Spatiotemporal Impacts of Invasive Species Removal and Reinvasion

by

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Abstract

Invasive species are a major driver of native species declines and reduce ecosystem function. Though eradication of invasive species is often beneficial, it can create other ecological issues and if not implemented correctly, can result in reinvasion. A model invasive species to test the effects of removal is the red-imported fire ant (*Solenopsis invicta,* hereafter RIFA), which depredates and competes with native species, though these impacts are debated. Eradication attempts of RIFA often result in reinvasion, though patterns of reinvasion, which give insight into the efficacy of removal, are not well understood. I hypothesized that RIFA would reinvade treated areas with higher densities due to elimination of competition from native species. I also hypothesized that RIFA removal would positively influence altricial Peromyscus species, due to increased survival of young in the nest, but would not impact semi-precocial cotton rats (*Sigmodon hispidus*), which are mobile more quickly after birth and thus at less risk of depredation by RIFA. To test our hypotheses, I applied a granular insecticide (Extinguish® Plus) on two 400-500 ha study sites, and left two 400-800 ha areas untreated. On all sites, I trapped ant species and small mammals. Extinguish® Plus effectively removed RIFA, but they reinvaded about 14 months after treatment with higher densities than on untreated areas, which indicates that treatment could have negative outcomes for native ant species. Results for small mammals were dependent upon species, with some results contrary to what I had expected, indicating that both the magnitude and mechanism of effects on small mammals require further investigation. In managing for invasive species, impacts on all species should be considered. Removal of long-established invasives involves many trade-offs, and if not eradicated, reinvasion of the species can result in worse ecological outcomes for native species.

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List of Abbreviations

RIFA	Red-imported fire ant

Chapter 1: Using the red-imported fire ant to study invasive species removal and reinvasion

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Abstract

Invasive species are a major driver of native species declines, often resulting in a reduction of ecosystem function. Though eradication of invasive species is often beneficial, it can create other ecological issues, and if implemented incorrectly, can result in reinvasion. A model invasive species to test the effects of removal is the red-imported fire ant (*Solenopsis invicta,* hereafter RIFA), which depredates and competes with native species. Eradication attempts often result in reinvasion, though patterns of reinvasion, which give insight into the efficacy of removal, are poorly understood. I compared patterns of RIFA relative abundance on sites treated with a granular insecticide (Extinguish® Plus) in southwest Georgia, USA. I hypothesized that RIFA would recolonize from untreated borders and reinvade treated areas, achieving higher densities due to elimination of competition from native species. Extinguish® Plus effectively removed RIFA, but they reinvaded about 14 months after treatment with higher densities than on untreated areas, which indicates that treatment could have negative outcomes for native ant species. There was evidence of reinvasion from the edges, but recolonization from within the property also occurred. When invasive species are removed using short-term management, as in this study, the response can include rapid recolonization and even increased abundance of the target invasive species. Management strategies for invasive species should incorporate multiple techniques and knowledge of reinvasion patterns to be most successful.

Keywords: red-imported fire ant, invasive species, Extinguish® Plus, *Solenopsis invicta*, reinvasion

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INTRODUCTION

Invasive species are a major driver of species endangerment (Wilcove et al. 1998; Bellard et al. 2016), and a leading cause of decline in biodiversity, thereby reducing ecosystem function (Vitousek et al. 1997; Mack et al. 2000; Pejchar and Mooney 2009; Pyšek and Richardson 2010; Crystal-Ornelas and Lockwood 2020a). Invasive species also have a large economic impact, with estimates from invasive insects alone at $70 billion USD per year (Bradshaw et al. 2016). As of 2005, over 50,000 invasive species were estimated to have been introduced to the United States (Pimentel et al. 2005) and this number is likely growing (Early et al. 2016). These species cause damages to crops, pastures, and forests, and billions are spent on pest control (Pimentel et al. 2005).

Further, human disturbance to an ecosystem, which is increasing in frequency and magnitude, can increase the likelihood of invasion in a community (Hobbs and Huenneke 1992; Vitousek et al. 1997). Coupling disturbance with climate change creates additional avenues of invasion for species (Walther et al. 2009; Seebens et al. 2015; Early et al. 2016). Each species has different impacts on the ecosystem it invades (Sax et al. 2007) and many factors interact to determine the impact that an invasive species will have (Ricciardi et al. 2013; Crystal-Ornelas and Lockwood 2020b). Consequently, there is much left unknown about the effects of specific species, including ramifications if a well-established invasive is removed (Simberloff et al. 2013).

Though eradicating an invasive species can benefit native species, and control measures are often recommended (Bergstrom et al. 2009; Lockwood et al. 2013; Simberloff 2014), removal of an invasive species often presents its own challenges when trying to manage for a healthy ecosystem (Courchamp et al. 2017). The methods used should account for the biology of the species and impacts following removal should be understood, especially when eradication exacerbates the issues (Caut et al. 2009; Zipkin et al. 2009; Ruscoe et al. 2011). Removal is further complicated when multiple invasive species are present in an ecosystem (Zavaleta et al. 2001; Bergstrom et al. 2009; Ballari et al. 2016), which will likely be an increasing occurrence as human disturbances increase (Airoldi and Bulleri 2011), or when an invasive species has been established for a long time (Simberloff et al. 2013). The right method for removal and the consequences of removal should be understood when managing an invasive species (Crystal-Ornelas and Lockwood 2020b).

A model species to test the effects of removal of an invasive species from an ecosystem is the red-imported fire ant (*Solenopsis invicta*, hereafter RIFA). RIFA are an invasive species in the southeastern United States that thrive in recently disturbed areas, commonly appearing in areas maintained by mowing or clearing. Invasive ants are often reliant upon anthropogenic disturbance for long-distance dispersal (Suarez et al. 2010). RIFA arrived near Mobile, Alabama around 1930 (Vinson 1997) and have rapidly expanded their territory since. In their original range in South America, RIFA were adapted to take advantage of natural disturbances, but in places where RIFA have invaded, anthropogenic disturbances have created a gap for them to thrive (King and Tschinkel 2008). RIFA utilize high reproductive output and effective dispersal in addition to their dispersal itself being aided by humans to effectively invade new ecosystems (Tschinkel 2006; King and Tschinkel 2008; Lach et al. 2010). RIFA are estimated to account for $1.3 billion/year (USD, adjusted to 2020) in economic impact from livestock and crop losses and damages as well as control costs (Pimentel et al. 2005)

Many studies have found negative impacts of RIFA on species in the surrounding ecosystem. RIFA have been linked to decreases in native ant and invertebrate abundance and species richness (Porter and Savignano 1990; Epperson and Allen 2010; Morrow et al. 2015). They have been found to decrease songbird nest survival (Campomizzi 2008), depredate young reptiles (Allen et al. 1994), and impact small mammal behavior (Pedersen et al. 2003; Holtcamp et al. 2010; Darracq et al. 2016). However, other studies have shown that RIFA density neither competitively limits native ants nor changes species richness (King and Tschinkel 2006; Stuble et al. 2009) or instead that native ant and arthropod diversity was positively associated with RIFA density (Morrison and Porter 2003), indicating a need for further research.

In addition to the debate over positive versus negative effects, there is also debate on the impact of removing RIFA (Lach et al. 2010). Though chemcials have been used for decades to remove RIFA from sections of the landscape, nationwide eradication from the United States is considered unattainable (Hoffmann et al. 2010). Further, the long-term effectiveness and patterns of reinvasion are not well understood. If control is not adequately implemented, a removed invasive species can reinvade, and as such, reinvasion is a critical component to consider when removing an invasive species, as is evaluation of the efficacy of the treatment (Hoffmann et al. 2016). Studying the reinvasion mechanism of RIFA in this project, whether they emerge from pockets of remaining RIFA in the landscape or from the edges of untreated areas, will give insight into the efficacy of the current methods of removal. Because chemical toxicants are recommended for control of RIFA populations on agricultural lands (Nester 2018), it is important to understand whether it is working as intended and what the long term consequences are.

Using RIFA as a model invasive species, I tested the impact of removing an invasive species from an area. Using a chemical toxicant, RIFA were removed to test effectiveness of removal, reinvasion patterns, and efficacy of the toxicant. I hypothesized that after an initial decline post-treatment, RIFA would recolonize treated areas from the edges as they reinvaded from nearby, untreated areas. Because RIFA take advantage of disturbed areas, the removal of ants with a chemical toxicant creates an easy area for RIFA to colonize. Nearby untreated areas would serve as source populations for these newly ant-free areas. One of the traits that makes RIFA an invasive species is their ability to quickly colonize and out-compete native ant species, which I hypothesize will lead to more RIFA on treated areas than untreated following recolonization. The reinvasion mechanisms and consequences are important factors to consider when managing invasive species.

METHODS

Study Area

I evaluated RIFA reinvasion patterns in the southeastern US. The study sites comprised four large (Treated A: 505 hectares, Untreated A: 870 hectares, Treated B: 407 hectares, Untreated B: 472 hectares) private properties located near Albany, Georgia in Dougherty and Terrell Counties (Figure 1.1) managed for hunting northern bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), and white-tailed deer (*Odocoileus virginianus*). Management practices include prescribed fire, mowing and chopping, timber volume management, and supplemental feeding for northern bobwhite. The sites were dominated by an overstory of loblolly pine (*Pinus taeda*) with old field ground cover and patches of longleaf pine (*Pinus palustris*). The average annual precipitation for Albany, Georgia was 51.4 inches, with an average annual temperature of 66.2°F and summer (June, July, August) average of 81.4°F (NOAA 2020).

Ant Sampling

I treated experimental units (n = 2; Figure 1.1) with a one-time broadcast application at 1.68 kg/ha of granular Extinguish® Plus (0.365% hydramethylnon, 0.25% s-methoprene; Central Life Sciences, Schaumburg, IL) when weather conditions were appropriate (soil temperature >18°C, low wind, no rain forecast for three days). Extinguish® Plus is a toxicant and sterilant that contains an adulticide and insect growth regulator, killing worker ants while also sterilizing the queen (Central Life Sciences 2018). Worker ants transport the bait back to the colony where it is consumed by other worker ants, as well as the queen. Decline of the colony can begin as early as a week after being treated (Central Life Sciences 2018). Specifically, I applied Extinguish® Plus to the western unit in May 2018 and the eastern unit in June 2018. Untreated units (n = 2; Figure 1), which did not receive Extinguish® Plus, were chosen based on similarity in habitat and management and paired with the treated units to create replicate study areas. Treated units were separated by a distance of 450 m, meeting the assumption of independence based on mean dispersal distances of the study species. RIFA queens usually fly less than 400 m before landing to create a colony (Tschinkel 2006).

To assess changes in ant populations as well as spatiotemporal reinvasion of RIFA following the application of Extinguish® Plus, I sampled ants using baited vials in grids that were randomly placed in both treated and untreated experimental units. I chose grid locations using stratified random sampling in ArcGIS v10.6 (ESRI, Redlands, CA, USA). I classified the treated units into four distance bands (0-250 m, 251-500 m, 501-1000 m, and >1000 m) from the nearest source (non-treated unit). Then, I used the Create Random Points tool within each distance band to randomly place points for grids. Two sampling grids were randomly placed in each distance band in the treated units, and an equal number of sampling units were randomly placed on untreated units, creating eight sampling grids per experimental unit. Each sampling grid consisted of 16 points in a 4×4 grid with 50 m spacing (Figure 1.2).

