our simulated and observed results did agree with low juvenile abundance.

Our model showed sensitivity to amount of non-grass cover needed to reduce predation risk and cotton rat simulated abundance was significantly decreased when non-grass cover was reduced on the landscape. Furthermore, our model provides support that non-grass cover is the main driver for cotton rat population dynamics. Cover is important to reduce predation risk for various prey species, including rodents (Brown, 1988). Our model will be adaptable to simulate various prey species with similar behaviors. Prey species are important to model because of their interconnectedness to other species, both plants and animals (Dickman, 1999). Our study is a good example of how our model could be used and why IBMs are important to include in wildlife management decisions. Habitat management techniques that reduce complexity in understory habitat structure should be simulated to better understand lower thresholds to avoid.

For our questions, our model provided us with general patterns that allowed us to broadly assess how rodents would respond in future switchgrass-pine management years and with different habitat characteristics. Our previous research did not suggest switchgrass-pine plots were ecological traps, sinks, or sources, so we did not include immigration or emigration in our current model. However, as seen from our results, immigration and emigration could be important for future model versions if the purpose is to obtain more precise predictions when varying habitat characteristics.

We developed, tested, and implemented an IBM to project cotton rat abundances for the initial 10-years of a switchgrass-pine system. We calibrated our model with our field data from years 1-3 (Larsen et al., 2016, In prep), and validated our model with year 7 data (King et al., 2014). Currently, our model's spatial scale matches our trapping grid scale, but we could increase our model's spatial scale to a standard pine management stand to test how cotton rats would respond to a larger switchgrass-pine system. In addition, our model could include marsh rice rats (*Oryzomys palustris*) and harvest mice (*Reithrodontomys* sp.) because all 3 rodents were trapped in our switchgrass-pine system and are known to impact one another's populations (Cameron, 1977; Kincaid and Cameron, 1982b). Including additional species in our model would allow us to more accurately predict community level changes. Our model could also include weather data to test potential effects of precipitation and temperature under different climate change scenarios (Clark et al., 2001). Weather impacts vegetation growth and therefore the survival and reproduction of rodent species. Furthermore, our model's habitat patches could be modified to test how changing the timing of switchgrass harvest would affect cotton rats and other rodent species. Understanding potential affects of fall versus spring switchgrass harvest could help inform switchgrass-pine management decisions.

Our model is not only useful for cotton rats in a switchgrass-pine system in Mississippi. Our model could also be used by anyone wanting to predict how prey species respond to heterogeneous habitat characteristics. Our model is particularly useful for other systems because it includes behaviors that emerge, fitness maximizing decisions, and a standardized territory submodel (Zakrzewski, 2016). Depending on specific research questions, IBMs can be useful in complex (Grimm and Berger, 2016) and simplified (Grimm, 1999) forms. For additional complexity, our model could include geographic information system (GIS) files to explore effects of spatial aspects such as elevation, habitat fragmentation, and urbanization on wildlife populations. On the other hand, simplifying our model further could allow for a greater understanding of the underlying mechanisms of population abundance fluctuations or stability. As previously stated, wildlife researchers commonly collect field data for 1-3 years following a habitat disturbance, but are not able to collect long-term data. Our model could be calibrated with short-term field data and then simulated to predict future responses, as we did. Field data could then be collected years after the initial disturbance to validate such a model. Although we used our field data as part of model calibration, previous literature contains the majority of necessary parameter values for several species. Overall, our study suggests a different approach to relate habitat management to biodiversity conservation.

## Acknowledgements

We thank Weyerhaeuser Company and Catchlight Energy LLC, National Council for Air and Stream Improvement, Inc. for funding. Weyerhaeuser Company employees operated under a Statement of Work with CLE during this study. We also thank U.S. Environmental Protection Agency (EPA) for funding. This publication was developed under STAR Fellowship Assistance Agreement no. FP-91763501-0 awarded by the U.S. EPA. It has not been formally reviewed by EPA. The views expressed in this publication are solely those of the authors, and EPA does not endorse any products or commercial services mentioned in this publication. Additionally, we thank American Society of Mammalogists, North Carolina Academy of Science, and University of North Carolina at Greensboro for funding. We would also like to thank Dr. Steven Railsback and Dr. Steven Lytinen for sharing their knowledge of individual-based models.

