

Altered Understory Characteristics Affect Spatial and Foraging Behaviors and Reproduction Patterns

By: Angela L. Larsen, Jessica A. Homyack, T. Bently Wigley, Darren A. Miller, and [Matina C. Kalcounis-Rueppell](#)

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Abstract:

Understanding how changes to habitat characteristics affect behaviors is necessary to integrate biodiversity goals with land management. Managed forests are a significant landscape component in the southern United States and provide opportunities for conservation alongside production of wood products. We investigated behavioral responses of rodents to differences in understory habitat characteristics from intercropping 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 abundance 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 spatial 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, and monocrop plots may 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 populations and produce forest products.

Keywords: Biodiversity | Conservation behavior | Forest management | Intercropping | *Panicum virgatum* | *Sigmodon hispidus*

Article:

1. 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 (areas used, but not defended by individuals) 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 and Greis, 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 intensively managed pine stands 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 healthy ecosystems (Dickman, 1999).

We hypothesized that differences in grass and vertical vegetation cover due to planting switchgrass would affect cotton rat behavior (Fig. 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, 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 and increased food availability 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.

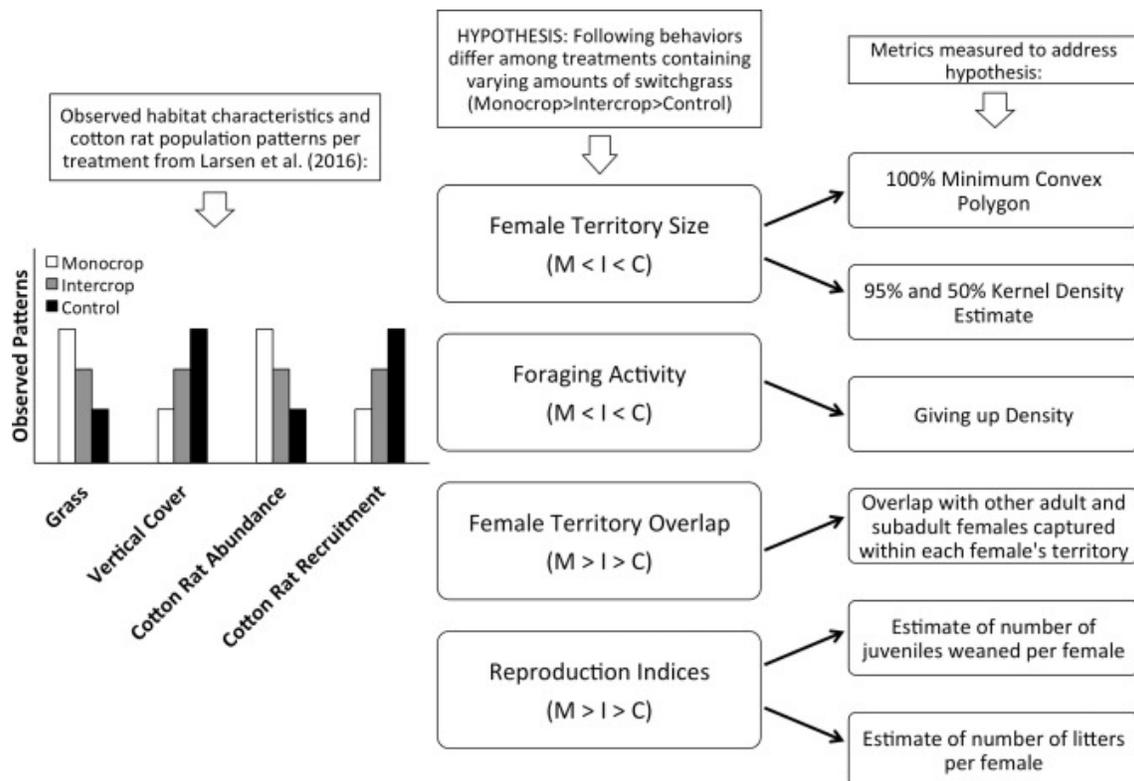


Fig. 1. Descriptive figure of habitat and cotton rat population patterns observed in Larsen et al. (2016) with the current study's hypothesis and measurements. Predictions of treatment pattern for each cotton rat behavior are listed in parentheses (M = Monocrop, I = Intercrop, C = Control). We based 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.