To sample foraging ants at each point, I used a 20 mL scintillation vial baited with 1 g of hot dog (Seymour 2007; Caldwell et al. 2017). The vial was placed on the ground, then picked up 30 min later (Porter and Tschinkel 1987) to prevent RIFA from fully consuming the bait and leaving the trap. I began sampling for a day 20 min after sunrise and continued until sampling of all grids was completed, no later than sundown. A single grid on each experimental unit was sampled at any given time, with paired treated and untreated grids sampled simultaneously. For each sampling session, observers rotated between sampling treated and untreated areas and the order the grids were sampled was rotated to minimize bias from time of day and observer.

Foraging and activity of RIFAs has been quantified relative to soil temperature such that 22-36 °C is optimal, but foraging at higher soil temperatures occurs (Porter and Tschinkel 1987). RIFA tunnel exits reach within 30 to 50 cm of every part of a RIFA colony's territory, so foragers spend up to 90% of their travel time in these underground tunnels (Porter and Tschinkel 1987). As such, the heat of day was not expected to significantly reduce foraging on this study area. However, cold temperatures are more limiting than heat, so winter temperatures would be likely to limit foraging (Tschinkel 2006). Therefore, ant sampling consisted of one sampling session of 30 min on each grid per month from April through September in both 2018 and 2019 to identify spatiotemporal changes. In total, I placed 6,144 vials for sampling. After collecting the samples, I filled the vials with ethanol and sealed them. Ants were then identified to species (MacGown 2014) and counted in the laboratory.

Statistical Analysis

I examined two indices of RIFA abundance, the proportion of vials per grid that contained RIFA and the count of RIFA for all vials in a grid for each sampling session. For each analysis, I used generalized linear mixed models (GLMM), creating a model set based on *a priori* hypotheses about the data. Variables considered were the following: session (all sampling that occurred for a given month), treatment (the comparison of treated and untreated properties), and distance (the distance from a sampled grid to the boundary between treated and untreated areas). Models examined comparisons of the following: a session effect, a treatment × session interaction, and a treatment × session × distance interaction. Models with treatment or distance main effects without an interaction with session were considered implausible and therefore were not tested. Sampling grid was included as a random effect; I initially examined including experimental unit as a random effect but omitted it because the associated random effects variance estimate was 0 for each analysis. After initial examinations of models with spatial autocorrelation in residuals indicated very weak or no autocorrelation after accounting for treatment effects, I proceeded with non-spatial models.

I modeled the proportion of vials with RIFA per grid as a binomial count. Based on preliminary model fits, I determined that a beta-binomial GLMM was appropriate to account for overdispersion and clustering of vials in grid sessions (Bolker et al. 2009) with residual dispersion varying by session. I modeled the count of RIFA per grid as a negative binomial GLMM. I chose this distribution due to overdispersion in preliminary model fits resulting from a wide range of counts. For both analyses, models were fit with R package *glmmTMB* (Harrison 2015; Brooks et al. 2017). Standard likelihood ratio tests were checked with a parametric bootstrapping comparison when the significance was between 0.001 and 0.1, using package *lme4*

(Bates et al. 2015). I treated 95% confidence intervals excluding 1 on the odds ratio scale or p-values <0.05 as evidence of a meaningful effect. All statistical analyses were conducted in R version 3.6.3 (R Core Team 2018).

RESULTS

Of 6,144 vials that were placed for sampling, 2,849 (46.4%) contained ants when collected. Of vials containing ants, 1,534 contained RIFA. The total number of ants collected was 260,651, of which 175,707 (67.4%) were RIFA. In total, 38 ant species were identified (Appendix 1).

In beta-binomial modeling of proportions of sample vials with RIFA, the model with a session × treatment interaction was favored over the simpler model with only a session effect ($\chi^2 = 106.7$, df = 12, $p<0.001$). There was not support for an effect of distance (likelihood ratio test of three-way session × treatment × distance interaction model vs. session × treatment model) ($\chi^2 = 40.4$, df = 24, bootstrap $p = 0.054$). However, because our hypotheses were related to distance, I investigated the distance model to assess the biological effects of distance on treated areas over time. Overall, distance did not affect the probability of a vial containing RIFA on untreated areas (95% confidence limits all bracketed 1; Table 1.1), but the effect of distance on the probability a vial contained RIFA varied by session in treated areas. In July 2018, RIFA were 1.16 (1.01-1.43; 95% CL) times as likely to be present in a vial on treated areas per 100 m closer to an untreated edge. A similar effect was also observed in September 2018, and April and May 2019 (Table 1.1).

In June 2018, at 500m from the boundary edge, RIFA were 3.71 (2.12-7.18; 95% CL) times as likely to be present in a vial on an untreated grid compared to a treated grid (Figure 1.3).

A similar pattern was seen through May 2019. However, by September 2019, RIFA on a treated grid were 1.69 (0.99-3.03; 95% CL) times as likely to be present in a vial compared to an untreated grid (Figure 1.3) and by August of 2019, the predicted proportion of vials containing RIFA exceeded that of untreated areas (Figure 1.4).

For the RIFA count analysis, the model with a session × treatment interaction was strongly supported over the simpler model with only a session effect ($\chi^2 = 71.0$, df = 12, bootstrap $p<0.0001$). The model with a three-way interaction of session × treatment × distance was not supported vs. the simpler model of session × treatment ($\chi^2 = 33.6$, df = 24, bootstrap $p = 0.22$). Based on the session × treatment model, in June 2018, an untreated grid had 5.38 (1.81-16.52; 95% CL) times as many RIFA as a treated grid. Untreated grids had increasingly more RIFA than treated grids until June 2019, when the effect neared 0 for the remainder of sampling (Figure 1.5).

DISCUSSION

Extinguish® Plus effectively removed RIFA from the treated properties, but RIFA reinvaded to greater numbers than in the untreated areas by the end of the study period. Although there was evidence of distance to the treatment border playing a role in the initial reinvasion, the effect of distance was not important over the entire reinvasion period. These results support my second hypothesis that RIFA would reinvade treated areas with higher numbers, but not my first hypothesis that reinvasion would occur from the edges. While Extinguish® Plus does kill RIFA, the higher RIFA numbers by the end of the study indicate that it could have negative ecological outcomes for the area, and that other management techniques could be preferable.

Distance was important for reinvasion in the period immediately following treatment. Most colony founding for RIFA occurs between April and August (Tschinkel 2006), so RIFA likely began recolonizing the treated properties immediately after treatment occurred. Because very few queens (<3%) have been reported to fly up to 400 m away to form a new colony (Tschinkel 2006), females would begin founding new colonies close to untreated boundaries or surviving colonies on treated areas and reinvade from there. In the months immediately following treatment for RIFA, they were more likely in the areas close to the borders and less likely in the interior of the treated property, evidenced in June and July 2018 (Figure 1.4). Because recolonization distances are so short, the collection of RIFA from the interiors of the properties in the months following treatment indicates that some colonies did remain following treatment. As such, reinvasion is occurring from both outside and within the treated areas.

When an invasive species is temporarily reduced, but not entirely eradicated, reinvasion is highly likely. Therefore, management actions should anticipate this. To most effectively use chemical toxicants in light of RIFA reinvasion at borders immediately following treatment, border areas could be treated again following initial treatment to extend the efficacy of the treatment without requiring an entire additional reapplication. Treatment could also be maximized by utilizing natural borders of uninhabitable or less inhabitable areas to make reinvasion more difficult for RIFA. Because RIFA thrive in disturbed areas, borders areas could include areas with minimal disturbance, and to discourage reinvasion, treated areas could minimize disturbance during the period of reinvasion. Application of toxicants for RIFA should consider the management strategies of adjacent properties to where the treatment will be applied.

While there are techniques to increase the effectiveness of chemical controls, the ecological costs likely outweigh the benefits of use, so management decisions should also consider other repercussions to the area following treatment. I found that the Extinguish® Plus treatment stopped being effective near the end of summer 2019, 14-16 months post-treatment. Even if initially successful, removal of invasive species can have unintended consequences, resulting from density-dependent relationships and interactions within species assemblages (Zipkin et al. 2009; Ruscoe et al. 2011). In my study, I found that more RIFA were detected on treated areas than on the untreated areas once the treatment was no longer effective. While this might be an initial reinvasion peak that dissipates over time, these results match with previous research that has indicated treatment of RIFA leads to higher RIFA densities after the treatment, likely due to an elimination of native ant species that competed with RIFA (Summerlin et al. 1977; Showler and Reagan 1987; Stimac and Alves 1994). Because RIFA are an efficient invasive species, they are able to take advantage of the disturbance of the chemical toxicant and will continue to reinvade, unless entirely eliminated. In a previous study across millions of treated acres, colonies experienced 98-100% mortality, but reinvasion by RIFA still occurred (Williams et al. 2001). If reinvasion results in higher densities of RIFA, then the amount and frequency of application are likely to increase over time, resulting in decreasing cost effectiveness. Additionally, Extinguish® Plus kills native ants as well as RIFA, which in combination with the increased densities of RIFA following treatment, could lead to a greater ecological impact for native ant species than simply not treating RIFA. Unless serving a specific purpose such as protecting agricultural crops, chemical treatments could be doing more damage than good. Though they can be effective in certain situations, other management techniques might be better suited and less ecologically harmful.

Given our results, alternative solutions should be explored to effectively control RIFAs long-term. Alternative control techniques might include biocontrol which has proven success against agricultural pests in certain conditions (Pejchar et al. 2020). Integrated pest management involves using multiple tools to effectively manage a species over the long-term, a strategy which should be used for RIFA. Leaving an invasive species alone is controversial because of the unknown or future impacts they can have (Simberloff 2014), but in some scenarios, this might be the best strategy for long-term management of RIFA. RIFA are a long-established invasive species in the United States, and while the United States might have a future without RIFA, the application of chemicals on a property-by-property basis is not going to get us there.

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Tables and Figures

Table 1.1 Odds ratio results for the probability a vial captured RIFA for each 100 m closer to an untreated boundary in a study on RIFA reinvasion in southwest Georgia from April 2018 – December 2019. Odds ratio of 1.0 = no effect of distance. Bold items indicate confidence limits that do not bracket 1. No meaningful distance effects were detected for untreated areas, but the effect of distance on likelihood of RIFA being detected on grids varied by session for treated areas.