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# Appendix A

## NetLogo Code

```
; The purpose of the model is to simulate population abundance and spatial distribution of
cotton rats in pine plantations intercropped with
; switchgrass based on field data and data from previous literature, for management
technique assessment.

; In current version, only female individuals are modelled.

; NOTE: The model design and code were adapted from Zakrzewski (2016) and Liu et al.
(2013). Specifically, we modified Zakrzewski (2016)'s Habitat-Based Models Building
Block:
; Territory Emergence for our territory submodel. We modified Liu et al. (2013)'s season,
reproduction, and CheckAgeandStatus submodels.

extensions [ r profiler csv ]

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

globals [
        year ; in which year the model is
        date ; 1~360
        month ; can exceed 12, ticks/30 + 1
        month-in-year ; 1 ~ 12
        calendar ; "Jan", "Feb", ..., "Dec"
        month-list ; [ Jan ~ Dec ]
        season ; "Spring", "Summer", "Autumn", "Winter"
        season-list ; [ "Spring" "Summer" "Autumn" "Winter" ]

        breeding-season-list ; [ 2~10 ]
        breeding-season? ; boolean, shows whether it is in breeding season or not
        spring-list ; [ 2 3 4 ]
        summer-list ; [ 5 6 7 ]
        autumn-list ; [ 8 9 10 ]
        winter-list ; [ 11 12 1 ]
  hrsizestest.csv
]
```

```
turtles-own [  ; ONLY FEMALE rats are modelled in this version
            age  ; state variable, units: in days

            my-range-patches  ; agentset: group of patches,
            HR-last-time ; last time that the rat has this group of patches as "my-range-
patches"
            HR-duration  ; time duration of how long my-range-patches can be stable

            max-life-span ; longevity
            checked? ; to facilitate counting, avoid duplicate counting in "counter-in-poor-
nest"
          ]

breed [ juveniles juvenile ] ; new born, not weaned, dependent on mother
breed [ subadults subadult ] ; weaned (independent) subadult, not sexually mature yet
breed [ adults adult ] ; sexually mature, able to reproduce
breed [ homeranges homerange ] ;; for territory visualisation

homeranges-own
[
  name
]

adults-own [
            litters-per-year ; max nr of litters each year
            litters-left ; number of litters remaining to be reproduced
            litter-size ; 1-3 based on our field data

            pregnant? ; boolean: whether pregnant or not
            pregnancy-counter ; state variable, count days of being pregnant, until giving
birth
                         ; after giving birth, enter the status of lactating
            pregnancy-duration ; time length of gestation

            lactating? ; boolean: whether in the state of lactating and taking care of the
juveniles
            lactation-counter ; state variable, count days of lactation,
                         ; if lactating is finished, they can get pregnant again
            lactation-duration  ; time length of lactation

            breed-start ; time to start first breeding, introduce variance in pop growth

            cover ; sum of habitat quality - considered vertical vegetation cover
            energy ;; sum of available resources hold by current territory
```

```
             territory ;; patch-set defining exclusive range
             enforcement ;; ability to win conflicts

              size-territory-before ;; territory size from step before
              size-territory-now ;; territory size from current step
              malnutrition
              predation

           ]

juveniles-own   [ wean-age
                predation
                mother
] ;  when it becomes independent subadults and leaves parental nest
subadults-own [
               mature-age  ; 2 months after birth when it becomes sexually mature adult

                predation
             ]

patches-own [
             habitat-type ; pine, mixed, grass
             habitat-quality ; cover

             owner ; 'who' of the turtle which owns the patch in its normal range at this time
step
                    ; but not necessarily visited and used, c.f. "todays-feeding-sites"
             resource ; food/grass

             cluster ;; the cluster of patches within the territory the patch belongs to
              ;  cluster-id ;; debug only, number assigned to patch within territory to
determine number of independend clusters

           ]

to setup
  clear-all
  reset-ticks

  ;; for evaluation purposes
  r:eval "library(adehabitatHR)"

  setup-season ; time scale
  setup-patches ; spatial scale
```

```
  create-adults starting-adults
  [setup-adults
  set age 80 + random 160
  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to go
  update-season ; time (day) & season
  update-patches ; Patch procedure, change crop height, farming disturbance, etc

  CheckAgeandStatus ; Turtle procedure
  update-territory
  adult-modify-territory
  reproduce ; adults only
; do-plots
 ;  if ( ticks > 10 ) [ calc-territory mark-territory ]
  ;  if all? individuals [energy >= housekeeping-demand] [ stop ]
  if (ticks > initial-phase)
  [
    check-for-malnutrition
    check-for-predation
  ]
 ; if (year = 1 and month = 6) [calc-territory]
  if (count turtles = 0) [ stop ] ;; all dead
  if (year = stop-year) [ stop ]
  tick

end


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


to setup-season ; the beginning date is 1st Jan
  set month 1
  set year 1
  set season ""
  set breeding-season? "No"
  set calendar ""
  set breeding-season-list [ 3 4 5 6 7 8 9 10 ] ;
```

```
  set spring-list [ 2 3 4 ]
  set summer-list [ 5 6 7 ]
  set autumn-list [ 8 9 10 ]
  set winter-list [ 11 12 1 ]
  set season-list [ "Spring" "Summer" "Autumn" "Winter" ]
  set month-list [ "Jan" "Feb" "March" "Apr" "May" "June"
                  "July" "Aug" "Sep" "Oct" "Nov" "Dec" ]
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;ALL the same/ homogeneous
landscape - NEED to unconstrain adults, update patches, and make smaller world: only
used for testing
;to setup-patches ; divide into 4 fields, with different rotation orders
;
;;; 1.5m*1.5m patch:
; ask patches with [
;
;    pxcor <= 29 and pycor <= 29
;      ]
;[
;    set habitat-type "grass"
;    set pcolor green
;    set habitat-quality  0.5
;    set resource  0.5
;    set owner nobody
;]
;
;end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;Random Heterogeneous landscape -
NEED to unconstrain adults, update patches, and make smaller world: only used for
testing
;to setup-patches ;
;
;;; 1.5m*1.5m patch:
; ask patches with [
;
;    pxcor <= 29 and pycor <= 29
;      ]
;[
;    set habitat-type "grass"
;    set habitat-quality random-float 1
;    set resource  random-float 1
;    set pcolor green - 2 * (habitat-quality + resource)
```

```
;    set owner nobody
;]
;
;end
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;to setup-patches ;  - NEED to unconstrain adults, update patches, and make smaller
world: only used for testing
;;
;;;; 1.5m*1.5m patch:
; ask patches with [            ; low food and cover
;
;    pxcor <= 9 and pycor <= 29
;
;  ] [
;    set pcolor brown
;    set habitat-quality random-float  0.5
;    set habitat-type "pine"
;    set resource random-float 0.5
;    set owner nobody
;  ]
;
;  ask patches with [            ; intermediate food and cover
;
;    pxcor > 9 and pxcor <= 19 and pycor <= 29
;
;  ] [
;    set pcolor orange
;    set habitat-quality 0.25 + random-float  0.5
;    set habitat-type "edge"
;    set resource 0.25 + random-float  0.5
;    set owner nobody
;  ]
;  ask patches with [            ; high food and cover
;
;    pxcor > 19 and pycor <= 29
;
;  ] [
;    set pcolor green
;    set habitat-quality 0.5 + random-float  0.5
;    set habitat-type "grass"
;    set resource 0.5 + random-float 0.5
;    set owner nobody
;  ]
```

```
;
;end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to setup-patches ; set up rows of grass, edge, and pine

;; 1.5m*1.5m patch:
 ask patches with [           ; setting up grass

    pxcor = 3 and pycor <= 199 or
    pxcor = 7 and pycor <= 199 or
    pxcor = 13 and pycor <= 199 or
    pxcor = 17 and pycor <= 199 or
    pxcor = 23 and pycor <= 199 or
    pxcor = 27 and pycor <= 199 or
    pxcor = 33 and pycor <= 199 or
    pxcor = 37 and pycor <= 199 or
    pxcor = 43 and pycor <= 199 or
    pxcor = 47 and pycor <= 199 or
    pxcor = 53 and pycor <= 199 or
    pxcor = 57 and pycor <= 199 or
    pxcor = 63 and pycor <= 199 or
    pxcor = 67 and pycor <= 199 or
    pxcor = 73 and pycor <= 199 or
    pxcor = 77 and pycor <= 199 or
    pxcor = 83 and pycor <= 199 or
    pxcor = 87 and pycor <= 199 or
    pxcor = 93 and pycor <= 199 or
    pxcor = 97 and pycor <= 199 or
    pxcor = 103 and pycor <= 199 or
    pxcor = 107 and pycor <= 199 or
    pxcor = 113 and pycor <= 199 or
    pxcor = 117 and pycor <= 199 or
    pxcor = 123 and pycor <= 199 or
    pxcor = 127 and pycor <= 199 or
    pxcor = 133 and pycor <= 199 or
    pxcor = 137 and pycor <= 199 or
    pxcor = 143 and pycor <= 199 or
    pxcor = 147 and pycor <= 199 or
    pxcor = 153 and pycor <= 199 or
    pxcor = 157 and pycor <= 199 or
    pxcor = 163 and pycor <= 199 or
    pxcor = 167 and pycor <= 199 or
```

```
    pxcor = 173 and pycor <= 199 or
    pxcor = 177 and pycor <= 199 or
    pxcor = 183 and pycor <= 199 or
    pxcor = 187 and pycor <= 199 or
    pxcor = 193 and pycor <= 199 or
    pxcor = 197 and pycor <= 199 or
    pxcor = 8 and pycor <= 199 or
    pxcor = 12 and pycor <= 199 or
    pxcor = 18 and pycor <= 199 or
    pxcor = 28 and pycor <= 199 or
    pxcor = 32 and pycor <= 199 or
    pxcor = 38 and pycor <= 199 or
    pxcor = 48 and pycor <= 199 or
    pxcor = 52 and pycor <= 199 or
    pxcor = 58 and pycor <= 199 or
    pxcor = 188 and pycor <= 199 or
    pxcor = 192 and pycor <= 199 or
    pxcor = 178 and pycor <= 199 or
    pxcor = 168 and pycor <= 199 or
    pxcor = 172 and pycor <= 199 or
    pxcor = 158 and pycor <= 199 or
    pxcor = 148 and pycor <= 199 or
    pxcor = 152 and pycor <= 199 or
    pxcor = 138 and pycor <= 199 or
    pxcor = 128 and pycor <= 199 or
    pxcor = 132 and pycor <= 199 or
    pxcor = 198 and pycor <= 199 or
    pxcor = 118 and pycor <= 199 or
    pxcor = 108 and pycor <= 199 or
    pxcor = 112 and pycor <= 199 or
    pxcor = 98 and pycor <= 199 or
    pxcor = 88 and pycor <= 199 or
    pxcor = 92 and pycor <= 199 or
    pxcor = 78 and pycor <= 199 or
    pxcor = 68 and pycor <= 199 or
    pxcor = 72 and pycor <= 199 or

     pxcor = 2 and pycor <= 199 or   ; originally grass and moved to edge for less grass, more cover scenario
     pxcor = 22 and pycor <= 199 or
     pxcor = 42 and pycor <= 199 or
     pxcor = 62 and pycor <= 199 or
     pxcor = 182 and pycor <= 199 or
     pxcor = 162 and pycor <= 199 or
```

```
     pxcor = 142 and pycor <= 199 or
     pxcor = 122 and pycor <= 199 or
     pxcor = 102 and pycor <= 199 or
     pxcor = 82 and pycor <= 199
      ]
[
    set habitat-type "grass"
    set pcolor green
    set habitat-quality random-float 0.5
    set resource 0.5 + random-float 0.5
    set owner nobody
]

ask patches with        ; set up edge
  [
    pxcor = 1 and pycor <= 199 or    ; Originally edge, but move to grass when testing for
more grass, less cover simulation
    pxcor = 21 and pycor <= 199 or
    pxcor = 41 and pycor <= 199 or
    pxcor = 61 and pycor <= 199 or
    pxcor = 81 and pycor <= 199 or
    pxcor = 101 and pycor <= 199 or
    pxcor = 121 and pycor <= 199 or
    pxcor = 141 and pycor <= 199 or
    pxcor = 161 and pycor <= 199 or
    pxcor = 181 and pycor <= 199 or

    pxcor = 11 and pycor <= 199 or
    pxcor = 31 and pycor <= 199 or
    pxcor = 51 and pycor <= 199 or
    pxcor = 71 and pycor <= 199 or
    pxcor = 91 and pycor <= 199 or
    pxcor = 111 and pycor <= 199 or
    pxcor = 131 and pycor <= 199 or
    pxcor = 151 and pycor <= 199 or
    pxcor = 171 and pycor <= 199 or
    pxcor = 191 and pycor <= 199 or

    pxcor = 6 and pycor <= 199 or
    pxcor = 16 and pycor <= 199 or
    pxcor = 26 and pycor <= 199 or
    pxcor = 36 and pycor <= 199 or
    pxcor = 46 and pycor <= 199 or
    pxcor = 56 and pycor <= 199 or
```

```
pxcor = 66 and pycor <= 199 or
pxcor = 76 and pycor <= 199 or
pxcor = 86 and pycor <= 199 or
pxcor = 96 and pycor <= 199 or
pxcor = 106 and pycor <= 199 or
pxcor = 116 and pycor <= 199 or
pxcor = 126 and pycor <= 199 or
pxcor = 136 and pycor <= 199 or
pxcor = 146 and pycor <= 199 or
pxcor = 156 and pycor <= 199 or
pxcor = 166 and pycor <= 199 or
pxcor = 176 and pycor <= 199 or
pxcor = 186 and pycor <= 199 or
pxcor = 196 and pycor <= 199 or

pxcor = 4 and pycor <= 199 or
pxcor = 9 and pycor <= 199 or
pxcor = 14 and pycor <= 199 or
pxcor = 19 and pycor <= 199 or
pxcor = 24 and pycor <= 199 or
pxcor = 29 and pycor <= 199 or
pxcor = 34 and pycor <= 199 or
pxcor = 39 and pycor <= 199 or
pxcor = 44 and pycor <= 199 or
pxcor = 49 and pycor <= 199 or
pxcor = 54 and pycor <= 199 or
pxcor = 59 and pycor <= 199 or
pxcor = 64 and pycor <= 199 or
pxcor = 69 and pycor <= 199 or
pxcor = 74 and pycor <= 199 or
pxcor = 79 and pycor <= 199 or
pxcor = 84 and pycor <= 199 or
pxcor = 89 and pycor <= 199 or
pxcor = 94 and pycor <= 199 or
pxcor = 99 and pycor <= 199 or
pxcor = 104 and pycor <= 199 or
pxcor = 109 and pycor <= 199 or
pxcor = 114 and pycor <= 199 or
pxcor = 119 and pycor <= 199 or
pxcor = 124 and pycor <= 199 or
pxcor = 129 and pycor <= 199 or
pxcor = 134 and pycor <= 199 or
pxcor = 139 and pycor <= 199 or
pxcor = 144 and pycor <= 199 or
```

```
    pxcor = 149 and pycor <= 199 or
    pxcor = 154 and pycor <= 199 or
    pxcor = 159 and pycor <= 199 or
    pxcor = 164 and pycor <= 199 or
    pxcor = 169 and pycor <= 199 or
    pxcor = 174 and pycor <= 199 or
    pxcor = 179 and pycor <= 199 or
    pxcor = 184 and pycor <= 199 or
    pxcor = 189 and pycor <= 199 or
    pxcor = 194 and pycor <= 199 or
    pxcor = 199 and pycor <= 199  ]

  [
    set habitat-type "edge"
    set habitat-quality 0.25 + random-float 0.5
    set pcolor orange
    set resource 0.25 + random-float 0.5
    set owner nobody
]

  ;; Create pines
  ask patches with [

    pxcor = 0 and pycor <= 199 or
    pxcor = 5 and pycor <= 199 or
    pxcor = 10 and pycor <= 199 or