2. Methods

2.1. 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 pineplots, 1 switchgrass intercropped in loblolly pine plot, and 1 switchgrass monocrop plot; Fig. 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 Loman et al., 2014, Larsen et al., 2016.

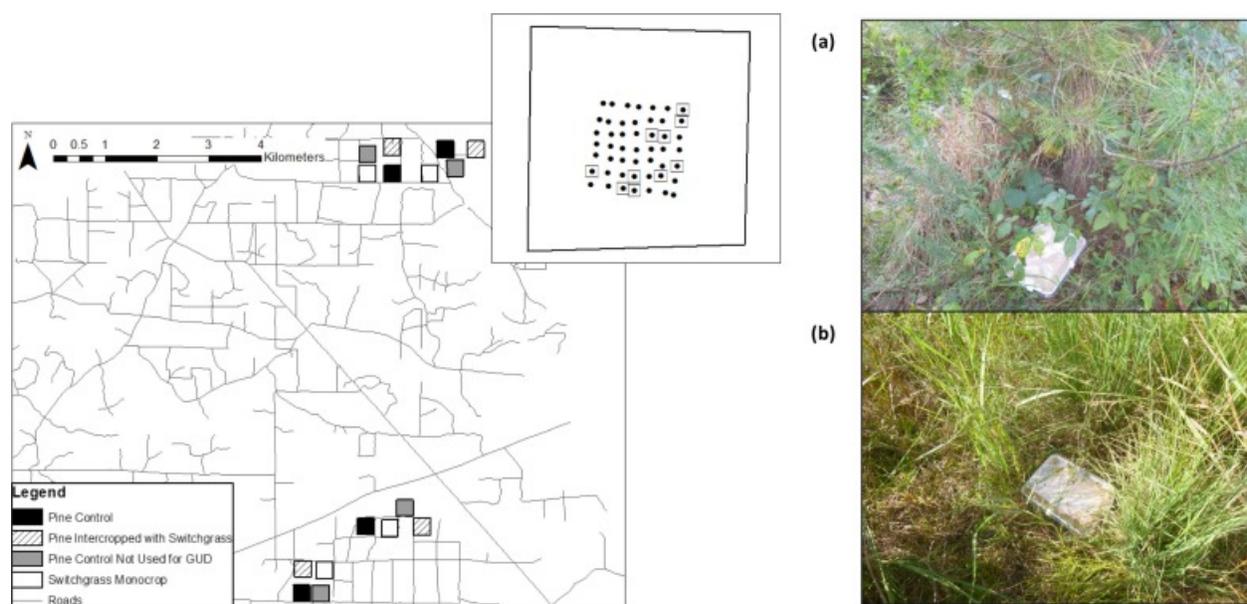


Fig. 2. Modified study area map from Larsen et al. (2016) of Kemper County, Mississippi, USA. Map depicts which trapping plots we used to collect giving-up density (GUD) data. The inset map is one of our treatment plots showing the trapping grid of 49 trapping stations (circles). The 10 trapping stations 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 pinebed (a) and 1 placed in the row (b).

2.2. Trapping

We live-trapped rodents using a 7×7 trapping grid (20 m spacing, 49 trap stations, Fig. 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 UIC IACUC 14-001.0 and the American Society of Mammalogists guidelines (Sikes and Gannon, 2011).

2.3. Space use

To determine territory area, we radio-tagged (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 (Howell, 1954, Doonan and Slade, 1995), while other studies suggest cotton rats use home ranges (Fleaharty 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 g. We radio-tagged 6 individuals per treatment in 2013 and 10 individuals per treatment in 2014 and 2015. To ensure they returned to normal behavior before measuring triangulation fixes, we located all radio-tagged individuals via homing using a R4000 or R4500S receiver with a 3 element folding yagi antennae (ATS) 24 h after they were radio-tagged. We also homed on individuals at least once per week during daylight. Lastly, for each radio-tagged individual, we obtained 6 triangulation fixes between 18:00 and 09:00 for 4–6 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 triangulation errors for each observer by taking bearings of radiotransmitters at known locations in a plot of each treatment type. We trained all observers until triangulation errors were $\leq 5^\circ$. Furthermore, we used trapping locations and location points from daytime homing to ground truth triangulation fix locations and to increase locations when needed to calculate territories. We removed any triangulation fix locations that were unrealistic before calculating territories. We considered locations from triangulation fixes to be unrealistic when they were ≥ 60 m from the nearest neighboring location. We used 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 triangulation fixes and explorative bouts by cotton rats. We did not detect any pattern to suggest our unrealistic locations were influenced by treatment.