		Treated		**Untreated**	
		Odds Ratio	**95% CL**	**Odds Ratio**	**95% CL**
2018	April	0.92	(0.82, 1.02)	1.08	(0.99, 1.19)
	May	1.01	(0.92, 1.11)	1.00	(0.94, 1.06)
	June	1.10	(0.99, 1.23)	1.00	(0.94, 1.05)
	July	**1.16**	**(1.01, 1.43)**	1.02	(0.96, 1.09)
	August	0.94	(0.83, 1.08)	0.99	(0.94, 1.05)
	September	**1.16**	**(1.00, 1.49)**	1.01	(0.95, 1.06)
2019	April	**1.16**	**(1.00, 1.54)**	1.00	(0.94, 1.05)
	May	**1.14**	**(1.01, 1.33)**	0.97	(0.93, 1.03)
	June	1.00	(0.92, 1.12)	0.97	(0.92, 1.02)
	July	1.04	(0.97, 1.12)	1.04	(0.99, 1.10)
	August	0.95	(0.88, 1.01)	1.00	(0.95, 1.05)
	September	0.97	(0.90, 1.05)	1.05	(0.99, 1.12)

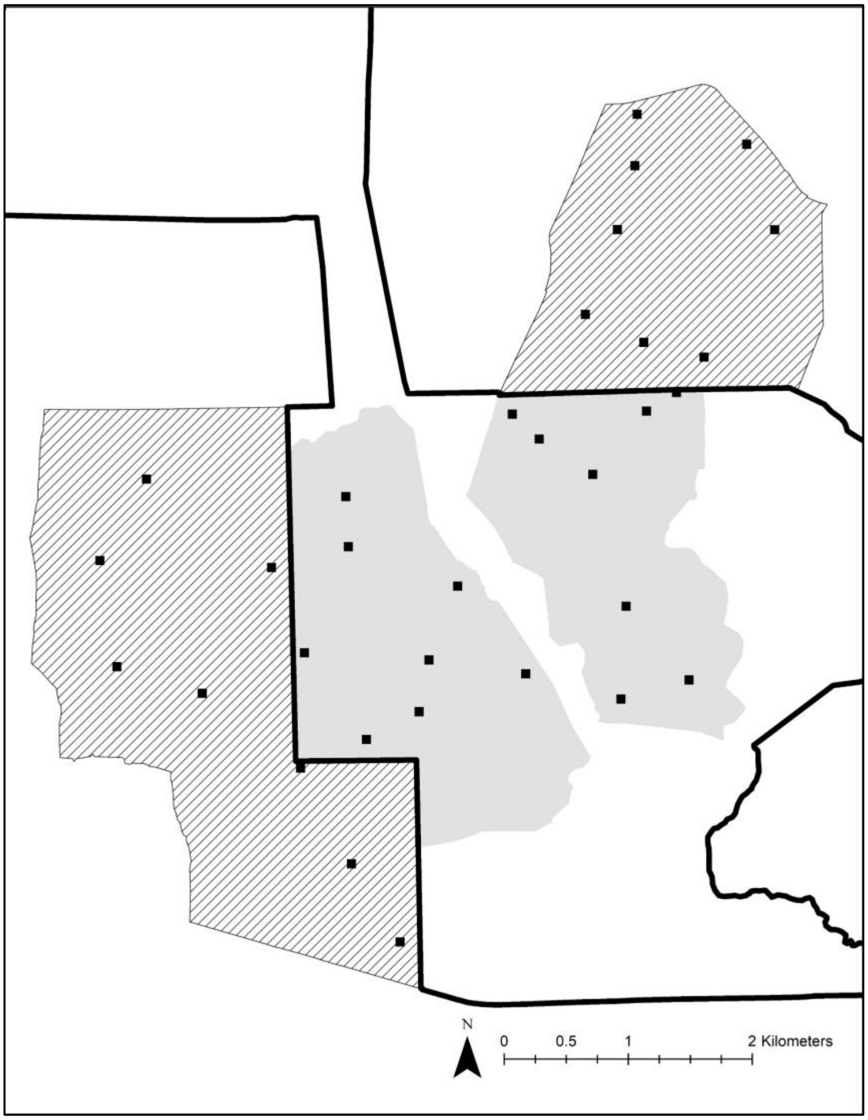

Fig. 1.1 Locations of ant sampling grids in a study of RIFA reinvasion in southwest Georgia from April 2018 – September 2019 (hatched = control, gray = treated). The interior of the thick black line represents the total treated area. The treated sites occur on the same property, but are separated by a buffer zone to minimize movement of individuals across replicates and maintain independence. Ant sampling grids were randomly placed across the properties (squares within experimental units).

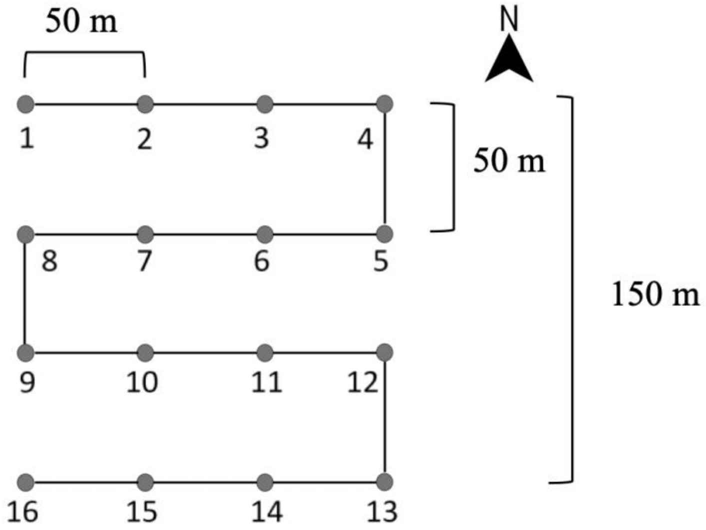

Fig. 1.2 4 × 4 grids were used for sampling of ants in a study of RIFA reinvasion in southwest Georgia from April 2018 – September 2019. Grids were walked in the indicated order and vials with a hot dog bait were placed on the ground for 30 minutes to collect ants.

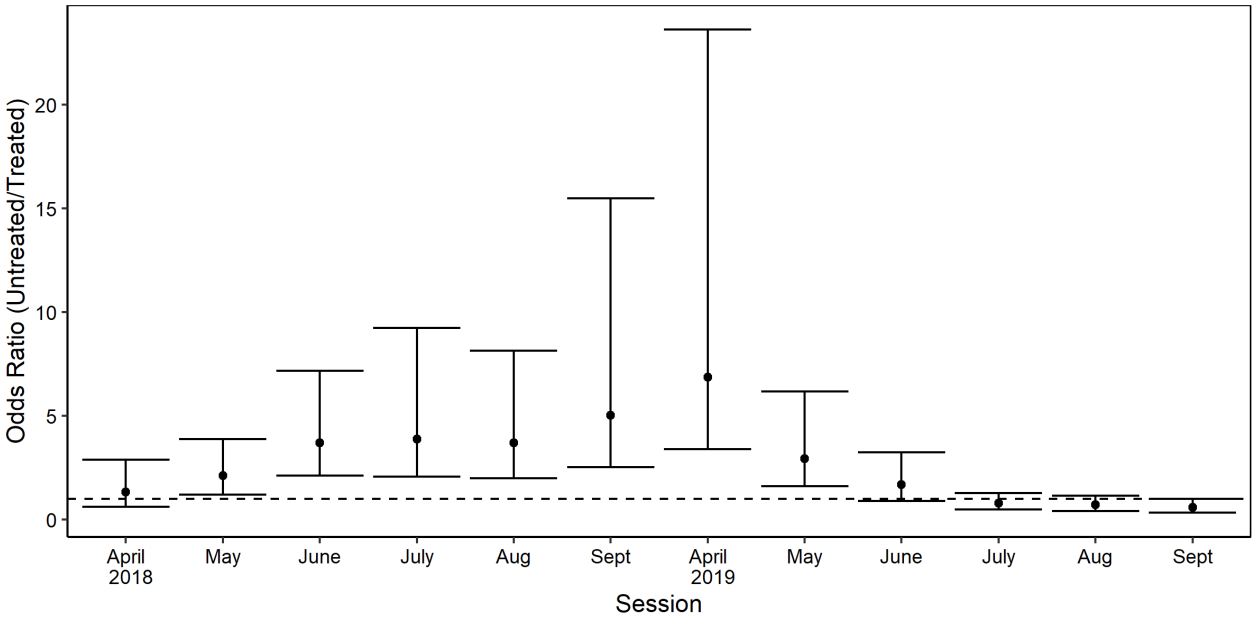

Fig 1.3 The odds ratio (untreated / treated) of a vial containing RIFA at 500 m from the untreated edge in a study on RIFA reinvasion in southwest Georgia from April 2018 – December 2019. A value >1 indicates higher likelihood of RIFA captures on untreated areas, while a value <1 indicates higher likelihood on treated areas, and a value of 1 (dashed line) indicates no effect. Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect.

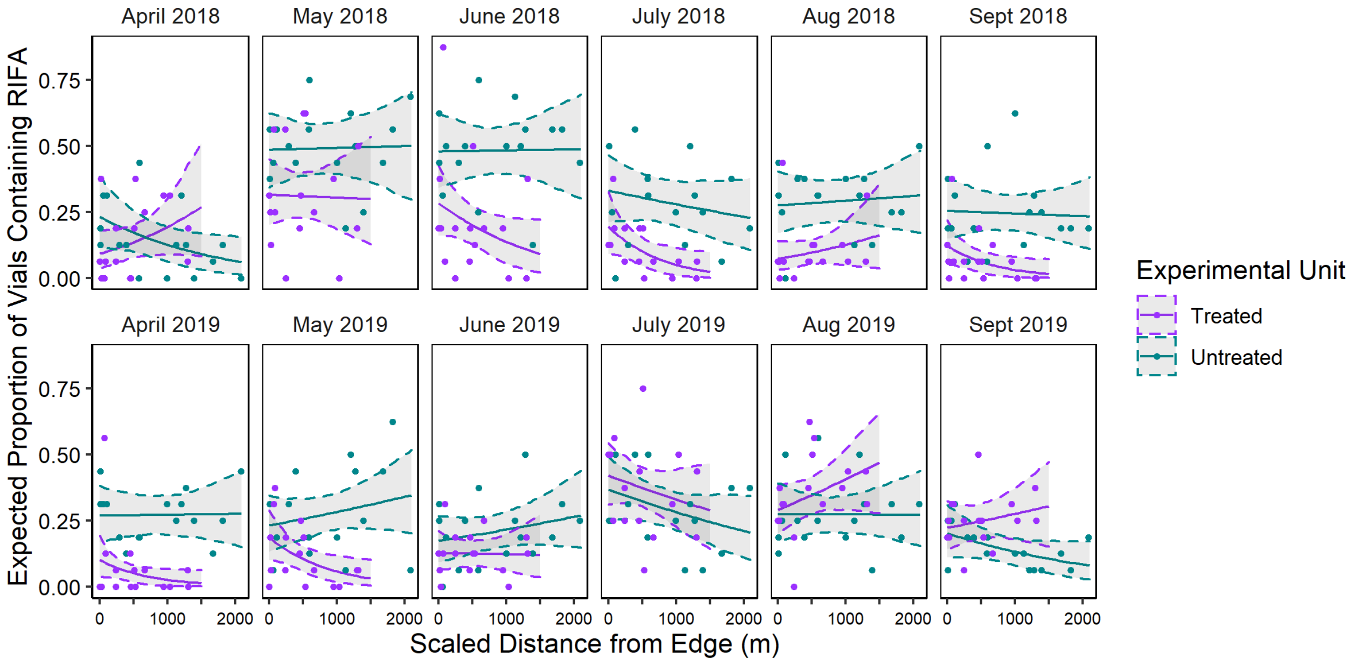

Fig. 1.4 The session × treatment × distance model was not supported against the session × treatment model, but illustrated the change in effect of distance over the reinvasion period in a study on RIFA reinvasion in southwest Georgia from April 2018 – December 2019. Dots indicate the recorded proportion of vials collected that contained RIFA. The regression line models a beta binomial distribution of predicted proportions for each treatment × session combination evenly spaced across the distances with 95% confidence intervals (dashed lines).