    pxcor = 15 and pycor <= 199 or
    pxcor = 20 and pycor <= 199 or
    pxcor = 25 and pycor <= 199 or
    pxcor = 30 and pycor <= 199 or
    pxcor = 35 and pycor <= 199 or
    pxcor = 40 and pycor <= 199 or
    pxcor = 45 and pycor <= 199 or
    pxcor = 50 and pycor <= 199 or
    pxcor = 55 and pycor <= 199 or
    pxcor = 60 and pycor <= 199 or
    pxcor = 65 and pycor <= 199 or
    pxcor = 70 and pycor <= 199 or
    pxcor = 75 and pycor <= 199 or
    pxcor = 80 and pycor <= 199 or
    pxcor = 85 and pycor <= 199 or
    pxcor = 90 and pycor <= 199 or
    pxcor = 95 and pycor <= 199 or
    pxcor = 100 and pycor <= 199 or
```

```
  pxcor = 105 and pycor <= 199 or
  pxcor = 110 and pycor <= 199 or
  pxcor = 115 and pycor <= 199 or
  pxcor = 120 and pycor <= 199 or
  pxcor = 125 and pycor <= 199 or
  pxcor = 130 and pycor <= 199 or
  pxcor = 135 and pycor <= 199 or
  pxcor = 140 and pycor <= 199 or
  pxcor = 145 and pycor <= 199 or
  pxcor = 150 and pycor <= 199 or
  pxcor = 155 and pycor <= 199 or
  pxcor = 160 and pycor <= 199 or
  pxcor = 165 and pycor <= 199 or
  pxcor = 170 and pycor <= 199 or
  pxcor = 175 and pycor <= 199 or
  pxcor = 180 and pycor <= 199 or
  pxcor = 185 and pycor <= 199 or
  pxcor = 190 and pycor <= 199 or
  pxcor = 195 and pycor <= 199
] [
  set pcolor brown
  set habitat-quality 0.5 + random-float  0.25
  set habitat-type "pine"
  set resource random-float 0.5
  set owner nobody
]

ask patches with [
  pxcor = 54 and pycor = 54 ]
 [
  set pcolor black ]

  ask patches with [
  pxcor = 54 and pycor = 146 ]
 [
set pcolor black
]
    ask patches with [
   pxcor = 146 and pycor = 54 ]
 [
set pcolor black
]
  ask patches with [
   pxcor = 146 and pycor = 146 ]
```

```
   [
  set pcolor black
   ]
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to setup-adults

   set color one-of remove green base-colors + random 3 + 1 ;; random color to better
distinguish territories
   setxy 54 + random-float 92 54 + random-float 92

   move-to patch-here uphill resource ;; moves to center of current patch and then to
neighboring patch with highest resource abundancy
   set owner self ;; and claim land

   set territory patch-set patch-here

   set enforcement random-float 1
   set malnutrition 0

   set shape "default" ; turtle shape
   set size 4  ; ajusted to world size
   set max-life-span 360 ; 1 year

   set litters-per-year 3 ; max, actual nr dependent on individual situation
   set litters-left litters-per-year
   set litter-size one-of [1 2 3] ; baseline, also in "to give-birth"; halved because only
modeling female rats

   set pregnancy-duration 27
   set lactation-duration 21
   set pregnant? false
   set lactating? false

   set breed-start 80 + random 10  ; to provide some variation of when a female starts
breeding
                              ; some can breed as early as 60 days in nature, but for simplicity of
adults we set to 80 up to 90 days
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
```

```
to setup-juveniles
    set age 1
   ; create-links-with adults-here [hide-link]
    set mother myself ; myself is the calling turtle, i.e. the turtle giving birth
    set color who * 10 + 3

    set size 4.5 ; enlarge the size otherwise covered by adults (default shape) and not visible
    set wean-age 22
    set shape "dot" ; dot shape means "don't move"
    set predation random (allowed-risk * 1.2)  ; Maximum 0.2 probability of predation based on survival estimates in Conner et al. 2011
  ; 0.25 probability of predation as juvenile in addition to death if mother dies - need to change if allowed-risk is changed

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to update-season
  set month ceiling ( ticks / 30 )
; need to add parenthesis, otherwise calculate as (ceiling ticks)/30
  set year ceiling ( ticks / 360 ) ; assume each year 360 days
  ifelse remainder month 12 = 0
  [ set month-in-year 12 ]
  [ set month-in-year remainder month 12 ]
; (remainder month 12) returns 0~11, need to transform 0 to 12

  ifelse remainder ticks 360 = 0 ; no need to setup initial value as 0, because the default at setup stage is 0 already
  [ set date 360 ]
  [ set date remainder ticks 360 ]


  set calendar item ( month-in-year - 1 ) month-list ; item index start counting from 0
  ifelse member? month-in-year breeding-season-list ; whether the month belongs to the breeding-season-list
  [ set breeding-season? "Yes" ]
  [ set breeding-season? "No"  ]

  ifelse member? month-in-year spring-list
  [ set season "Spring" ]
  [
    ifelse member? month-in-year summer-list
```

```
    [ set season "Summer" ]
    [
      ifelse member? month-in-year autumn-list
      [ set season "Autumn" ]
      [ set season "Winter" ]
    ]
  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to update-patches

if year <= 7 [               ; to allow grass to grow throughout the summer months
  if month <= 6 and date = 30 or date = 60 or date = 90 or date = 120 or date = 150 or date
= 180 or date = 210 or date = 240 or date = 270 or date = 300 or date = 330 or date = 360
  [
    ask patches
    [
      if habitat-type = "grass"
      [set habitat-quality random-float 0.5 ]
    ]
  ]]

  if year <= 7 [
   if month = 7 and date = 30 or date = 60 or date = 90 or date = 120 or date = 150 or date
= 180 or date = 210 or date = 240 or date = 270 or date = 300 or date = 330 or date = 360
  [
    ask patches
    [
      if habitat-type = "grass"
      [set habitat-quality 0.5 + random-float 0.25 ]
    ]
  ]]

  if year <= 7 [
   if month = 8 and date = 30 or date = 60 or date = 90 or date = 120 or date = 150 or date
= 180 or date = 210 or date = 240 or date = 270 or date = 300 or date = 330 or date = 360
  [
    ask patches
    [
      if habitat-type = "grass"
      [set habitat-quality 0.5 + random-float 0.5 ]
```

```
    ]
  ]]
if year <= 7 [
    if month >= 9 and date = 30 or date = 60 or date = 90 or date = 120 or date = 150 or
date = 180 or date = 210 or date = 240 or date = 270 or date = 300 or date = 330 or date =
360
                              ; grass harvested in early fall and will remain low to the ground
throughout the winter months
  [
    ask patches
    [
      if habitat-type = "grass"
      [set habitat-quality 0.2 + random-float 0.3 ]
    ]
  ]]

  if year = 8 and date = 360    ; by year 8, pine trees will begin to shade out the grass,
descreasing grass amount - leading to less food and less cover
  [
    ask patches
    [
      if habitat-type = "grass"
      [set resource 0.5 + random-float 0.2
      set habitat-quality 0.3 + random-float 0.2
      ]
    ]
  ]

  if year = 9 and date = 360
  [
    ask patches
    [
      if habitat-type = "grass"
      [set resource 0.4 + random-float 0.2
      set habitat-quality 0.25 + random-float 0.5
      ]
    ]
  ]

  if year >= 10 and date = 360
  [
    ask patches
    [
      if habitat-type = "grass"
```

```
    [set resource random-float 0.5
    set habitat-quality 0.25 + random-float 0.5
    ]
   ]
  ]

  if year = 1 and date = 1 ; pine trees on the plots are continuously growing so cover will increase throughout the years. Natural succession
  [
   ask patches
   [if habitat-type = "pine"
    [set habitat-quality 0.5 + random-float 0.25 ]
   ]
  ]

  if year = 2 and date = 1
  [
   ask patches
   [if habitat-type = "pine"
    [set habitat-quality 0.5 + random-float 0.3 ]
   ]
  ]

  if year = 3 and date = 1
  [
   ask patches
   [if habitat-type = "pine"
    [set habitat-quality 0.5 + random-float 0.35 ]
   ]
  ]

  if year = 4 and date = 1
  [
   ask patches
   [if habitat-type = "pine"
    [set habitat-quality 0.5 + random-float 0.4 ]
   ]
  ]

   if year = 5 and date = 1
  [
   ask patches
   [if habitat-type = "pine"
    [set habitat-quality 0.5 + random-float 0.45 ]
```

```
    ]
   ]

    if year = 6 and date = 1
   [
     ask patches
     [if habitat-type = "pine"
       [set habitat-quality 0.5 + random-float 0.5 ]
     ]
   ]

    if year >= 7 and date = 1 ; Change in cover from year 7 to year 10 will be minimal to
perspective of rats on plots - mainly growing tall now.
   [
     ask patches
     [if habitat-type = "pine"
       [set habitat-quality 0.5 + random-float 0.5 ]
     ]
   ]

   ask patches with [                    ; setting edge of trapping grid for comparison purpose
     pxcor = 54 and pycor = 54 ]
    [
     set pcolor black ]

     ask patches with [
     pxcor = 54 and pycor = 146 ]
    [
   set pcolor black
   ]
       ask patches with [
      pxcor = 146 and pycor = 54 ]
    [
   set pcolor black
   ]
     ask patches with [
      pxcor = 146 and pycor = 146 ]
    [
   set pcolor black
     ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
```

```
to CheckAgeandStatus
 ask turtles
 [
  set age age + 1
  if age = max-life-span ; once reaches longevity, die

  [
     ask juveniles with [mother = myself] [ die ] ; myself is the turtles asking the juveniles to do something
    die
  ]
;     set counter-too-old counter-too-old + 1

 ]

 if date = 1
 [
  ask adults
  [
    set litters-left litters-per-year ; each year can reproduce max 3 litters, start new counting (reset) at the beginning of each year
    set breed-start 80 + random 10  ; will need to change if change breeding season
  ]
 ]

 ask juveniles
 [
  ; if mother = myself [ die ] ; myself is the turtles asking the juveniles to do something

  if age = wean-age ; develop into subadults
  [
    set breed subadults
    set predation random-float (allowed-risk * 1.2) ; to give a 0.2 probability of predation as subadult. Same as juvenile because can move to avoid predation but also could emigrate
    set size 4
    set shape "triangle 2" ; slightly different shape with adults to distinguish
    set mature-age 80 ; trigger the change of breed to adults

    SET HR-last-time TICKS ; so newly weaned juv can be called in "to define-normal-range"
    SET HR-duration 0
  ]
 ]
```

```
ask subadults
  [
    if age = mature-age ; develop into adults
    [
;      set counter-juv-to-ad counter-juv-to-ad + 1
      set breed adults
      setup-adults
      set predation 0
      set breed-start 80 + random 10  ; will need to change if change breeding season
    ]

  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;;;TERRITORY
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to update-territory ;; observer procedure - updates territory statistics

  ask adults
  [
    ;; find and remove fragmented (e.g. unconnected4) territory structure
    find-clusters
    remove-clusters
  ]
  ask adults
  [
    set size-territory-now count territory

    set energy sum [resource] of territory ;; update of available resources

    if (energy = 0) [die] ;; no territory, no energy, no life

    set cover sum [habitat-quality] of territory ;; update of available cover

    move-to one-of territory ;; to be still inside the own territory
  ]
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to adult-modify-territory ;; observer procecure
```

```
ask adults
  [
    set size-territory-before count territory

    if(energy <= (housekeeping-demand * 2))

    [ ;; if smaller grow range

      grow-territory
      ]

     if(cover <= (pred-avoidance * 2))

    [ ;; if smaller grow range

      grow-territory
      ]

    if (count territory >= 3969)   ; 63 (1.5mx1.5m) patches since our max territory in
intercrop was 8942.19269 meters squared
    [ ;; if greater shrink range
      shrink-territory
    ]

  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to grow-territory ;; individuals procedure

  let expander self

  let neighborline no-patches ;; will be the patches next to my territory
  let enclosed no-patches ;; fill possible holes in territory
                          ;  let pot-comp no-patches ;; possible extension pattern

  set neighborline edge-patches territory false ;; calls 'edge-patches' of the current
territory, 'false' to return outer edge - e.g. not part of own territory

  ask territory ;; to include further patches in the consideration
  [
```

```
    set enclosed (patch-set enclosed neighbors with [count neighbors4 with [owner = expander] = 4] ) ;; patch-set that holds fully by territory enclosed patches, e.g. all neighbors4 of patch are part of territory

;   set pot-comp (patch-set pot-comp neighborline with [owner != nobody and [status] of owner < my-status]) ;; possible extension pattern
  ]


  let target check-competition neighborline enforcement ;; calls 'check-competition' with outer-edge patches of territory and own 'enforcement' for possible interactions to find a target for expansion

  set territory (patch-set territory target enclosed) ;; combine new patches and former territory

  ask territory
  [
    update-patch-status false expander ;; 'false' because no release and expander as new owner
  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to shrink-territory ;; individuals procedure

  let droppables edge-patches territory true ;; uses edge-patches procedure to subset possible patches for release, 'true' for inner edge e.g. part of territory

  let tobedropped min-one-of droppables [resource + habitat-quality] ;; selects one of possible patches with minimum resource availability

  if (tobedropped != nobody) ;; (catches expections)
  [
    set territory (patch-set territory with [self != tobedropped]) ;; removes patch from territory

    ask tobedropped ;; updates patch attributes
    [
      update-patch-status true nobody ;; 'true' to release patch from own influence
    ]
  ]
```

```
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


;;;;;;;;;;;;;;;;;;;;;;;;;
;;; cluster legal note ;;;
;;;;;;;;;;;;;;;;;
;;; To the extent possible under law, Uri Wilensky has waived
;;; copyright and related or neighboring rights to the cluster idea.
;;; Opened out by Neil Carter et al. (2015) and further extended.
;;;;;;;;;;;;;;;;;;;;;;;;;

to find-clusters ;; individuals procedure

  ask territory [ set cluster nobody ] ;; start fresh each tick

  loop
  [
    ;; pick a random patch of territory that isn't in a cluster yet
    let seed one-of territory with [(cluster = nobody)]
                                          ;; if we can't find one, then we're done!
    if (seed = nobody)
    [
      ;      mark-clusters ;; only if debugging
      stop
    ]