For our territory analyses, our goal was to use 25 locations per radio-tagged individual based on previous research elsewhere (Cameron and Spencer, 1985, Morris et al., 2011a, Morris et al., 2011b) and because it represented an upper range of locations per individual in our study in 2013. Furthermore, Cameron and Spencer (1985) found that about 15–20 locations were needed before cotton rat home range was independent of location sample size. We considered triangulation fixes, daytime homing, and trap stations as locations. For all individuals with > 25 locations, we randomly selected a subset of locations to balance number of locations per individual. Based on visual comparisons in ArcMap 10.2.2 (ArcGIS, 2014), our randomly selected subsets approximated all available locations per individual. Although our goal was 25 locations per individual, we also used individuals with as few as 12 locations in our primary

analyses to maintain our sample size and to have a balanced sample across treatments and years. We used a minimum of 12 locations because territories calculated based on 12 or more locations were comparable to other territories in our data. Furthermore, territory areas tend to be under-, but not over-estimated with fewer locations, particularly when using minimum convex polygon (MCP) (Swihart and Slade, 1985, Blundell et al., 2001, Girard et al., 2002). We also conducted all space use analyses with individuals with <25 locations removed to evaluate potential bias.

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. We calculated both MCP and KDE to ensure both resulted in the same pattern and for comparison to previous studies (Morris et al., 2011a, Morris et al., 2011b, Farmer and Ault, 2014). 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 evaluate 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.

2.4. 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 $33 \times 23 \times 5$ cm aluminum foil, oblong cake pans with clear plastic lids as GUD foraging trays. To allow rodents access to the trays, we removed two squares, approximately 5×5 cm, that we cut out of two adjacent sides of each tray. 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; Fig. 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 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 15 g 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 used the same insecticide during each trapping session, so the rodents were acclimated to the insecticide (Larsen et al., 2016). We checked each tray every 24 h 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-h checks with a new 5 g of seed to reset the tray for the next 24-h

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-h 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 $\sim 0.20 * \text{Total (MNKA)} + 0.19$; $F_{1,22} = 28.38$, $p < .01$, $R^2_{\text{adj}} = 0.54$). 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.

2.5. Social behavior and reproductive output

We measured social behavior with female spatial 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 (2014), and used the Spatial Join tool to determine which trap stations each territory contained. To measure female spatial overlap, we used the MNKA of all adult and subadult female cotton rats within a radio-tagged 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.

2.6. 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-tagged individuals, so we were unable to balance individuals among stands. For this analysis, therefore, we assumed 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-tagged individuals were balanced among treatments.

We also 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 $\neq 0$), 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 differences in 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 (Logan, 2010). We used rank transformations of raw data if data did not meet assumptions as either raw or log-transformed and if the statistical model did not include an interaction term. If the model did include an interaction term, we used aligned rank transformations instead (Blair et al., 1987, Sawilowsky et al., 1989, Beasley, 2002). We investigated pairwise contrasts using a Tukey HSD for main effect models and least-square mean contrasts in Package *ARTool* (Kay and Wobbrock, 2016) for all interaction models. We used Program R (R Core Team, 2014) for all analyses.

3. Results

3.1. Space use

We used 25 locations for 82% of radio-tagged individuals for our territory analysis. However, as indicated previously, we did not have 25 locations for some individuals (10 in 2013 with 1 individual having 12 locations, 1 having 18, 5 having 20, and 3 having 24 locations; 2 in 2014 having 24 locations; 2 in 2015 with 1 having 13 and 1 having 24 locations). Using all individuals ($n = 78$), we found 100% MCP and 95% KDE territory sizes did not differ among treatments, but territories were about 2 times larger in 2013 than both 2014 and 2015 ($F_{2,69} = 8.05$, $p < .01$ and $F_{2,69} = 12.74$, $p < .01$; respectively, Fig. 3). Similarly, we found 50% KDE core area sizes did not differ among treatments but were slightly more than 2 times larger in 2013 ($F_{2,69} = 16.90$, $p < .01$) than in 2014 and 2015. When we excluded individuals with < 25 locations ($n = 64$), year was still the only significant effect and consistently, 2013 was significantly greater than 2014 and 2015 (year effect: 100% MCP $F_{2,55} = 4.41$, $p = .02$; 95% KDE $F_{2,55} = 4.22$, $p = .02$; 50% KDE core $F_{2,55} = 5.95$, $p < .01$). Therefore, we used all radio-tagged individuals with at least 12 locations for data interpretation.