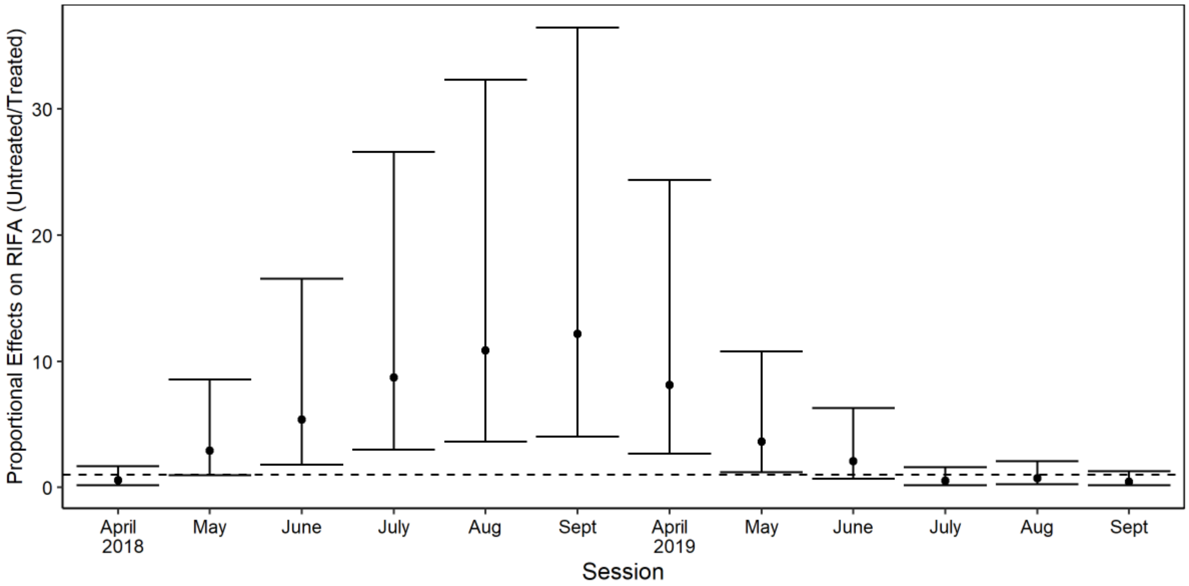

Fig 1.5 The proportional effect of treatment on RIFA count per grid in a study on RIFA reinvasion in southwest Georgia from April 2018 – December 2019. A value >1 indicates expected captures are higher on untreated areas, while a value <1 indicates expected captures are higher on treated areas, and a value of 1 (dashed line) indicates no effect. Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect.

Chapter 2: Changes in native small mammal populations with removal of invasive ant*

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Abstract

Invasive species often cause the decline of native species. Thus, removal studies provide important information on how native species may rebound that is necessary for informing best management practices. Using red-imported fire ant (*Solenopsis invicta,* hereafter RIFA) as a model species, I hypothesized that its removal would positively influence altricial *Peromyscus* species, due to increased survival of young in the nest and thus increased recruitment to the population, but would not impact semi-precocial cotton rats (*Sigmodon hispidus*), which are mobile more quickly after birth and thus at less risk of depredation by RIFA. I compared small mammal populations on sites treated with a granular insecticide (Extinguish® Plus) to remove RIFA in southwest Georgia, USA from April 2018 – December 2019 (n = 2 sites per treatment, sites = 400-800 ha each). As expected, I observed no detectable difference in cotton rat recruitment. However, the same was true for cotton mice (*Peromyscus gossypinus*) and oldfield mice (*Peromyscus polionotus*), altricial species for which I expected a difference. Further, RIFA removal resulted in increased survival of both cotton rats and cotton mice, increasing average population rate of change (λ) on treated sites during the study period. Although treatment resulted in lower survival of oldfield mice, λ estimates were similar on treated and untreated sites, although low sample sizes were problematic for this species. My results show that removal of invasive species can have positive impacts for native species, but both the magnitude of RIFA effects on small mammals and mechanisms by which impacts occur are complex.

Keywords: invasive species, Extinguish® Plus, population parameters, *Sigmodon hispidus*, *Peromyscus gossypinus*, *Peromyscus polionotus*, *Solenopsis invicta*

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INTRODUCTION

Invasive species can have broad-reaching negative impacts on populations and ecosystems (Crowl et al. 2008, Simberloff et al. 2013). They can alter food webs (Wardle et al. 2001), reduce species richness (Sala et al. 2011, Crystal-Ornelas and Lockwood 2020), and disrupt abiotic processes (Wardle et al. 2009). Invasive species are more dangerous as predators than native species (Salo et al. 2007), can reduce fitness of native species (Gurnell et al. 2004), and are a leading cause of species extinctions (Clavero and Garcia-Berthou 2005). Given the adverse consequences of invasive species, there are many success stories of native populations rebounding when invasive species are managed or removed (Hoffmann 2010, Monks et al. 2014, O'Donnell et al. 2017).

Invasive ants are a worldwide ecological and economic problem, with the red-imported fire ant (*Solenopsis invicta*, hereafter RIFA), one of the most studied (Suarez et al. 2010). RIFA is a model species to study effects of their removal on native species as it is adapted to thrive under natural disturbance in their native range and have responded to human disturbance to spread in the southern United States (Tschinkel 2006, Lach et al. 2010). RIFA are highly studied, accounting for up to 18% of the literature on invasive insects (Kenis et al. 2009), but there is conflict among these studies as to whether RIFA have neutral, negative, or even positive effects on native species and ecosystem services (Morrison and Porter 2003, Allen et al. 2004, Lach and Hooper-Bui 2010). Thus, potential impacts of RIFA removal are even less well understood.

Small mammals are a useful group to test in response to RIFA populations, as they are an important component of the ecosystem due to their influence on vegetative composition through consumption and dispersal, role as consumers of insects and fungi, and function as a prey species (Sieg 1987, Root-Bernstein and Ebensperger 2013, Moorhead et al. 2017). Therefore, fluctuations in their populations can indicate broader ecosystem changes (Carey and Harrington 2001, Pearce and Venier 2005). Looking at effects of RIFA on small mammals specifically, impacts depend on species and life history (Lechner and Ribble 1996). Young of altricial or semi-precocial small mammals could be at risk of depredation by RIFA (Allen et al. 2004, Lach and Hooper-Bui 2010). Other demographic impacts are generally thought to be indirect, driven by direct or indirect effects on behavior. Species with diets similar to that of the omnivorous RIFA could face competition for resources and higher vulnerability to other predators (Orrock and Danielson 2004, Lach and Hooper-Bui 2010). Cotton rats (*Sigmodon hispidus*) changed habitat use in the presence of RIFA (Pedersen et al. 2003, Holtcamp et al. 2010), and oldfield mice (*Peromyscus polionotus*), cottons rats, and deer mice (*Peromyscus maniculatus*) altered foraging decisions in the presence of RIFA (Holtcamp et al. 1997, Orrock and Danielson 2004, Darracq et al. 2016). These changes in behavior could lead to increased risk of mortality. However, in other species, RIFA presence did not lead to altered habitat selection (Pedersen et al. 2003, Keenan 2017). A study on cotton rats found that RIFA impacts on survival were only detectable in the absence of other predators (Long et al. 2015).

Given the complexity of RIFA impacts, various responses to RIFA removal may be expected within a small mammal community. Small mammals are an especially useful group for assessing effects of invasive species removal because multiple species of varying life history traits typically reside in an area. This allows multiple comparative hypotheses to be tested in one study.

In this study, I tested several hypotheses about small mammal responses to large-scale removal of RIFA. I expected that survival of cotton rats, cotton mice (*Peromyscus gossypinus*), and oldfield mice would not differ on treated and untreated areas. Direct depredation of small mammals by RIFA is rare, and though there are indirect effects (competition for food, changed foraging patterns which increase risk of other depredation) (Holtcamp et al. 1997, Orrock and Danielson 2004), other studies have found RIFA effects on survival to be compensatory, rather than additive (Long et al. 2015). Next, I expected recruitment of altricial species (cotton mouse, oldfield mouse) would be higher in areas treated for RIFA, but no different for the semi-precocial cotton rat. Cotton rats are mobile within hours of birth (Meyer and Meyer 1944) and leave the nest within 4-7 days (Bergstrom and Rose 2004), while cotton and oldfield mice remain in the nest for 3-4 weeks (Wolfe and Linzey 1977, Whitaker and Hamilton 1998). Altricial species are more at risk of young in the nest being depredated by RIFA in the nest in areas where RIFA are present.

Finally, due to increased recruitment on treated areas, I expected cotton and oldfield mice to have increased population rate of growth (lambda, λ) on treated areas, but that there would not be a difference in population growth for cotton rats between areas.

METHODS

Study Area

To test my three hypotheses, I evaluated the impact of RIFA removal on native small mammals in the southeastern US. The study sites comprised four large (Treated A: 505 ha, Untreated A: 870 ha, Treated B: 407 ha, Untreated B: 472 ha) private properties located near Albany, Georgia in Dougherty and Terrell Counties (Figure 2.1) managed for hunting northern bobwhite (*Colinus virginianus*), wild turkey (*Meleagris gallopavo*), and white-tailed deer (*Odocoileus virginianus*). Management practices included prescribed fire, mowing and chopping, timber volume management, and supplemental feeding for northern bobwhite. The sites were dominated by an overstory of loblolly pine (*Pinus taeda*) with old field ground cover and patches of longleaf pine (*Pinus palustris*). The average annual precipitation for Albany, Georgia was 51.4 inches, with an average annual temperature of 66.2°F and summer (June, July, August) average of 81.4°F (NOAA 2020).

RIFA Removal

I treated experimental units (n = 2; Figure 1) with a one-time broadcast application at 1.68 kg/ha of granular Extinguish® Plus (0.365% hydramethylnon, 0.25% s-methoprene; Central Life Sciences, Schaumburg, IL) when weather conditions were appropriate (soil temperature >18°C, low wind, no rain forecast for three days). Extinguish® Plus is a toxicant and sterilant that contains an adulticide and insect growth regulator, killing worker ants while also sterilizing the queen (Central Life Sciences 2018). Worker ants transport the bait back to the colony where it is consumed by other worker ants, as well as the queen (Central Life Sciences 2018). Specifically, I applied Extinguish® Plus to Treated A in May 2018 and Treated B in June 2018. Untreated units (n = 2; Figure 2.1), which did not receive Extinguish® Plus, were chosen based on similarity in habitat and management and paired with the treated units to create replicate study areas. Ant sampling was conducted from April through September 2018 and 2019 on treated and untreated areas (see Chapter 1). Based on other analyses, treatment caused an immediate reduction of RIFA relative abundance with captures 83.0% lower on treated areas than control areas following treatment in 2018 (see Chapter 1). From April to June 2019, RIFA relative abundance remained lower on treated areas with 65.18% fewer captures. However, from July through the end of ant sampling in September, captures were 35.67% higher on treated areas.