    ;; otherwise, make the patch the "leader" of a new cluster
    ;; by assigning itself to its own cluster, then call
    ;; grow-cluster to find the rest of the cluster
    ask seed
    [
      set cluster self
      grow-cluster
    ]
  ]

end

to grow-cluster  ;; patch procedure

  ask neighbors4 with [(cluster = nobody) and (owner = [owner] of myself)] ;; neighbors4
to have territories not too stretched out
  [
```

```
    set cluster [cluster] of myself ;;
    grow-cluster ;; recursion to get all patches
  ]

end

to remove-clusters ;; adults procedure

                   ; determine how many different clusters my territory has:
  let clusters-in-my-territory no-patches
  ask territory
  [
    if not member? cluster clusters-in-my-territory ;; all patches in same cluster have their
former seed 'patch name' set as their cluster variable (see grow-cluster)
    [
      set clusters-in-my-territory (patch-set clusters-in-my-territory cluster) ;; if cluster
representative is not yet accounted in territory cluster-list, add it
    ]
  ]

  if count clusters-in-my-territory = 1 [ stop ] ;; nothing to remove

                                                  ;; determine largest cluster:
  let biggest-cluster nobody
  let nmax 0 ;; marks the maximum number of patches in cluster, gets increased when
bigger cluster is found
  ask clusters-in-my-territory
  [
;    let n count patches with [ cluster = [cluster] of myself ]  ;; counts number of patches
with same cluster variable as representative ('myself' is one of 'clusters-in-my-territory') ;;
chooses the cluster of biggest spatial extend
    let n sum [resource + habitat-quality] of patches with [ cluster = [cluster] of myself ]

    if n > nmax ;; if current cluster is bigger than the former maximum, update biggest-
cluster and new maxium patch per cluster count ('nmax')
    [
      set biggest-cluster self
      set nmax n
    ]
  ]

  ;; remove all but the biggest cluster:
  ask territory
  [
```

```
    if cluster != biggest-cluster
    [
      update-patch-status true nobody ;; 'true' to release patch from own influence
    ]
  ]

  set territory territory with [owner = myself] ;; update of remaining territory

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;; debug, uncomment to verify found clusters                              ;;
;; once all the clusters have been found, this is called                  ;;
;; to put numeric labels on them so the user can see                      ;;
;; that the clusters were identified correctly                           ;;
;to mark-clusters ;; patch procedure                                     ;;
;                                                     ;;
;  ask patches [ set plabel ""] ;; start fresh                           ;;
;  let counter 0 ;; amount of clusters in territory                        ;;
;  loop                                                  ;;
;  [ ;; pick a random patch we haven't labeled yet                        ;;
;    let p one-of territory with [(cluster-id = "") and (cluster != nobody)]      ;;
;    if (p = nobody)                                        ;;
;      [ stop ]                                          ;;
;    ;; give all patches in the chosen patch's cluster the same label            ;;
;    ask p                                               ;;
;    [                                                    ;;
;      ask patches with [(cluster = [cluster] of myself) and (owner != nobody)]   ;;
;      [                                                  ;;
;        set cluster-id counter                                ;;
;        set plabel cluster-id                                ;;
;      ]                                                  ;;
;    ]                                                    ;;
;    set counter counter + 1                                  ;;
;  ]                                                      ;;
;                                                         ;;
;end                                                       ;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;;;;;;;;;;;;;
;;; cluster end ;;;
;;;;;;;;;;;;;;;;;;;
```

```
to remove-artefacts ;; when graphics? has not been activated before to update visualization

  if-else (graphics?)
  [ ;; show home ranges
    ask patches with [owner != nobody] [ set pcolor [color] of owner]
    ask patches with [owner = nobody]  [if habitat-type = "grass"[set pcolor green ]]
    ask patches with [owner = nobody]   [if habitat-type = "edge"[set pcolor orange ]]
    ask patches with [owner = nobody]   [if habitat-type = "pine"[set pcolor brown ]]
;;;;;;;;UNCOMMENT to visualize current territories only - slows model
    hide-link
  ]
  [ ;; hide home ranges
  ;  ask patches [ set pcolor scale-color green resource 0 10 ]
    hide-link
  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to update-patch-status [ release? newowner ] ;; patch procedure

  if-else (release?)
  [ ;; remove ownerships
    set owner nobody

    ask patches with [owner = nobody]  [if habitat-type = "grass"[set pcolor green ]]
    ask patches with [owner = nobody]   [if habitat-type = "edge"[set pcolor orange ]]
    ask patches with [owner = nobody]   [if habitat-type = "pine"[set pcolor brown ]]
;;;;;;;;UNCOMMENT to visualize current territories only - slows model
;    ;    set cluster-id "" ;; uncomment if debugging

  if (graphics?) [ set pcolor scale-color green resource 0 10 ]

  ]
  [ ;; assign ownerships
    set owner newowner

   if (graphics?) [ set pcolor [color - 0.5] of newowner ]
  ]

end
```

```
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to-report edge-patches [ TERR inner? ] ;; individuals procedure, reports inner/outer
territory edge as seen on http://stackoverflow.com/questions/25412725/netlogo-selecting-
edge-patches-of-patch-set for inner line

    if-else (inner?)
  [ ;; inner edge of territory
    report TERR with [ ;; only reports territory patches
      any? neighbors4 with [ ;; that have neighbors4
        owner != [ owner ] of myself ;; which have a different owner than myself
      ]
    ]
  ]
  [ ;; outer edge
    let caller self ;; needed to be temporarily stored for comparision
    report patch-set [neighbors4 with [owner != caller] ] of TERR ;; returns a patch-set
(otherwise list of patch-sets) of neighbors4 of the HR which have a different owner than
the calling individuals
  ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to-report check-competition [ possiblepatches own-enforcement ] ;; adults procedure,
checks input for competition and returns target

  let restpatches no-patches ;; for possible recursion
  let target max-one-of possiblepatches [habitat-quality + resource] ;; chooses one-of
neighboring patches with highest resource abundance

  if-else (target != nobody)
  [
    ask target
    [
      if (owner != nobody) ;; check target for competition, if = competition, else =
acqusition
      [
        let other-enforcement [enforcement] of owner


        ;;;
        ;;;; when an invader tries to gain power over an enemy territory cell it needs to
overcome the home ground advantage
```

```
        ;;;
        let invasion-probability random-float 1 ;; is the invader successful?
        let homeground-advantage 0.5 ;; invaders need to have luck even though they are
stronger

        if-else (own-enforcement >= other-enforcement AND invasion-probability >
homeground-advantage) ;; check who is more persuasive, if = expander, else = defender
        [
          ask owner ;; former owner
          [
            set territory territory with [self != target] ;; remove current target from displaced
owner
          ]
        ] ;; endif current expander is stronger
        [
          ;; recursion with remaining patches from neighborline, IDEA: could be connected
with counter to allow only a limited number of tries
          set restpatches possiblepatches with [self != target]
        ] ;; endelse current expander is weaker
      ] ;; endif competition
    ]
  ] ;; endif there is a target
  [
    report nobody
  ] ;; endelse no patch left to report

  ;; check if target has not turned out as possible expansion option, true = recursion, false
= we have a winner
  if-else (restpatches != no-patches)
  [
    ;type who print "recursion" debugging, reports the ID of the adults that needs to find
another target because of competition - the amount of calls shows recursion runs
    report check-competition restpatches own-enforcement
  ] ;; endif recursion with less patches
  [
    report target
  ] ;; endelse expansion into target

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;; homerange calculation ;;;
```

```
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;; seen on and adjusted  ;;;;;;;;;;;
;;; http://r-ext.sourceforge.net/ ;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to calc-territory
  ;; load R package adehabitat - already in setup-procedure
  ; r:eval "library(adehabitatHR)"

  ;; create an empty data-frame
  r:eval "individuals <- data.frame()"

  ;; merge the Name-, X- and Y-lists of all animals to one data-frame
  ask adults
  [
    let XY [list pxcor pycor] of territory ; Creates a list of XY pairs
    let X map [ [?1] -> (item 0 ?1) ] XY           ; Extracts the X coordinates
    let Y map [ [?1] -> (item 1 ?1) ] XY           ; Extracts the Y coordinates

    (r:putdataframe "individual" "X" X "Y" Y)
    r:eval (word "individual <- data.frame(individual, Name = '" who "')")
    r:eval "individuals <- rbind(individuals, individual)"
  ]

  ;; split the data-frame into coordinates and factor variable
  r:eval "xy <- individuals[c('X','Y')]"
  r:eval "id <- individuals$Name"

  ; create SpatialPointsDataFrame
  r:eval "spdf <- SpatialPointsDataFrame(individuals[1:2], individuals[3])"
  r:eval (word "homerange <- mcp(spdf, percent = "mcp-percentage", unin = c('m'), unout
= c('m2'))")
  r:eval "hr.sizes <- as.data.frame(homerange)"
 ; r:eval "write.csv(hr.sizes, hrsizestest.csv)"
; r:eval (word "write.csv(hr.sizes, 'hr_sizes.csv')")
;observer> export-world (word "hr.sizes" random-float 1.0 ".csv") ; gave patch info, but
no MCP data

  ;;calculate homerange
;  r:eval "homerange <- mcp(xy, id)"

end
to mark-territory
```

```
 clear-drawing

 ask adults
 [
   pen-up

   ;; get the points of the homerange polygon for the current animal
   r:eval (word "temp <- slot(homerange,'polygons')[[which(slot(homerange,'data')$id ==
"who")]]@Polygons[[1]]@coords")

   let tempX r:get "temp[,1]"
   let tempY r:get "temp[,2]"

   let tempXY (map [ [?1 ?2] -> list ?1 ?2 ] tempX tempY)



   hatch-homeranges 1
   [
     hide-turtle
     set name [who] of myself
     set color [color] of myself
   ]

   ; draw the homerange boundary
   foreach tempXY
   [ [?1] ->
     ask homeranges with [name = [who] of myself]
     [
       move-to patch (item 0 ?1) (item 1 ?1)
       set pen-size 2
       pen-down
     ]
   ]

   ; connect the last point of the homerange with the first one, to close the polygon
   ask homeranges with [name = [who] of myself]
   [
     let lastpoint first tempXY
     move-to patch (item 0 lastpoint) (item 1 lastpoint)
     pen-up
   ]

   ask homeranges [ die ] ;; clean up
```

```
]

end
;;;;;;;;;;;;;;;;;;;;;;
;;; end homerange ;;;
;;;;;;;;;;;;;;;;;;;;;;

to reproduce

  if breeding-season? = "Yes"
  [
    ask adults
    [
      ifelse not pregnant?
      [
        ifelse not lactating?
        [
          if litters-left > 0 and energy > (housekeeping-demand * 1.5)
          [
              if age > breed-start and date < 255
; NOTE this date has to be changed if breeding season is changed
; in order for a mouse to finish pregnancy (27d) and lactation (21d),
; the last pregnancy should be before August 15 if breeding season ends on Sept 30.
              [
                set pregnant? true
                set pregnancy-counter 0
              ]

          ]
        ]
        [ lactate ]
      ]
      [ give-birth ] ; here assume no abortion
    ]
  ]

end
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
to give-birth

    ifelse pregnancy-counter = pregnancy-duration
    [
      set litter-size one-of [1 2 3]              ; in all months: baseline
```

```
      hatch litter-size
      [
        set breed juveniles
        setup-juveniles
      ]

;       set counter-new-born counter-new-born + litter-size

       set pregnant? false ; after giving birth, not in 'pregnant' state
       set lactating? true ; start lactating
       set lactation-counter 1
       set litters-left litters-left - 1
    ]
    [ set pregnancy-counter pregnancy-counter + 1 ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to lactate

    ifelse lactation-counter = lactation-duration
    [
      set lactating? false
    ] ; stop lactation
    [ set lactation-counter lactation-counter + 1 ]

end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to check-for-malnutrition

 ask adults
  [
    if (age > 140 AND energy < housekeeping-demand)
    [
        set malnutrition malnutrition + 1
    ]
     if (age > 140 AND energy > housekeeping-demand)
      [
        set malnutrition 0
      ]
        if (malnutrition > allowed-malnutrition)
```

```
       [
         ask territory [ update-patch-status true nobody ]
         ask juveniles with [mother = myself] [ die ] ; myself is the turtles asking the juveniles to do something

         die
           ]
  ]


end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to check-for-predation

 ask juveniles
  [if (predation > allowed-risk)
      [
        die
  ]]

 ask subadults
  [if (predation > allowed-risk)
      [
        die
  ]]

;   ask adults
;  [
;    if (age < 120 AND cover < (pred-avoidance / 2))
;    [
;   set predation predation + 1
;]
; if (predation > allowed-risk)
;      [
;         die
;  ]]
;

    ask adults
  [
    if (age > 140 AND cover < pred-avoidance)
    [
```

```
    set predation predation + 1
  ]
  if (age > 140 AND cover > pred-avoidance)
   [
    set predation 0
   ]
  if (predation > allowed-risk)
   [
     ask territory [ update-patch-status true nobody ]
     ask juveniles with [mother = myself] [ die ] ; myself is the turtles asking the juveniles to do something
     die
    ]
 ]
end

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
```