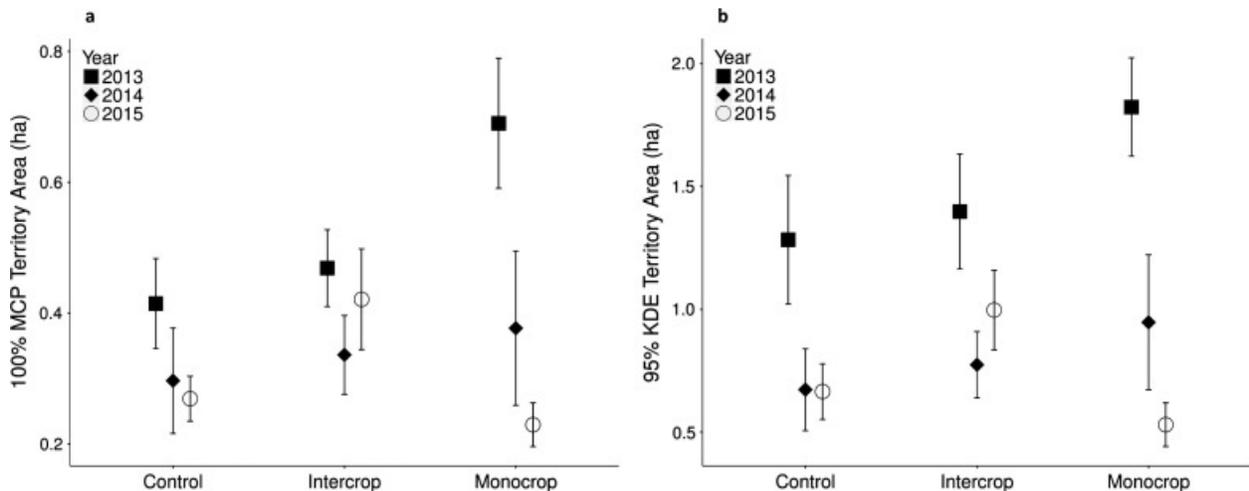


Fig. 3. Mean (\pm SE) female cotton rat territory areas based on 100% minimum convex polygon (MCP) [a] and 95% kernel density estimate (KDE) [b] plotted by treatment per year. We collected all locations necessary to calculate territory areas in Kemper County, Mississippi, USA in summers of 2013, 2014, and 2015. Both MCP and KDE territory areas were larger overall in 2013 but did not differ among treatments.

3.2. Foraging

Foraging activity was nearly 2 times greater in monocrop than control plots ($F_{2,6} = 5.29$, $p < .05$; Fig. 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 ($t = -2.05$, $df = 3$, $p = .13$) or control plots ($t = -0.98$, $df = 3$, $p = .40$).

3.3. Social behavior and reproductive output

Territory size was not significantly correlated with female spatial overlap ($r = -0.05$, $df = 75$, $p = .67$). We observed significantly higher adult female spatial overlap in 2013 than in 2014 and

2015, but adult female spatial overlap did not significantly vary among treatments ($F_{2,66} = 3.85$, $p = .03$ and $F_{2,66} = 1.84$, $p = .17$, respectively; Fig. 5a). When we combined subadult and adult females, territories in monocrop plots in 2014 had twice the overlap of intercrop and control plots ($F_{4,66} = 6.22$, $p < .01$; Fig. 5b). Across all years, adult female spatial overlap was positively related to percent grass in the reference female's territory in control (adult female spatial overlap $\sim 0.02 * \text{Grass} (\%) + 0.15$; $F_{1,21} = 9.17$, $p = .01$, $R^2_{\text{adj}} = 0.27$; Fig. 6a) but not intercrop or monocrop plots ($F_{1,24} = 1.75$, $p = .20$ and $F_{1,24} = 0.39$, $p = .54$; 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 spatial overlap $\sim 0.04 * \text{Grass} (\%) - 0.24$; $F_{1,21} = 26.53$, $p < .01$, $R^2_{\text{adj}} = 0.54$; Fig. 6b). We removed 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 spatial 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 spatial overlap, number of juveniles weaned per female, and number of litter per female) had a significant linear relationship with vertical vegetation cover.