Small Mammal Sampling

I assessed small mammal survival, recruitment, and abundance via capture-mark-recapture sampling. Locations of small mammal trapping grids were selected randomly within each experimental unit using ArcGIS v10.6 (ESRI, Redlands, CA, USA). Small mammal trapping followed the robust design (Pollock 1982), using 11 primary periods (sessions), with secondary periods of three nights per session. Each treated and untreated unit contained three, 49-trap grids with Sherman live traps (7.62 × 8.89 × 22.86 cm, H. B. Sherman Traps, Inc., Tallahassee, FL) arranged in a 7 × 7 trap design with 10 m spacing between each trap (Figure 2.2; Darracq et al. 2016). Primary sessions occurred every other month from April 2018 through December 2019, with the April 2018 trapping session occurring before the application of Extinguish Plus. For each session, grids within a treated-untreated pair (e.g., treated A and untreated A) were trapped simultaneously, followed by the other pair of experimental units. Due to a natural disaster at the field site, the B set of grids was not trapped in October 2018. Additionally, one untreated B grid was not trapped in December 2018 due to flooding at the site.

I baited traps with oats and opened them in the afternoon, then checked them beginning at sunrise each morning. When nightly temperatures were below 10°C, I placed nesting material in all traps to prevent cold-related trap mortality. Captured small mammals were ear-tagged with a unique identification number, and weight, sex, and reproductive status were recorded. Because RIFA can cause trap mortality (Masser and Grant 1986), very localized control of RIFA immediately at trap stations is standard for small mammal studies in the Southeast (Conner et al. 2011, Morris et al. 2011, Larsen et al. 2016). Therefore, I sprinkled Talstar (7.9% bifenthrin, FMC Corporation, Philadelphia, PA), a granular insecticide, within 0.25 m of each trap station to minimize trap mortalities.

Cotton rats were considered adults when they were >50 g (Bergstrom and Rose 2004, Morris et al. 2011). All individual cotton rats captured in a second session were adults by that time. Cotton mice were considered to be adults at >19 g (Bigler and Jenkins 1975). For oldfield mice, adults were individuals >7 g (Whitaker and Hamilton 1998), however, I did not capture enough juvenile individuals to create an age variable for this species.

Statistical Analysis

Capture histories were created for each individual for cotton rats, cotton mice, and oldfield mice. For each species, a multi-step model selection process was used due to the large number of biologically important variables to consider. I conducted preliminary modeling of detectability within the robust design framework with Huggins conditional likelihood (Huggins 1989, 1991) to determine a detectability model for each species when survival was held constant (Appendix 1). Detectability models from this step were used in two subsequent analyses. First, I used the robust design (Huggins form) with individual covariates to model survival and estimate abundance for each grid session. I then used Pradel seniority models to examine recruitment and population growth rate (λ).

Model sets chosen for each step were based on *a priori* hypotheses driven by the biology of the species. I did not expect treatment to be in the top survival models for any species or in the top recruitment models for cotton rats. If there was a treatment effect, I could expect to see in as a constant effect of treatment or an effect that varied over time since treatment. I also expected survival and recruitment to vary seasonally. Therefore, I investigated the time relationship with several possible forms of temporal variation – as a categorical variable (time), logit-linear trend (Time), and quadratic trend Time + Time^2 – to account for complex temporal variation and smoother changes after treatment. Similarly, I expected there to be variation in survival due to age and sex, so these variables were included in the models. The time variables and sex were included in the survival model sets as interactions with treatment to account for differences that could occur between the groups.

Survival and abundance - I modeled survival and estimated abundance using the robust design (Huggins form), which allowed use of individual covariates for p and S, with temporary emigration assumed 0. Temporary emigration was determined to not be important for my dataset due to very few individuals (<5%) having gaps between primary capture sessions if recaptured. After initial modeling of the full survival set, the models with sum weight of 0.95 were model averaged (Burnham and Anderson 2002, Grueber et al. 2011). Model rankings were determined using Akaike's Information Criterion, adjusted for small sample sizes (AICc, Burnham and Anderson 2002).

Population size estimates were derived from model averaged survival models. I used these estimates to perform an approximate comparison of average abundance of each species for each session. For each species and session, I calculated the proportional abundance, $\frac{\bar{N}\_treated}{\bar{N}\_untreated}$ using the ratio of summed abundances across the six grids of each treatment. I used the delta method in R package *msm* (Jackson 2011) to calculate the variance of this estimate of proportional abundance based on a modified version of the model-averaged variance covariance matrix. Because that matrix was not positive-definite, I used R package *Matrix* (Bates and Maechler 2019) to shift this to a positive-definite matrix before proceeding with the delta method.

Recruitment and population growth rate - Finally, I used the Pradel robust design model (Huggins form) with Phi (apparent survival) and seniority used to model recruitment and λ

(Pradel 1996). Seniority is the probability that an individual captured in a particular trap session was alive during the previous capture session. Seniority is a complement to recruitment, wherein 1 – seniority estimates the probability of recruitment (Nichols 2016). Though I had convergence issues with the Pradel robust design recruitment models for my dataset, the seniority form worked properly and allowed use of the reverse time goodness-of-fit test (Gimenez et al. 2018). The set of apparent survival models for the seniority stage included candidate apparent survival models with 0.90 summed weight from the robust design survival modeling. Models with a sum weight of 0.95 were model averaged and recruitment was derived (Burnham and Anderson 2002, Williams et al. 2002, Grueber et al. 2011). Model averaged seniority results were also used to derive log(λ) which was averaged, exponentiated, and reported as average(λ). For seniority, I considered the same model set as survival, but with individual covariates (age and sex) removed.

Goodness of fit was assessed using R package R2ucare (Gimenez et al. 2018) to examine for lack of fit of the open-population components each model (Cormack-Jolly-Seber survival and reverse-time seniority models), based on pooling detection histories to one observation for each animals for the 11 primary sessions. This examination tested for evidence of overdispersion, transience, and between-session trap response. I conducted all analyses using RMark (Laake 2013) in Program R (R Core Development Team 2020).

RESULTS

I captured and created capture histories for 1,066 cotton rats, 230 cotton mice, and 82 oldfield mice. I also caught, but did not use in analysis, 245 house mice (*Mus musculus*), 25 eastern harvest mice (*Reithrodontomys humulis*), 2 marsh rice rats (*Orzomys palustris*), and 1 golden mouse (*Ochrotomys nuttalli*), several short-tailed shrews (*Blarina brevicauda*) and 2 southern flying squirrels (*Glaucomys volans*). The average number of individuals caught per grid per session was 10.9 for cotton rats (range 0-51), 2.4 for cotton mice (range 0-15), and 0.8 for oldfield mice (range 0-5). After accounting for trap closures, I had 18,298 trap nights. Cotton rat individuals were caught in an average of 1.3 sessions per individual (range 1-8). Cotton mice individuals were caught in an average of 1.3 sessions (range 1-7). Oldfield mice individuals were caught in an average of 1.2 sessions (range 1-4).

Following preliminary detectability modeling, the top detectability model was used for each species in all further modeling (Appendix 1), either because one model had nearly all support at this stage (cotton rat) or because when modeling survival and seniority, competing p models produced very similar survival and abundance estimates in further preliminary analyses (cotton mouse, oldfield mouse). Average detection probability per trap night was 0.23 (range 0.035 – 0.49) for cotton rats, 0.22 (range 0.010–0.55) for cotton mice, and 0.21 (range 0.070 – 0.36) for oldfield mice. Top models for all species included a recapture effect (Appendix 1). Recapture within a session was 1.84 times as likely (1.32–2.57; 95% CL) for cotton rats, 3.82 times as likely (2.52–5.79; 95% CL) for cotton mice, and 3.17 times as likely (1.19–8.47) for oldfield mice as initial capture.

Cotton Rat

The top four models were strongly supported in initial survival modeling (0.97 cumulative weight) and were used in model averaging. A time × treatment interaction was in the top three models (Table 1). Model averaged survival estimates over time show that the time × treatment effect on survival varied (Figure 2.3), though overall survival was higher on treated areas (Figure 2.6). In most time periods, cotton rats on treated areas were more likely to survive than those on untreated areas (Figure 2.4). This effect was largest in time 1, April to June 2018, the period when treatment was applied to the treated properties. Using the top survival model, a cotton rat on a treated area was 1.78 (1.14–2.80; 95% CL) times as likely to survive as one on an untreated area.

For seniority modeling, the top 3 models were strongly supported (0.98 cumulative weight). Time and treatment effects for seniority (γ) were in all of the top supported seniority models (Table 2.2). Using the top seniority model, there were 5 time periods where a rat on a treated area was more likely to have been alive at the last session than on an untreated area (Figure 2.5). Recruitment of cotton rats varied by treatment and time, with higher estimates between the April and June sessions each year (Figure 2.3).

Abundance estimates ranged from 0-109.6 per grid for cotton rats, with a mean estimate of 18.7 across all sampling sessions (Appendix 2). The average coefficient of variation for grid-sessions with non-zero captures was 32.1 (range 8.7-95.1) Average abundance alternated between being higher on treated and untreated areas (Table 2.3). λ estimates for cotton rats varied from 0.4-3.0 per grid per session, with an average on treated areas of 1.10 (1.04–1.18; 95% CL) and an average of 0.99 on untreated areas (0.94–1.06; 95% CL, Figure 2.7). There were spikes in population growth between the April and June trapping sessions on the treated area in 2018 and on both areas in 2019 (Figure 2.3).

Cotton Mouse

For cotton mice, there was not strong support for any individual survival model. There were 24 models with cumulative model weight of 0.95 used in model averaging (Table 2.1). Sex and treatment were in the top weighted models. Survival was higher on treated areas (Figure

2.6), and using the top survival model, an individual was 1.05 (0.49–2.25; 95% CL) times as likely to survive on a treated area than an untreated area. There was interaction with sex in which females had higher survival than males on both treated and untreated areas, with a larger difference for males between the areas (Figure 2.8). Females on treated areas were 1.28 (0.59-2.78; 95% CL) times as likely and on untreated areas 3.05 (1.42-6.58; 95% CL) times as likely to survive as males.

The top nine seniority models were used in model averaging (0.96 cumulative weight, Table 2.2). All of these top models indicated a time or time + treatment effect for γ. Using the top model with a time + treatment effect for γ (second-ranked model overall), cotton mice on untreated areas were 1.04 times as likely to have been alive during the previous capture session as mice on treated areas (0.58-1.88; 95% CL). Recruitment varied by treatment and time, showing peaks in late fall of each year and being higher in treated areas for most of the sessions, though the treated and untreated areas were not statistically different from one another (Figure 2.8).