# Appendix B

## TRACE Document

This is a TRACE document ("TRAnsparent and Comprehensive model Evaludation") which provides supporting evidence that our model presented in:

> **Larsen, A.L., Grimm, V., Homyack, J.A., Wigley, T.B., Miller, D.A., Kalcounis-Rueppell, M.C. In prep. An Individual-Based Model of Hispid Cotton Rat Response to Habitat Variables in a Biofuel Feedstock Production System.**

was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:

> Schmolke A, Thorbek P, DeAngelis DL, Grimm V. 2010. Ecological modelling supporting environmental decision making: a strategy for the future. *Trends in Ecology and Evolution* 25: 479-486.

and uses the updated standard terminology and document structure in:

> Grimm V, Augusiak J, Focks A, Frank B, Gabsi F, Johnston ASA, Liu C, Martin BT, Meli M, Radchuk V, Thorbek P, Railsback SF. 2014. Towards better modelling and decision support: documenting model development, testing, and analysis using TRACE. *Ecological Modelling* 280:129-139.

and

> Augusiak J, Van den Brink PJ, Grimm V. 2014. Merging validation and evaluation of ecological models to 'evaludation': a review of terminology and a practical approach. *Ecological Modelling* 280:117-128.

## 1 Problem formulation

**This TRACE element provides supporting information on**: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.

**Summary:**

> **Population dynamics depend on individuals' interactions with their environment and other individuals. When understory habitat characteristics are altered, individual rodents can respond differently and therefore impact population dynamics. Furthermore, population level changes can affect the rodent community structure. The hispid cotton rat is used as a model species because it is a dominant, grassland specialist in our own field data and has been intensively studied. Therefore, adequate data exists in the literature to inform components of the individual-based model that our data could not.**

The model is designed to estimate the effects of planting switchgrass in loblolly pine plantations on rodent population dynamics over 10 years. Our previous research has shown that switchgrass-pine plots have intermediate cotton rat adult abundance, juvenile recruitment, and foraging levels and intermediate rodent diversity compared to switchgrass monocrop and pine only (control) plots during the first three years of management (Larsen et al., 2016, In prep). We measured 4 replicates of 10-ha switchgrass-pine plots for 3 consecutive summers. The switchgrass-pine can be effectively managed for about 10 years before the pine trees grow tall enough to shade the grass to the point it will not be economical to harvest. Although our current model's form is specific to our switchgrass-pine system, our model could be adjusted to other prey species with similar behaviors driven by food and cover. Therefore, stakeholders include wildlife biologists, forest managers, and animal behaviorists. Our specific questions are: 1) Do cotton rat populations persist in switchgrass-pine plots with predicted grass versus non-grass vegetation cover for 10 years after pine stand establishment? and 2) How do different levels of vegetation cover (grass and non-grass) effect cotton rat populations? We use adult abundance and juvenile abundance, as a recruitment index, as model outputs to answer our questions. Grass in our model is food for cotton rats, providing needed energy to survive and reproduce. Pine trees and other naturally occurring vegetation is considered non-grass cover, which is necessary to reduce predation risk for cotton rats. We use previous research (King et al., 2014) to validate our model at year 7. However, no data exists for years 4-6 and 8-10, so our model should not be used to assess yearly variation. We also do not input any climate data so we do not account for natural yearly variation due to weather, precipitation, etc. Extrapolation to a larger spatial scale is possible with data on cotton rat responses to a larger scale to ensure calibration and validation are possible. Future applications of the model will include simulating other management techniques that affect the amount of food and cover on population dynamics of prey species.

## 2 Model description

**This TRACE element provides supporting information on**: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

**Summary:**

**We present the model description in the ODD format as found in Larsen et al. (in prep).**

We followed the ODD (Overview, Design concepts, Details) protocol to describe our model below (Grimm et al. 2006, 2010). See Figure A.1 for a broad overview of the model. We implemented the model in NetLogo 6.0.1 (Wilensky 1999; program code in Appendix A).

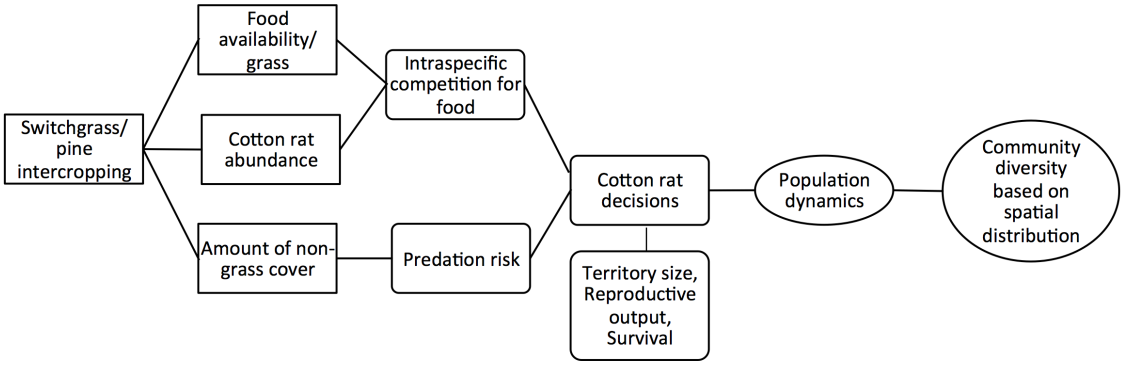


Figure A.1. Broad Overview of the Conceptual Model. We set components in the left hard-edged rectangles as initial parameters. Both grass and non-grass cover were updated throughout our 10-year simulation to represent natural succession and annual switchgrass mowing. Components in the middle soft edged rectangles were parts of our model to allow cotton rat decisions to emerge. Components in the right circles were direct (population dynamics) and indirect (community diversity based on spatial distribution) outputs from our model.