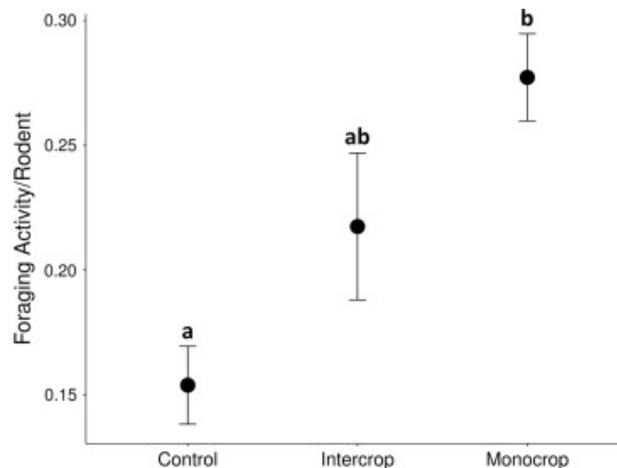


Fig. 4. Mean (\pm SE) foraging activity per minimum known alive number (averaged across trapping sessions) of rodents on each plot by treatment. We measured foraging activity using giving up density trays in Kemper County, Mississippi, USA in summer of 2015. Foraging activity significantly differed among treatments. Letters denote significant treatment pairwise comparisons.

Females in control plots weaned 2 times higher number of juveniles per female than in monocrop plots ($F_{2,6} = 14.22$, $p < .01$; Fig. 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 ($F_{4,18} = 3.97$, $p = .02$; Fig. 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

($F_{2,6} = 6.02$, $p = .04$; Fig. 8). Intercrop plots had an intermediate proportion of juveniles that did not significantly differ from control and monocrop plots' proportions of juveniles.

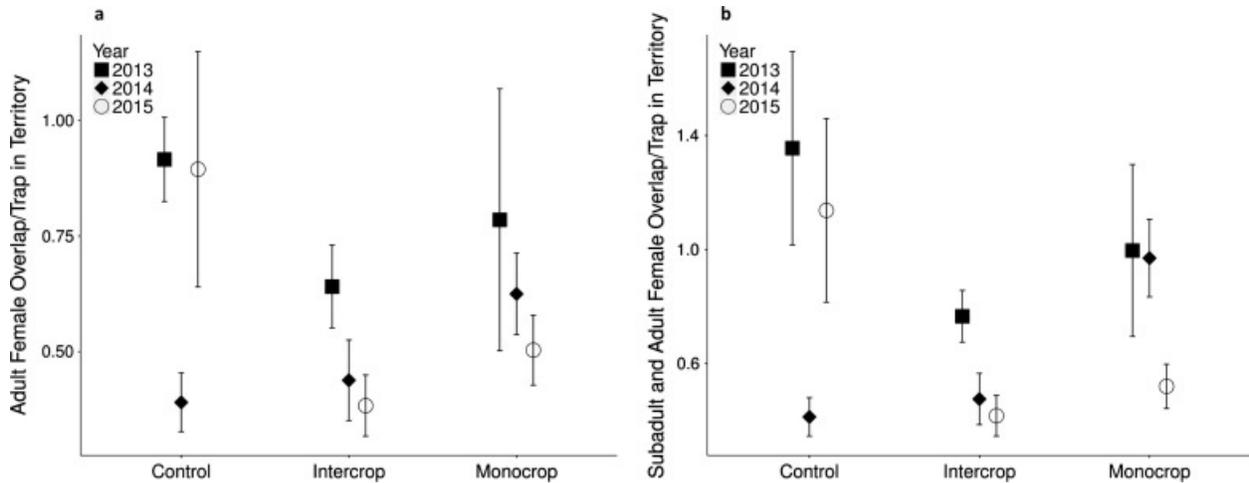


Fig. 5. Mean (\pm SE) minimum known alive number of adult only (a) and adult and subadult (b) female cotton rats in territories of radio-tagged female cotton rats plotted by treatment per year. We radio-tagged and followed adult female cotton rats to determine territory areas and live-trapped rodents 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 spatial overlap in 2013 than in 2014 and 2015. In 2014, we also found subadult and adult female spatial overlap was highest in monocrop plots.