Abundance estimates ranged from 0-80.3 per grid for cotton mice, with a mean estimate of 5.3 across all sampling sessions (Appendix 2). The average coefficient of variation for grid-sessions with non-zero captures was 51.8 (range 18.9-119.2). Average abundance was higher for untreated than treated sites in the first two sessions, but higher for treated sites in all following sessions which had captures on both areas (Table 2.3).

Estimates of λ ranged from 0.5 – 3.5 per grid per session. The average on treated areas of 1.08 (0.999–1.18; 95% CL) was higher than the (0.95; 0.88–1.02; 95% CL) on untreated areas (Figure 2.7). Population growth was highest in late fall to winter of each year on both treated and untreated areas (Figure 2.8).

Oldfield Mouse

For the model averaged survival results for oldfield mice, 15 models with a cumulative weight of 0.96 were used (Table 2.1). Using model averaged results, oldfield mice had higher survival on untreated areas throughout the study (Figure 2.6), though the difference between treated and untreated areas varied by time (Figure 2.9). Using the top model, an oldfield mouse on an untreated area was 4.32 (1.17-15.96; 95% CL) times as likely to survive as one on a treated area.

For oldfield mice, 31 models were used in seniority model averaging (0.96 cumulative weight). The top 2 models for seniority were the null model for γ (Table 2.2). Using the model averaged results, recruitment was higher on treated areas, though treated and untreated areas did not differ statistically from one another and there was not much seasonal variation (Figure 2.9).

Abundance estimates ranged from 0-19.8 per grid for cotton mice, with a mean estimate of 2.0 across all sampling sessions (Appendix 2). The average coefficient of variation for grid-sessions with non-zero captures was 81.0 (range 36.3-185.2). Average abundance was higher on untreated areas for most sessions (Table 2.3).

Estimates of λ ranged from 0.6 – 1.1 per grid per session. The averages on both treated and untreated areas, 0.91 (0.74 – 1.12; 95% CL) and 0.90 (0.74 – 1.10; 95% CL), respectively, indicate declining populations (Figure 2.7). Population growth was similar between treated and untreated areas throughout the year (Figure 2.9).

DISCUSSION

My findings indicate that effects of RIFA on small mammals are dependent upon species. I had expected similar life history strategies and altricial young of cotton mice and oldfield mice to yield similar results to RIFA removal, including increased recruitment. However, I did not find a change in recruitment for any of the focal species. Additionally, I did not expect to see changes in survival, but there were increases for both cotton rats and cotton mice on treated areas.

For cotton rats, a semi-precocial species, there were no impacts on recruitment which supported my hypothesis. However, this was also true for the altricial species, cotton mice and oldfield mice, for which I had expected RIFA removal to increase recruitment. I detected changes in recruitment associated with seasonal breeding peaks for each species: early summer for cotton rats; winter for cotton mice; and no seasonal change for oldfield mice. RIFA are thought to impact small mammals through depredation of the young of altricial species while still in the nest (Lach and Hooper-Bui 2010, Lach et al. 2010), but population level impacts of this were not supported by my data. I had expected this for the semi-precocial cotton rat, as young likely leave the nest early enough that direct depredation of young is not a major influence on recruitment. However, it also seems that recruitment of cotton mice and oldfield mice was not impacted, indicating that direct depredation of young in the nest by RIFA was not an important factor for population level recruitment, though some depredation could still be occurring.

RIFA removal resulted in increased survival of both cotton rats and cotton mice, increasing λ on treated sites during the study period. Previous studies have shown changes in cotton rat habitat use and foraging patterns when RIFA are present (Pedersen et al. 2003, Holtcamp et al. 2010, Darracq et al. 2016). These changes in behavior due to RIFA could lead to increased mortality from other predators, though a previous study found impacts on survival from RIFA only in the absence of other predators (Long et al. 2015). However, private hunting lands, as the ones my study was conducted on, often remove meso-predators from their properties, which could make my study areas more similar to predator free areas and indicate that what I found was a compensatory response. Further studies with more direct comparisons of predator impacts could draw out these relationships. Additionally, increases in survival could be linked to competition for food or changes in foraging behaviors. Stings from RIFA are associated with less efficient foraging of cottons rats (Darracq et al. 2016) and fear of envenomation could lead to changes in small mammal demographics (Orrock and Danielson 2004, Preisser et al. 2005).

Removal of RIFA resulted in a larger increase in survival for males than for females for cotton mice, so the effects of RIFA which influence cotton mouse survival are more important for males than for females. Male cotton mice have larger home ranges than females (Wolfe and Linzey 1977), which could result in more behavior changes when RIFA are present. Moving over larger areas to find mates and forage could leave them more vulnerable to depredation from other species if they change behaviors around RIFA.

Although treatment resulted in lower survival and proportional abundance of oldfield mice, λ estimates were similar on treated and untreated sites, though low samples sizes were problematic for this species. Further, I found an overall declining population of oldfield mice on both treated and untreated areas. Oldfield mice have been shown to change behaviors and reduce foraging time in the presence of RIFA (Orrock and Danielson 2004). Behavior changes are not always linked to demographic changes, but since I found that survival was higher with RIFA present, perhaps the oldfield mice have adapted to risk of RIFA envenomation while foraging or utilize higher value resources for a shorter time. Still, oldfield mice are present on the study area in lower abundances than cotton mice and had an overall declining population, so their populations might be more unstable and respond negatively to changes in the system, such as the removal of ants. This shows the complexity of invasive species removal, if removal of a long-established invasive species adds stress to a potentially declining species.

Overall, both the magnitude of RIFA effects on small mammals and mechanisms by which impacts occur require further investigation. While removal had slightly positive effects for cotton rats and cotton mice, it had negative impacts for oldfield mice. If RIFA had been removed for a longer period of time in this study, clearer impacts on survival and recruitment might have been evident. Our study did not investigate specific behaviors, but it would be beneficial for future studies to link behavioral changes around RIFA to changes in survival for small mammals, leading to better understanding of the processes that are occurring. Further, additional studies on additive or compensatory effects of RIFA on survival would provide valuable management information.

The various impacts on the small mammal species in my study illustrate the complicated nature of invasive species removal, especially for a long established species (Simberloff 2014). Species that have been established for a long time, as the RIFA, which has been in the United States for close to 90 years, can become established in local ecosystems. This does not mean that no action should be taken, but instead, that removal should be well-studied and chosen based on the best-science available for that species (Mack et al. 2000, Zavaleta et al. 2001, Hulme 2006). Slight increases in non-target small mammal populations are likely not enough on their own to justify widespread use of chemical toxicants, due to other impacts (see Chapter 1). However, RIFA range is likely to expand within the United States with increasing temperatures from climate change (Korzukhin et al. 2001, Tschinkel 2006), and increased human disturbance can allow RIFA to spread or increase density of populations (King and Tschinkel 2008, Lebrun et al.

2012). These changes could cause greater impacts to small mammal populations, highlighting the importance of understanding the changes that occur.

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Tables and Figures

Table 2.1 The model sets used to model average survival and population estimate results for the cotton rat, cotton mouse, and oldfield mouse from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. These model sets comprised ≥0.95 cumulative weight of the full model sets.

Species	Model	AICc	ΔAICc	*w*	npar
Cotton rat	~time * treatment + sex + ageclass	6490.28	0.00	0.68	69
	~time * treatment + sex	6492.70	2.42	0.20	68
	~treatment * sex + treatment * time	6494.67	4.39	0.08	69
	~time + treatment + sex + ageclass	6495.79	5.51	0.04	60
Cotton mouse	~treatment * sex	1496.36	0.00	0.17	26
	~treatment + sex	1496.58	0.22	0.15	25
	~sex	1497.29	0.93	0.11	24
	~treatment * sex + Time	1498.19	1.82	0.07	27
	~Time + sex	1498.34	1.98	0.06	25
	~treatment * sex + ageclass	1498.40	2.03	0.06	27
	~Time + treatment + sex	1498.51	2.15	0.06	26
	~treatment + sex + ageclass	1498.71	2.34	0.05	26
	~sex + ageclass	1499.47	3.11	0.04	25
	~treatment * sex + treatment * Time	1499.97	3.61	0.03	28
	~treatment * Time + sex	1500.33	3.97	0.02	27
	~treatment * sex + Time + I(Time^2)	1500.44	4.08	0.02	28
	~Time + I(Time^2) + sex	1500.47	4.11	0.02	26
	~Time + sex + ageclass	1500.49	4.13	0.02	26
	~Time + treatment + sex + ageclass	1500.62	4.26	0.02	27
	~Time + I(Time^2) + treatment + sex	1500.74	4.38	0.02	27
	~treatment	1500.85	4.49	0.02	24
	~1	1500.90	4.54	0.02	23
	~Time	1502.14	5.78	0.01	24
	~treatment * Time + sex + ageclass	1502.39	6.03	0.01	28
	~treatment * sex + time	1502.53	6.17	0.01	35
	~Time + I(Time^2) + sex + ageclass	1502.63	6.26	0.01	27
	~Time + treatment	1502.80	6.44	0.01	25
	~Time + I(Time^2) + treatment + sex + ageclass	1502.86	6.50	0.01	28

Oldfield mouse	~Time + I(Time^2) + treatment	477.85	0.00	0.20	17
	~Time + I(Time^2) + treatment + sex	478.03	0.19	0.19	18
	~Time + treatment	479.46	1.61	0.09	16
	~Time + I(Time^2) + sex	480.20	2.35	0.06	17
	~Time + treatment + sex	480.23	2.38	0.06	17
	~treatment	480.49	2.64	0.05	15
	~treatment * sex + Time + I(Time^2)	480.66	2.82	0.05	19
	~treatment + sex	480.77	2.92	0.05	16
	~Time + I(Time^2)	480.78	2.93	0.05	16
	~treatment * Time	480.97	3.12	0.04	17
	~Time	481.24	3.40	0.04	15
	~Time + sex	481.36	3.51	0.04	16
	~sex	481.73	3.88	0.03	15
	~treatment * Time + sex	481.85	4.01	0.03	18
	~1	482.29	4.44	0.02	14

Table 2.2 The model sets used to model average seniority results for the cotton rat, cotton mouse, and oldfield mouse from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. These model sets comprised ≥0.95 cumulative weight of the full model sets.