*Purpose*

The purpose of our model is to simulate cotton rat population abundance and spatial distribution in switchgrass-pine plots based on field data and data from previous literature, for management technique assessment. Our model is used to predict how cotton rat populations respond in future management years and under different management scenarios.

*Entities, state variables, and scales*

Our model entities are habitat patches to make up the landscape, and female cotton rats (Table A.1). Each habitat patch is 1.5 m x 1.5 m and defined as pine, edge (mix of woody and herbaceous vegetation), or grass. Our model world is 300 m x 300 m for a total of 9 ha, which is large enough to buffer cotton rat movement around the 1.96 ha trapping grid area (Larsen et al., 2016). Our model does not allow simulated individuals to leave one boundary and enter back into the landscape from the opposite boundary. We contain our simulated rats to the interior 1.96 ha area of our world to best represent our sampled trapping grid area. We only consider female cotton rats in our model because: 1) cotton rats are promiscuous, so reproduction is mainly limited by the number of females, not males (Liu et al., 2013) and 2) our previous studies only obtained female behavior data, not male behavior (Larsen et al., 2016). Each time step in our model is one day.

Table A.1. State Variables for Habitat Patches and Cotton Rats. A brief explanation of each variable, possible values, and units where necessary are included.

| | Variables | Explanation | Possible Values | Units |
|---|---|---|---|---|
| **Habitat Cell** | location | x and y coordinate | | |
| | habitat type | pine, edge/mixed, grass | | |
| | habitat quality | amount of cover | (pine>edge>grass) | % |
| | resource | amount of food | (pine<edge<grass) | % |
| | owner | rat(s) that own patch as part of territory | | |
| **Rat** | ID | # | | |
| | age | juveniles – not sexually mature and remains at nest | juveniles - 1-21 (Meyer and Meyer, 1944) | days |
| | | subadults – dispersing/establishing a territory | subadults - 22-80 (Clark, 1972) | |
| | | adults – reproductive and established territory | adults - 81-360 (max lifespan is 360) (Clark, 1972; Larsen et al., 2016) | |
| | territory | set of habitat cells | Range of patches will be based on our territory data (Larsen et al., In prep) | |
| | | enforcement | Territory program from Zakrzewski (2016) | |
| | reproductive traits | Breeding season | February-October | |
| | | pregnant or not | gestation - 27<br>Needs 1.5 times amount of base energy in territory to reproduce (Clark, 1972; Randolph et al., 1977) | days |
| | | lactating or not | | days |

| | | |
|---|---|---|
| | | lactating - 21 (Meyer and Meyer, 1944) |
| | litter size | random number in range of 1-3; only modeling females so halved 1-7 (Cameron, 1977; Larsen et al., In prep; Meyer and Meyer, 1944) |
| | litters per year | random number in range of 1-3 (Cameron, 1977; Larsen et al., In prep; Meyer and Meyer, 1944) |
| survival | malnutrition | Driven by energy needed vs. energy obtained in territory (Inversely calibrated) |
| | predation | Driven by cover needed vs. cover obtained in territory (Inversely calibrated) |
| | juvenile and subadult | Minimum 0.80 probability (based on adult survival in control plots of Conner et al. (2011); and inversely calibrated) |

*Process overview and scheduling*

Every time step goes through the process outlined in Figure A.2 and in the following. Each submodel is underlined in the description below. State variables update immediately after each action and entities perform actions in a randomized sequence each time step. Update Patches and Update Breeding Season: Habitat patches and time steps are updated first to allow subsequent submodels to respond to updated settings. Habitat quality (cover) is updated to represent cut grass from fall to spring with growing grass throughout summer months. Furthermore, habitat quality (cover) increases throughout the years in pine patches to represent pine trees continuously growing and shading out grass, reducing resources (food; Jose et al., 2009). Furthermore, for each habitat patch, habitat quality and resources vary randomly within a range of observed and expected percentage patterns to create a dynamic and heterogeneous landscape.

Maturation: Cotton rats age by one day for each time step that our model progresses and changes life stages as cotton rats reach maturation ages. When a juvenile is born, its age is set to 1. Once a juvenile becomes a subadult, that individual is no longer dependent on their mother because our classification is based on weaning age (Meyer and Meyer, 1944). Once a subadult becomes an adult, that individual establishes a territory.

Establish Territory: Cotton rats establish territories based on food, cover, and competitive interactions with other females. Once an individual becomes an adult it begins to establish its territory based on the sum of food and sum of cover within its territory. If the sum of food or cover is below the malnutrition or risk avoidance parameter values respectively, the individual continues to add patches to grow its territory. The individual can not grow its territory if the number of patches have already reached the maximum number, which is based on our field data (Larsen et al., In prep). The individual removes patches if the sum of food or cover within its territory is more than double what it needs to survive. If a territory has a detached cluster of patches, the detached cluster of patches is also removed. The edge patches with the lowest sum of food and cover combined are removed when an individual is shrinking its territory. If 2 individuals compete for the same patch, first the original owner receives a 0.5 probability of winning to provide the owner of the patch with home advantage. Second, the randomly assigned competitive value is compared between the 2 individuals and the individual with the higher competitive outcome takes ownership of the patch. Our territory submodel is an adaptation of Zakrzewski's (2016) Habitat-Based Models Building Block: Territory Emergence with the addition of the predation component. For details of the base submodel refer to Zakrzewski (2016).

Reproduce: Reproduction is possible if adults have more energy (food resources) than the malnutrition threshold times 1.5 in their territory (Randolph et al., 1977). Our model updates number of litters, days of pregnancy, birth, and days of lactation per adult within each breeding season.

Survive: Survival in our model depends on age. For juveniles and subadults, predation is considered random. For adults, survival is based on cover within their territory to reduce predation risk and food within their territory to reduce malnutrition risk. Furthermore, juveniles die if their mother dies. Lastly, adults die if individuals age to the maximum lifespan of 360 days.

Plot Cotton Rat Adult, Subadult, and Juvenile Abundance over Time: Cotton rat abundance per age group is measured and plotted over time.

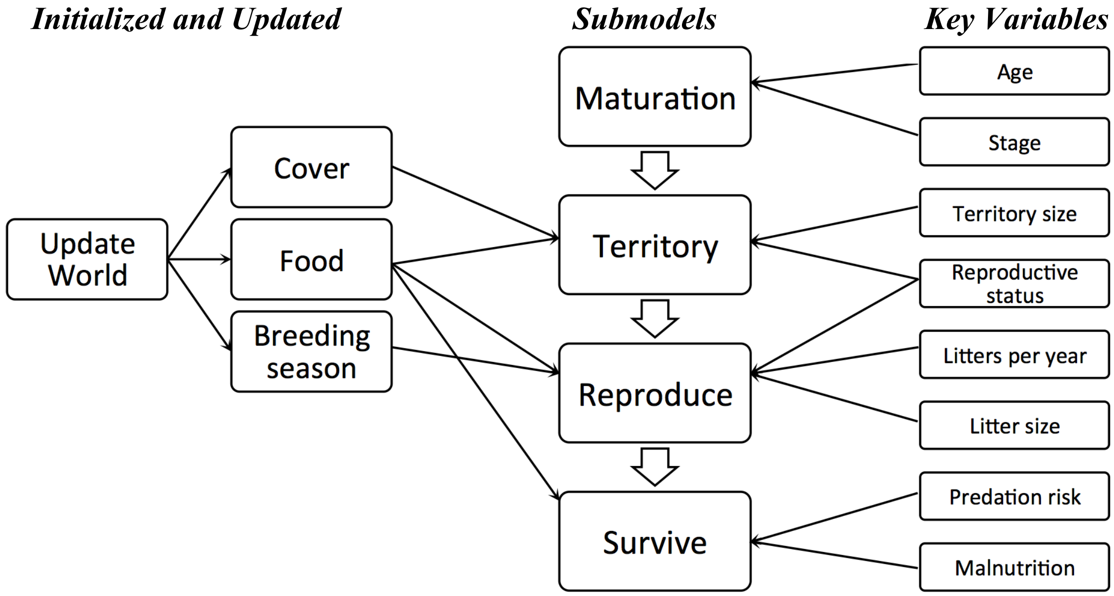


Figure A.2. Overview of Model Processes with Landscape Factors on the Left and Key Variables on the Right of the List of Submodels (maturation, territory, reproduce, and survive). At each time step, our model processed the submodels in the same order.

*Design concepts*

*Basic principles*. Key processes are cotton rat territory establishment, reproduction, and survival. All processes are affected by cover and food availability and lead to population dynamic changes. Concepts in our model are influenced by earlier models; territory (Zakrzewski 2016, Van Moorter et al., 2009), reproduction (Liu et al., 2013), and survival in terms of obtaining enough energy to avoid malnutrition while finding enough cover to avoid predation (Roese et al., 1991).

*Emergence*. Population dynamics and spatial distribution of territories emerge from individuals' behaviors and interactions with other rats and their environment. When different grass and cover amounts are introduced, individuals' behavior (movement and reproduction) impact population dynamics and spatial distribution of territories.

*Adaptation*. Adaptation is based on reducing predation risk by obtaining enough cover in an individual's territory. However, individuals are still required to obtain food so individuals may add habitat patches with low cover but high food to their territories. Our previous results suggested cotton rats had to forage in monocrop plots even though cover is poor ((Larsen et al., In prep).

*Prediction*. Our model includes an indirect prediction that cover is negatively correlated with predation risk (mortality rate).

*Sensing*. In our model, cotton rats sense 1) habitat quality, defined as food and cover amounts, of environment within their territory, 2) presence of other rats in their local environment.

*Interaction*. Cotton rats compete for habitat patches to add to their territories.

*Stochasticity*. Litter size is randomly determined within a range of 1-3 pups. We based the 1 on our field data of captured juveniles (Larsen et al., In prep). We used 3 as half of 7, which is the number of pups observed when cotton rats gave birth in our traps (4-7 pups; average=5.67 pups/female; (Larsen et al., In prep)) and previous literature (Cameron, 1977; Meyer and Meyer, 1944). We halved the maximum because we are only modeling female cotton rats. Number of litters per female is also randomly determined within a range of 0-3 per breeding season because our trapping data showed females were pregnant 0-3 times each breeding season (average=1.05 litters/female; (Larsen et al., In prep)). Maximum lifespan, gestation, and lactation duration are all constants in the model. Environmental fluctuations (weather and climate) are not included to keep our model as general and simple as possible.