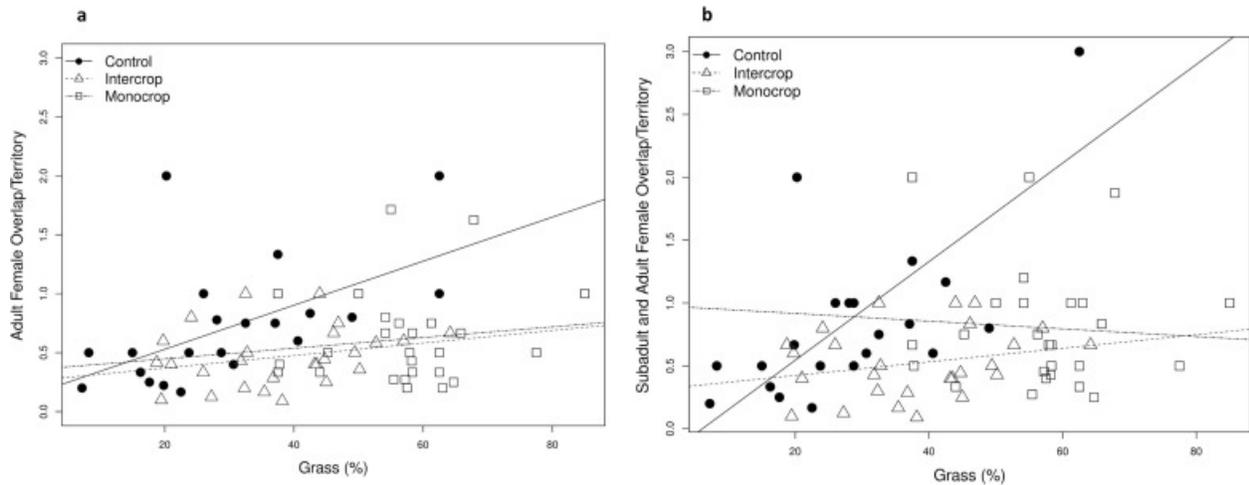


Fig. 6. Scatterplot of the minimum number known alive of adult (a) and subadult and adult (b) female cotton rats trapped in radio-tagged female cotton rat territories over the average percentage of grass measured at trap stations within each territory. Shapes denote the treatment each territory was in, 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.

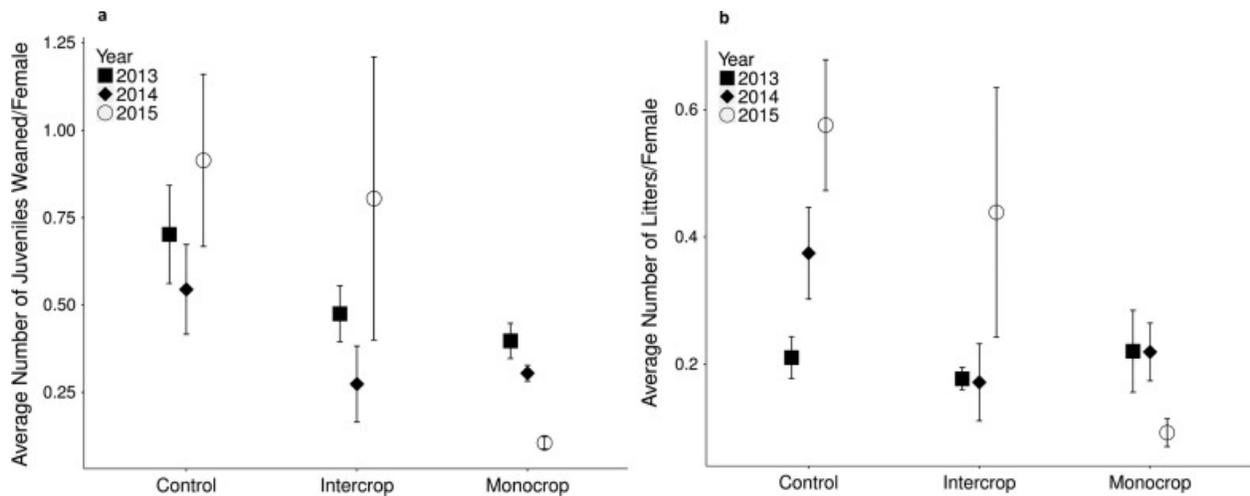


Fig. 7. Average number of juveniles weaned per adult female cotton rat (a) and average number of litters per adult female cotton rat (b). We based averages on trapping data of cotton rats. We live-trapped rodents to determine the number of juvenile and adult cotton rats throughout the summers of 2013, 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).