	Phi	**Gamma**	**AICc**	**ΔAICc**	***w***	**npar**
Cotton rat	~time * treatment	~time * treatment	11136.56	0.00	0.64	86
	~time * treatment	~time + treatment	11137.94	1.38	0.32	77
	~time * treatment	~time	11141.98	5.43	0.04	76
	~time * treatment	~Time + I(Time^2) + treatment	11186.00	49.44	0.00	70
	~time + treatment	~Time + I(Time^2) + treatment	11223.49	86.93	0.00	61
Cotton mouse	~treatment * Time	~time	2430.83	0.00	0.63	36
	~treatment * Time	~time + treatment	2433.15	2.32	0.20	37
	~treatment	~time	2436.85	6.02	0.03	34
	~Time	~time + treatment	2437.16	6.33	0.03	35
	~Time + treatment	~time	2437.16	6.33	0.03	35
	~1	~time + treatment	2437.34	6.51	0.02	34
	~treatment	~time + treatment	2439.07	8.24	0.01	35
	~Time + I(Time^2)	~time + treatment	2439.16	8.33	0.01	36
	~Time + treatment	~time + treatment	2439.20	8.37	0.01	36
Oldfield mouse	~Time	~1	833.72	0.00	0.17	16
	~Time + I(Time^2)	~1	834.84	1.13	0.10	17
	~Time + treatment	~treatment	835.47	1.76	0.07	18
	~Time	~Time	835.60	1.88	0.07	17
	~Time + I(Time^2) + treatment	~treatment	835.91	2.19	0.06	19
	~Time	~treatment	836.10	2.38	0.05	17
	~Time + treatment	~1	836.32	2.60	0.05	17
	~Time + I(Time^2)	~Time	836.55	2.84	0.04	18
	~treatment	~treatment	836.74	3.02	0.04	17
	~treatment * Time	~treatment	837.20	3.48	0.03	19
	~Time + I(Time^2)	~treatment	837.28	3.56	0.03	18
	~Time + treatment	~Time + treatment	837.35	3.64	0.03	19
	~Time + I(Time^2) + treatment	~1	837.49	3.78	0.03	18

~treatment	~Time + treatment	837.51	3.80	0.03	18
~Time + I(Time^2) + treatment	~Time + treatment	837.54	3.82	0.03	20
~Time	~Time + treatment	838.02	4.30	0.02	18
~Time	~Time + I(Time^2)	838.09	4.37	0.02	18
~treatment	~1	838.23	4.52	0.02	16
~Time + treatment	~Time	838.24	4.52	0.02	18
~Time + I(Time^2)	~Time + I(Time^2)	838.64	4.93	0.01	19
~treatment * Time	~1	838.67	4.96	0.01	18
~treatment	~Time	838.89	5.17	0.01	17
~Time + I(Time^2) + treatment	~Time + I(Time^2) + treatment	839.00	5.29	0.01	21
~Time + I(Time^2)	~Time + treatment	839.03	5.32	0.01	19
~Time + I(Time^2) + treatment	~Time	839.25	5.53	0.01	19
~treatment * Time	~Time + treatment	839.41	5.69	0.01	20
~Time + treatment	~Time + I(Time^2) + treatment	839.71	5.99	0.01	20
~Time + treatment	~treatment * Time	839.81	6.09	0.01	20
~treatment	~Time + I(Time^2) + treatment	840.02	6.31	0.01	19
~treatment	~treatment * Time	840.11	6.39	0.01	19
~Time + I(Time^2) + treatment	~treatment * Time	840.30	6.58	0.01	21

Table 2.3 The proportional abundance (treated / untreated) of cotton rats, cotton mice, and oldfield mice from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. There is a difference in abundance between areas if confidence limits do not cross 1, indicated by bold text. A proportional abundance >1 indicates higher abundance on treated areas, while <1 indicates higher abundance on untreated areas. Proportional abundances in December 2018 account for a grid closure on an untreated area.

Species		**Session**	**Proportional Abundance (Treated to Untreated)**	**95% CL**
Cotton rat	2018	April	0.78	(0.51, 1.18)
		June	0.94	(0.74, 1.18)
		August	**2.06**	**(1.79, 2.36)**
		October	**2.18**	**(1.59, 3.00)**
		December	**0.41**	**(0.29, 0.58)**
	2019	February	**0.63**	**(0.42, 0.93)**
		April	1.12	(0.86, 1.46)
		June	**1.19**	**(1.08, 1.31)**
		August	0.94	(0.77, 1.14)
		October	0.96	(0.77, 1.18)
		December	**1.71**	**(1.28, 2.29)**
Cotton mouse	2018	April	**0.23**	**(0.05, 0.96)**
		June	**0.55**	**(0.40, 0.76)**
		August	**5.87**	**(1.97, 17.50)**
		October	0.00	(0.00, 0.00)
		December	1.34	(0.70, 2.56)
	2019	February	1.26	(0.98, 1.63)
		April	**2.29**	**(1.75, 2.98)**
		June	**3.12**	**(1.40, 6.96)**
		August	1.32	(0.58, 3.02)
		October	0.78	(0.43, 1.43)
		December	1.47	(0.85, 2.55)
Oldfield mouse	2018	April	1.03	(0.68, 1.55)
		June	**0.35**	**(0.12, 0.97)**
		August	0.85	(0.12, 5.96)
		October	0.28	(0.00, 253.30)
		December	0.88	(0.41, 1.91)
	2019	February	0.62	(0.04, 9.06)

April	1.61	(0.49, 5.27)
June	0.60	(0.30, 1.21)
August	1.21	(0.00, 2720.31)
October	0.88	(0.10, 7.45)
December	0.74	(0.24, 2.29)

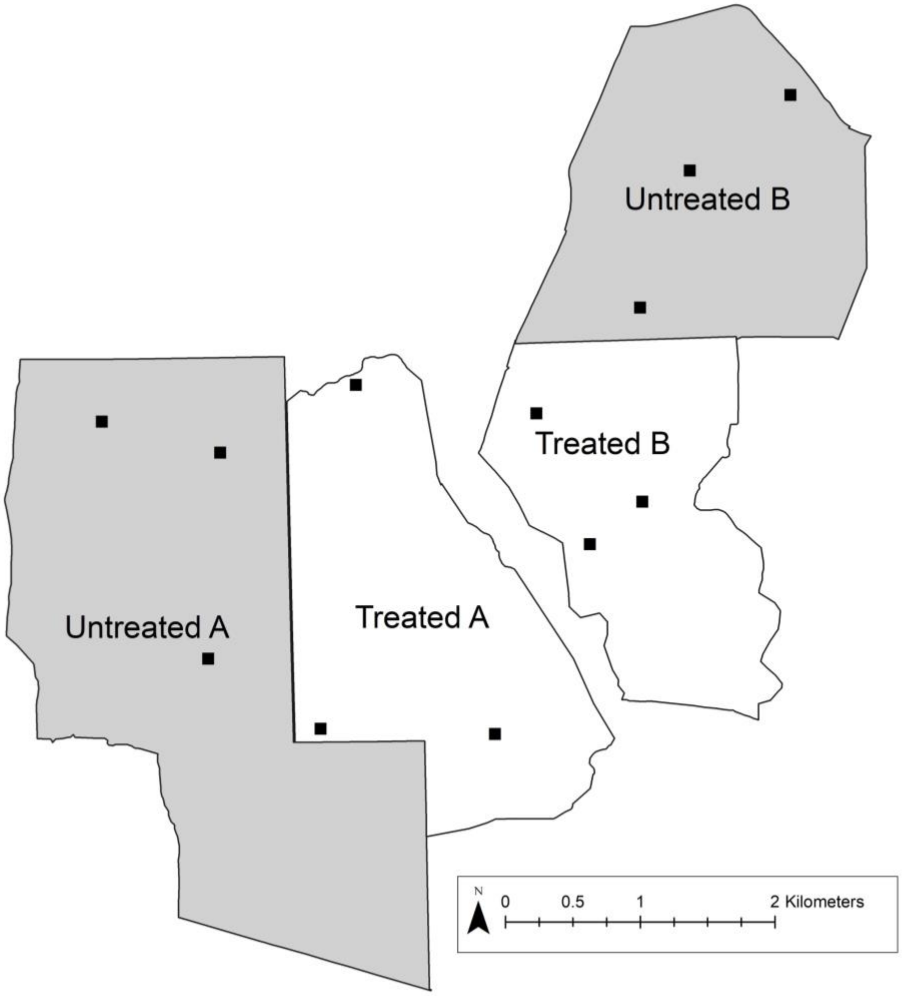


Figure 2.1 The experimental units near Albany, Georgia for a study on cotton rat, cotton mouse, and oldfield mouse response to RIFA removal from April 2018 – December 2019. Each experimental unit had three, 49-trap small mammal trapping grids (black square) randomly placed across the unit.

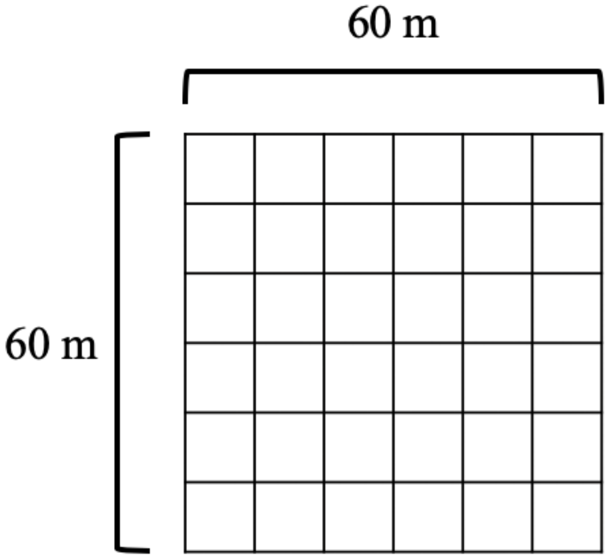


Figure 2.2 The small mammal sampling grids used to study cotton rat, cotton mouse, and oldfield mouse response to RIFA removal from April 2018 – December 2019 in southwest Georgia. Each grid included 49 Sherman traps in a 7x7 layout, with 10-m spacing between traps, with trap placement indicated by line intersections in the figure.