*Collectives*. Each territory is defined as a collection of all patches each individual decides to own.

*Observation*. Population abundance as number of adults, subadults, and juveniles is output and displayed from the model. Population abundance provides information about the population dynamics and how individual behavior impacts the population level. Territory shapes and spatial distribution is observed and used to assess spatial availability for other rodent species.

### *Initialization*

Our model is initialized with a set number of adult cotton rats randomly distributed throughout the trapping grid area. Our starting number of adults is 10, based on our field data (Larsen et al., 2016). The model starts on January 1st. The landscape starts with the switchgrass-pine system and the number of patches of edge and grass can be changed to conduct different simulations to test responses. The initial landscape is a row of pine (1 patch wide), a row of edge (1 patch wide), a row of grass (2 patches wide), a row of edge (1 patch wide), and this habitat patch pattern is repeated for the entire ‘length’/x-axis of the world to represent switchgrass-pine plots. Pine trees are set in rows as would be in a traditional pine plantation. Then grass is set in the middle of the space between the pine trees (in the interbed or row). Finally, we define the naturally occurring vegetation that grows between the pine beds and grass rows as edge.

### *Input data*

Our model does not use any input data.

### *Submodels*

*Maturation*. In our model, cotton rats age by 1 day at each time step. Cotton rats are juveniles from 1 to 21 days, subadults from 22 to 80 days, and adults from 81 to 360 days (Clark, 1972; Meyer and Meyer, 1944). Average cotton rat lifespan is 6 months (Clark, 1972), but maximum lifespan is set to 360 days (1 model year) because we recaptured individuals 1 year after initial capture, but never more than 1 year.

*Territory*. Our model includes an adapted version of Zakrzewski’s Habitat-Based Models Building Block: Territory Emergence. Only adult cotton rats establish territories.

Adults grow their territories if cover and food are lower than needed for survival. If an individual's territory is near a neighboring cotton rat, the two individuals need to compete if both individuals want to add the same patch to their own territory. Adults will shrink their territories if their territory has grown beyond the maximum allowed number of patches (based on observed field data; (Larsen et al., In prep).

*Reproduce*. An adult reproduces if it is breeding season and the individual has 1.5 times the amount of baseline energy within its territory (Randolph et al., 1977). After a gestation period of 27 days (Clark, 1972), an individual gives birth to a litter of 1-3 pups (half of 1-7 range given we are only modeling females). Lactation then occurs for 21 days, unless all pups die. Once 21 days is over, or all pups die, the female is fertile again.

*Survive*. If a female cotton rat survives to 360 days, that individual dies because maximum lifespan is 360 days. If a female cotton rat dies in the model and has juveniles, all juveniles die too because they are not weaned and therefore depend on their mother. Malnutrition and predation are the risks for adults in our model. Juveniles and subadults are susceptible to random predation events, but their 'death' could also be considered emigration. Probability of death from predation increases when an adult does not have the baseline amount of cover in their territory. Similarly, probability of death from malnutrition increases when an adult does not have the baseline amount of food in their territory.

*Plotting*. Our model is set to plot population size as number of adults, subadults, and juveniles and is updated each time step.

## 3 Data evaluation

**This TRACE element provides supporting information on**: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

**Summary:**

> **The majority of cotton rat parameters were based on our field data or previous literature. Parameters of malnutrition and predation were inversely calibrated using on our observed field patterns of abundance and territory size and spatial distribution.**

Our model mainly used our field data from our previous research (Larsen et al., 2016, In prep). We also used previous literature as cited in Larsen et al. (in prep) to verify our data and assign values to parameters that we did not have measurements for. Both adult survival components of our model (malnutrition and predation) were inversely calibrated based on observed abundance and territory patterns. We used the initial 3 years at our study site for calibration and assumed constant malnutrition and predation risk throughout all 10 years of our simulations.

## 4 Conceptual model evaluation

**This TRACE element provides supporting information on**: The simplifying assumptions underlying a model's design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

**Summary:**

> **The conceptual model is shown in Figure 4.1 of Larsen et al. (in prep). The design concepts are in section 2 of this TRACE document, Model description. A few simplifying assumptions are necessary to produce our model and are discussed.**

Our model is developed with the intention of it being useful but simplified to ensure generality for use with other management applications. Our habitat patches are set to match the overall pattern of natural vegetation succession, but are completely determined by the observer. We therefore assume the amount of grass and non-grass cover will change throughout the months and years of the simulation. We also assume that female cotton rats find mates if they are able to reproduce. In nature, finding mates and actually mating may vary but is not represented in our model directly. Reproduction is instead based on timing and the amount of energy a female obtains in her territory. We do not directly consider immigration and emigration in our model. However, subadult mortality is considered a combination of emigration and death, which is common to assume when conducting field work as well.

## 5 Implementation verification

**This TRACE element provides supporting information on**: (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

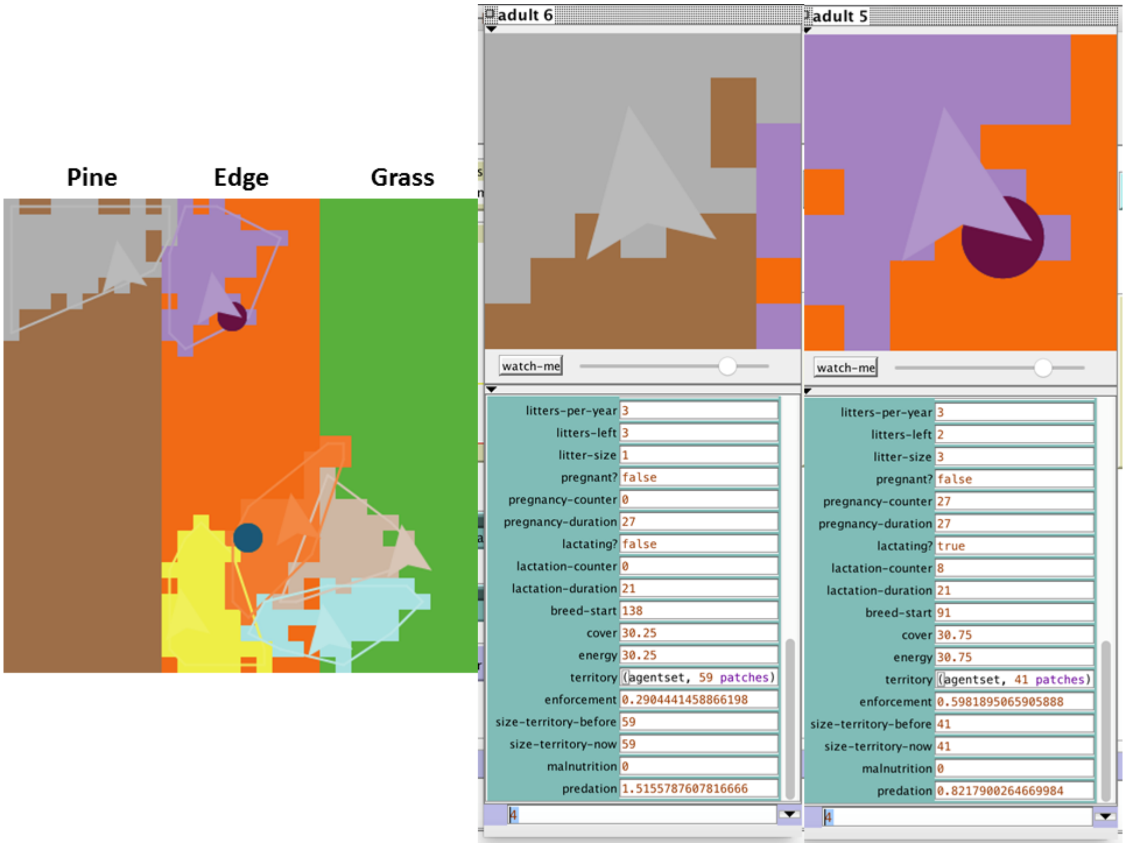
**Summary:**

> **We performed tests to ensure the computer code implementing the model worked as described in the ODD. We checked code syntax, used visual testing via the NetLogo interface and agent and patch monitors, used stress tests of extreme parameter and landscape values, and performed independent tests of each submodel prior to overall tests of our entire model.**

We thoroughly tested our model to ensure it performed as we described in our ODD protocol. Some of our tests were more simplistic, such as checking code syntax and using visual testing. We used all of our testing methods at each level of model development, such as running submodels in smaller landscapes and our full model. One example of a visual test we conducted by watching agent monitors is presented in Figure A.3. The gray individual had to obtain a larger territory (59 patches) to obtain slightly less cover (30.25) and energy (30.25) than the light purple individual who had a territory of 41 patches to obtain 30.75 for both cover and energy. The gray individual was in pine habitat type, which had lower amounts of available energy compared to the edge habitat type the light purple individual was in. Also, the light purple individual had a higher enforcement number (0.60) compared to the gray individual (0.29). Therefore, the light purple individual had a high probability of keeping its territory, even though the gray individual had a high probability of using the edge habitat type.

We also conducted stress tests with extreme parameters. For example, if predation risk was high, we would expect populations to go extinct. We set allowed-risk to 0 days to represent high predation risk and the population quickly went extinct each run. Similarly, we set allow-risk to 30 days (exceptionally high) and populations increased quickly. We did the same stress test with allowed malnutrition. We also conducted stress tests by altering the landscape and one example of the territory and landscape testing can be found in Larsen et al. (in prep).

We implemented our model in NetLogo 6.0.1 (Wilensky 1999). The code for our model is in Appendix A of Larsen et al. (In prep).



| | adult 6 | adult 5 |
|---|---|---|
| litters-per-year | 3 | 3 |
| litters-left | 3 | 2 |
| litter-size | 1 | 3 |
| pregnant? | false | false |
| pregnancy-counter | 0 | 27 |
| pregnancy-duration | 27 | 27 |
| lactating? | false | true |
| lactation-counter | 0 | 8 |
| lactation-duration | 21 | 21 |
| breed-start | 138 | 91 |
| cover | 30.25 | 30.75 |
| energy | 30.25 | 30.75 |
| territory | (agentset, 59 patches) | (agentset, 41 patches) |
| enforcement | 0.2904441458866198 | 0.5981895065905888 |
| size-territory-before | 59 | 41 |
| size-territory-now | 59 | 41 |
| malnutrition | 0 | 0 |
| predation | 1.5155787607816666 | 0.8217900264669984 |

Figure A.3. Example of Visual Testing Using 2 Agent Monitors. The left shows the landscape with the 3 habitat types (pine, edge, and grass) with 6 adult female cotton rats and their respective minimum convex polygon territory boundaries. Each adult female cotton rat is depicted with a colored arrowhead and juveniles are circles. We also show the monitors for agent 6 (gray) and agent 5 (light purple). This example verified our territory submodel worked as described in our ODD protocol.