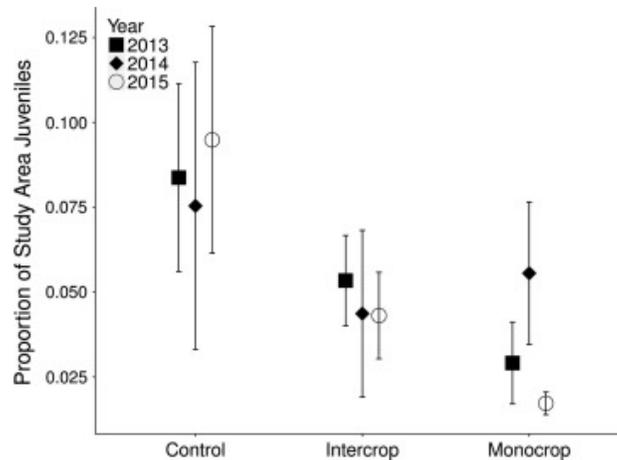


Fig. 8. Proportion of study area's juveniles captured per year and per treatment. We live-trapped rodents to determine the number of juvenile throughout the summers of 2013, 2014, and 2015 in Kemper County, Mississippi, USA. We found control plots contained higher proportions of our study area's juveniles compared to monocrop plots.

4. Discussion

We hypothesized that cotton rats would exhibit different behaviors in response to altered habitat characteristics from biofuel feedstock production. Female territory size did not differ among treatments, but foraging activity, female spatial overlap, and reproduction indices did differ among treatments, yet not as predicted (Fig. 1). There was more female spatial 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 may act as population sinks and possibly even ecological traps for cotton rats (Larsen et al., 2016). We did not measure individual movements in or out of treatment plots, so we cannot definitively state whether monocrop plots were acting as ecological traps or not (Kristan, 2003). 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 spatial 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). High cotton rat population densities in 2013 may have prevented individuals from maintaining territories and instead we may have been measuring home ranges (Grant, 1993, Maher and Lott, 2000). Territoriality in an area of high cotton rat density could be costly to a female cotton rat because of the increased risk of predation from exposure during territorial interactions and injury from intraspecific interactions (Wingfield et al., 2001). Thus, female cotton rats may have devoted less energy to territorial defense. In 2013, understory vegetation may not have been developed 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 vegetation became more complex, cotton rats may have acquired suitable 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 following senescence 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).

The GUD data suggested that cotton rats were risk averse in control plots, which may have increased individual fitness. Reproductive indices indicated that 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 could be consumed, lowering 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 vegetation structure could have affected predation risk. However, 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 determine if high foraging activity in monocrop plots was due to mismatched cues of predation risk or lack of food, future research should include artificially covered foraging trays (Mattos and Orrock, 2010). Regardless, our results of high cotton rat abundance and high foraging activity in monocrop plots suggest that cotton rats may be attracted to switchgrass only plots because of abundant grass [cotton rats' main food source; (Randolph et al., 1991)]. Although cotton rats may perceive monocrop plots as high quality habitat, the grass is not providing either adequate food or cover from predators, or both. As further evidence that monocrop plots are acting either as a sink or an ecological trap, we detected low recruitment which may be due to either a lack of dicots in diets of females which can adversely affect reproduction (Randolph et al., 1995) or increased predation risk, or a combination of both. Briones et al., (2013) showed *Peromyscus leucopus* shifted their diet in monocrop plots, but not intercrop, to include more C₄ plants, which includes switchgrass.

The location of grass in control plots limited cotton rat territories. 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). For example, dispersal (Stafford and Stout, 1983, Diffendorfer, 1998), social structure (Summerlin and Wolfe, 1973), and how social structure affects other behaviors (Spencer and Cameron, 1983) could be particularly relevant cotton rat behaviors. 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 (i.e. constant territory size), which can be

detrimental in the long term (Berger-Tal and Saltz, 2016). We limited radio-tagging to females > 95 g and may have radio-tagged 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 could have improved estimates of female reproductive output, but 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 1–3 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 4–7 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).

4.1. Conclusions

Here, we confirmed 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 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 success. 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 differed among years but not 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). 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 may support 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).

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