## 6 Model output verification

**This TRACE element provides supporting information on**: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

**Summary:**

> **In this section we described how we inversely determined malnutrition and predation parameters via calibration to best represent adult survival. The majority of our parameters were based on our field data or previous literature. To determine adult survival via calibration, we ran the full model under various parameter settings and compared the output patterns of**

> **abundance and territory size and spatial distribution with our observed patterns from the field. We only have field data from the initial 3 years of the management practice, so we only used the first 3 years of simulations for calibration.**

We presented model output compared to field observations in Larsen et al. (in prep). All parameter values that we obtained from previous field data and previous literature were set first. Then, allowed malnutrition and allowed predation risk are set to 7 days each. Our model consisted of some minor habitat patch changes to represent switchgrass mowing and growing back over the summer months, and pine trees growing throughout the years. Individual cotton rats needed to respond to the habitat patch changes, as the changes altered the cotton rat's territory energy and cover. We allowed 7 days for each cotton rat to alter the habitat patches in its environment and if the individual was unable, it died. A 7-day period was considered enough time for a cotton rat to respond to a minor habitat characteristic disturbance and if not, its probability of death was expected to be high.

We inversely calibrated amount of energy and cover a female needed in her territory. We used the size and spatial distribution of territories measured in the field, adult abundance, and juvenile abundance. All abundances (field and simulated) were from June and July since we mainly trapped during both months. When we were comparing outputs from different parameter sets, we were particularly interested in making sure the overall patterns (increasing/decreasing) were consistently between our field data and simulated data. Some parameter sets were discarded because the simulated patterns were opposite of what we observed or underestimated our field data. Other than the first year, which was likely a high year in a cycle for cotton rats, we agreed with simulated data that overestimated rather than underestimated our data. Our trapping data was more likely to have underestimated the actual cotton rat population, especially juveniles which our model started counting at age 1 day.

## 7 Model analysis

**This TRACE element provides supporting information on**: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

**Summary:**

> **A sensitivity analysis was performed for the 2 adult survival parameters that were inversely calibrated. Since we had justification for all other parameters, our main interest was to find how sensitive our model was to our calibrated parameters. Results are in Table A.2.**

We altered our model's energy (housekeeping-demand) and cover (predation-avoidance) parameters independently by values of 1. From our calibrated parameter values, we varied each by ±2. We found our model output to be more sensitive to changes in the cover than the energy parameter (Table A.2).

Table A.2. Results of our Sensitivity Analysis for our Model's Energy and Cover Parameters. Absolute differences of simulated adult cotton rat abundance averages between the addition of 1 to the housekeeping-demand (a: energy) or predation-avoidance (b: cover) parameters per simulation year. Our model's calibrated parameter values were housekeeping-demand = 74 and predation-avoidance = 65. We presented each parameter set value ±2. We also presented average, minimum, and maximum absolute differences per parameter changes to best identify parameter sensitivity.

**a: ENERGY**

| Year | 72-73 | 73-74 | 74-75 | 75-76 | Average | Min | Max |
|---|---|---|---|---|---|---|---|
| 1 | 1.19 | 1.52 | 0.00 | 0.20 | | | |
| 2 | 0.05 | 1.41 | 0.82 | 1.90 | | | |
| 3 | 0.85 | 1.21 | 0.75 | 0.68 | | | |
| 4 | 2.14 | 1.80 | 0.48 | 2.28 | | | |
| 5 | 2.68 | 0.32 | 1.37 | 3.33 | | | |
| 6 | 3.80 | 0.39 | 3.13 | 3.62 | | | |
| 7 | 3.11 | 0.21 | 2.51 | 3.66 | | | |
| 8 | 2.89 | 1.20 | 1.01 | 1.84 | | | |
| 9 | 4.34 | 1.27 | 1.05 | 0.55 | | | |
| 10 | 0.94 | 1.46 | 1.42 | 1.82 | | | |
| | | | | | 1.63 | 0.00 | 4.34 |

**b: COVER**

| | 63-64 | 64-65 | 65-66 | 66-67 | | | |
|---|---|---|---|---|---|---|---|
| 1 | 1.04 | 1.69 | 1.50 | 2.04 | | | |
| 2 | 1.24 | 3.95 | 0.55 | 2.17 | | | |
| 3 | 2.22 | 4.78 | 2.15 | 2.60 | | | |
| 4 | 2.41 | 7.42 | 3.53 | 4.25 | | | |
| 5 | 0.99 | 6.70 | 3.73 | 6.62 | | | |
| 6 | 1.25 | 7.40 | 3.08 | 7.95 | | | |
| 7 | 1.24 | 3.83 | 4.38 | 9.33 | | | |
| 8 | 1.50 | 2.76 | 3.36 | 11.42 | | | |
| 9 | 1.56 | 0.77 | 4.67 | 9.30 | | | |
| 10 | 2.11 | 1.65 | 5.31 | 4.07 | | | |
| | | | | | 3.71 | 0.55 | 11.42 |

## 8 Model output corroboration

**This TRACE element provides supporting information on**: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence, which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

**Summary:**

> **The adult and juvenile abundance patterns from our simulations matched relatively well to year 7 abundance results in switchgrass-pine plots reported by King et al. (2014). We also used patterns from our other field treatment plots (Larsen et al., 2016) to compare with our scenario model output.**

Rodent populations fluctuate with environmental factors, which we did not include in our model. However, at year 7, our simulated model output matched results from a similar study conducted during management year 7 (King et al. 2014).

Our switchgrass monocrop plots were mostly grass with little to no non-grass cover. Our control plots were young pine plantations with more non-grass than grass cover. Overall, monocrop plots contained high adult, but low juvenile abundance (Larsen et al., 2016). Our control plots had low adult, but high juvenile abundance (Larsen et al., 2016). Our simulated scenarios consisted of: 1) decreased grass with increased non-grass cover compared to our baseline, 2) baseline; predicted grass and non-grass under current management, and 3) increased grass with decreased non-grass cover compared to baseline. Given the similarities in habitat characteristics, scenario 1 was expected to be more similar to control plots and scenario 3 was expected to be more similar to monocrop plots and therefore monocrop results.

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# CHAPTER V

# CONCLUSIONS

## Specific Aim I: Assess Effects of Understory Habitat Modification (treatment plot [monocrop, intercrop, control]) on Population Dynamics and Community Structure (Chapter II)

I, along with my co-authors, found monocrop plots contained high cotton rat abundance, low cotton rat juvenile recruitment, and low rodent diversity. Given my results, I considered monocrop plots to be sinks for cotton rats and recommended monocrop plots not be used for effective management. I also found control plots were opposite of monocrop plots with low cotton rat abundance, high cotton rat juvenile recruitment, and high rodent diversity. I considered control plots to be sources for the first few years after managers planted the pine trees because understory habitat characteristics were still relatively complex. I found intercrop plots were intermediate to monocrop and control plots in all measurements (abundance, recruitment, and diversity). Overall, I considered intercrop plots an appropriate management technique, because intercrop plots seemed to contain an adequate mixture of grass and cover. However, the question remained of whether cotton rats would eventually respond to the understory characteristics in a similar way as in monocrop or control plots.

## Specific Aim II: Assess Effects of Understory Habitat Modification (treatment plot [monocrop, intercrop, control]) on Spatial and Foraging Behaviors, and Patterns of Reproduction (Chapter III)

Although I, along with my co-authors, assessed the population and community responses in Chapter II, my results did not suggest which behaviors were acting as mechanisms to population and community responses. I found female cotton rat territory size was only affected by density, but not by treatment. I also found rodents foraged more in monocrop than control plots, with intermediate foraging in intercrop plots. I found female cotton rats tolerated more territory overlap in control than monocrop and intercrop plots, but only in control plots where grass cover was high. Lastly, I found reproductive indices were consistently higher in control than monocrop plots and intermediate in intercrop plots. My results suggest that monocrop plots act as sinks because cotton rat reproductive indices were low. However, adult cotton rat abundance in monocrops was high so it is possible monocrop plots are in fact ecological traps since cotton rats likely incorrectly perceive monocrop plots as good quality habitat. My results suggest that some cotton rat behaviors differ (foraging activity, female tolerance, and reproduction indices) more than others (territory size), at least during the initial 3 years of switchgrass and pine management. Although I found rodent behavioral responses in intercrop plots were intermediate, my results did not explain how behavioral, population, or community responses may change beyond the initial 3 years.

### Specific Aim III: Understand How Alterations in Behavioral Responses Drive Alterations at Population and Community Levels in Areas Where an Understory Habitat Modification has Occurred (treatment plot scale [monocrop, intercrop, control]; Chapter IV)

I, along with my co-authors, developed and calibrated an individual-based model (IBM) using 3 years of vegetation, behavior, and population field data from Chapters II and III. We also validated our IBM with a similar study conducted at year 7 of switchgrass-pine management. With my model, I was able to find under the current switchgrass-pine management technique, cotton rat populations would likely persist throughout the 10-years of pine stand establishment. A reduction in grass and increase in non-grass cover made cotton rat populations increase more than simulated cotton rat populations under current management. However, an increase in grass and reduction in non-grass cover caused simulated cotton rat populations to decline and remain extremely low for the 10 years. Switchgrass-pine plots will likely maintain cotton rat populations under current management, but I do not recommend management techniques that would reduce non-grass cover any further. My results suggest cotton rat population dynamics are driven by behavioral responses to the amount of non-grass cover in an area. My IBM could be altered to project prey species responses to various management techniques. My IBM could better inform management decisions that promote biodiversity conservation.

### Overall Conclusions

Overall, my results suggest intercropping switchgrass in pine plantations is an effective and sustainable management technique. Monocrop plots likely acted as ecological traps because cotton rats perceived the area as good habitat with high food resources, but did not correctly perceive low cover resources. Control plots, on the other hand, acted as sources because cotton rat reproductive indices were highest in control plots, but subadults likely emigrated when they perceived low food resources. Intercrop plots acted as an intermediate habitat type with a balance of food and cover resources. My IBM allowed me to fully assess the entire management time scale and habitat variation in the switchgrass-pine system. Furthermore, my model could be altered to investigate a larger spatial scale, additional rodent species, and how climate change could impact rodent response to switchgrass-pine system. Additionally, my model could be altered to test various prey species responses to habitat alterations in almost any system.