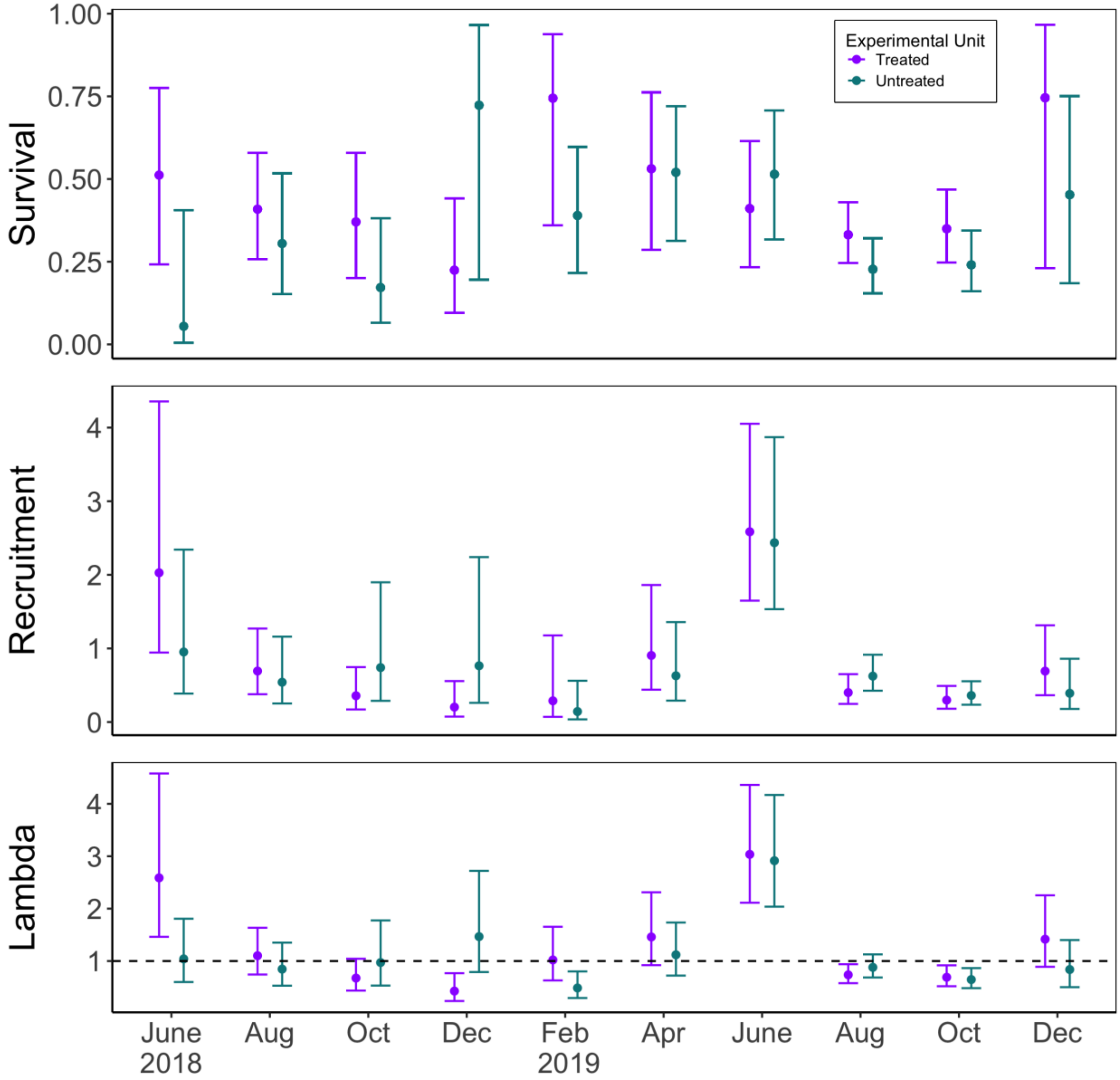


Figure 2.3 Model averaged survival, recruitment, and λ estimates of cotton rats from April 2018 – December 2019 from a study of response to RIFA removal in southwest Georgia. Error bars show 95% confidence limits. The model set for survival is from model averaged results of models presented in Table 2.1. The recruitment results are derived from the model averaged results of the model set in Table 2.2. The dashed line on the λ plot indicates no population growth. The labeled month indicates the end of the 2-month period for which the parameter is estimated.

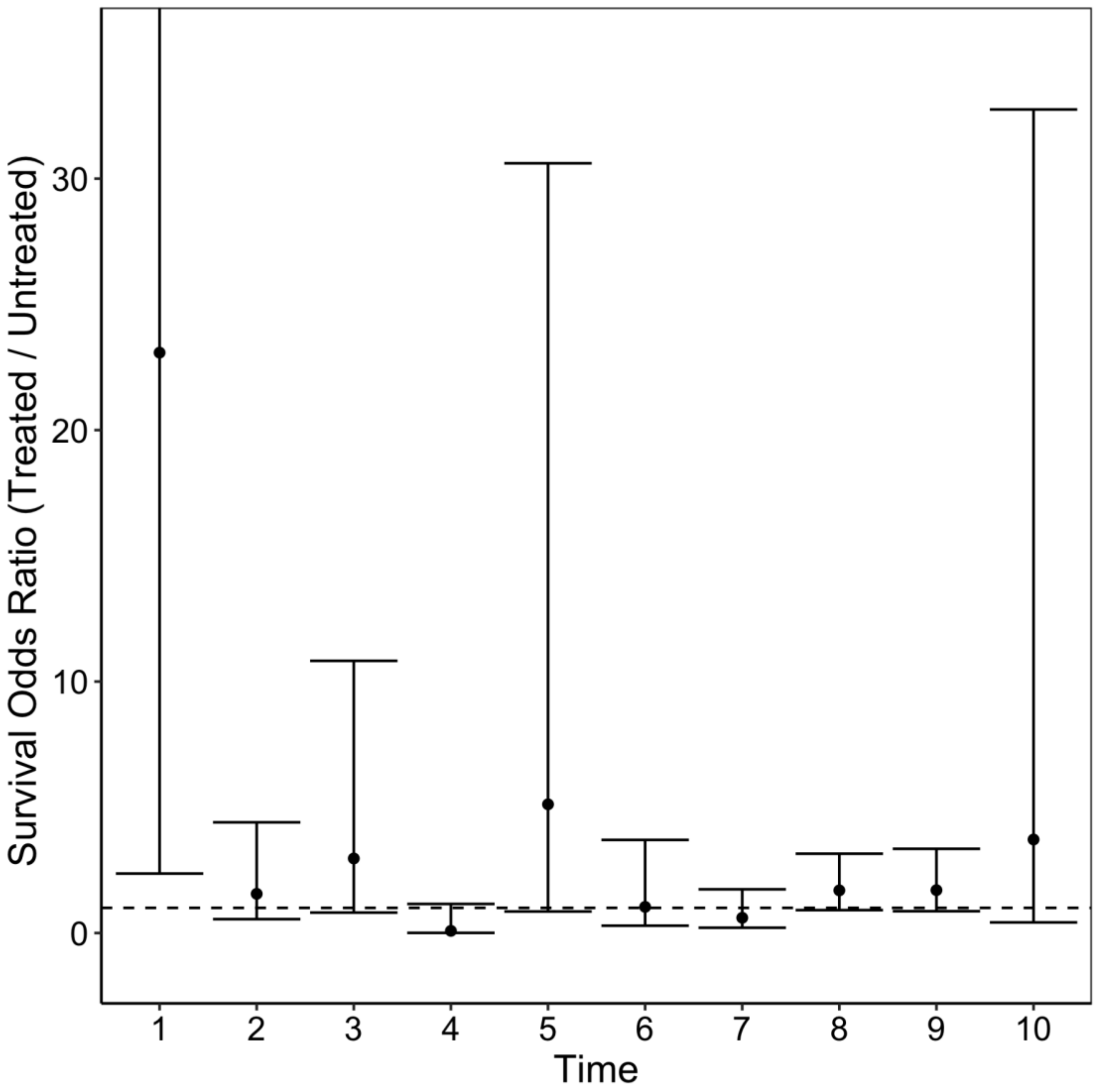


Figure 2.4 The odds ratio (treated / untreated) for between-session survival of cotton rats using estimates from the top ranked survival model (Table 1) from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. A value > 1 indicates higher likelihood of survival on treated areas, while a value <1 indicates higher likelihood on untreated areas, and a value of 1 (dashed line) indicates no effect. Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect. The error bar for time 1 continues to 225.35. Time 1 was the period during which Extinguish® Plus was applied to the treated properties.

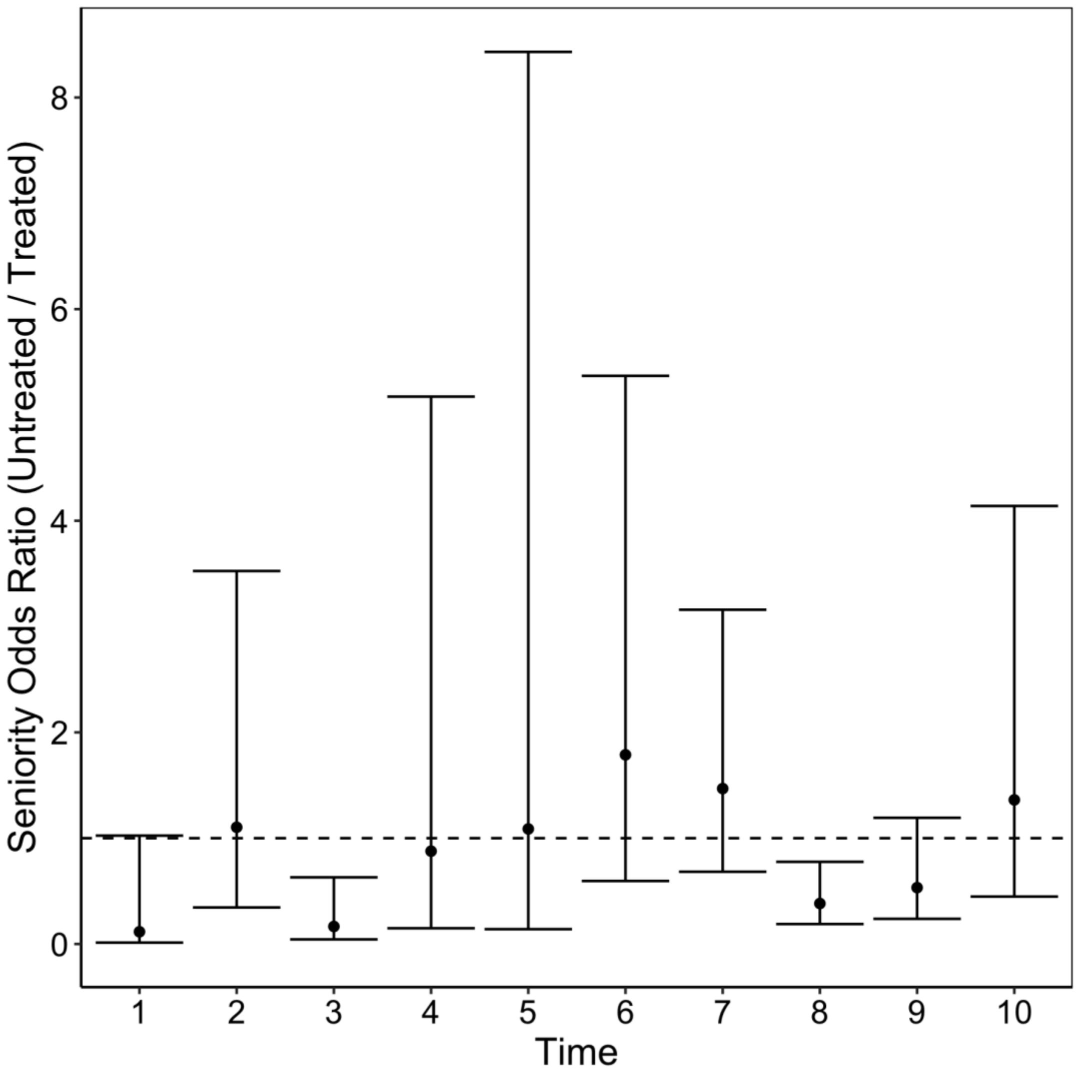


Figure 2.5 The odds ratio (untreated / treated) of seniority of cotton rats from a study of small mammal response to RIFA removal in southwest Georgia from April 2018 – December 2019. Seniority is the probability that an individual captured in a particular trap session was alive during the previous capture session. A value > 1 indicates higher likelihood of the rat having been alive on untreated areas, while a value <1 indicates higher likelihood on treated areas, and a value of 1 (dashed line) indicates no effect. Error bars represent 95% confidence limits. Error bars that do not cross 1 indicate a significant effect.

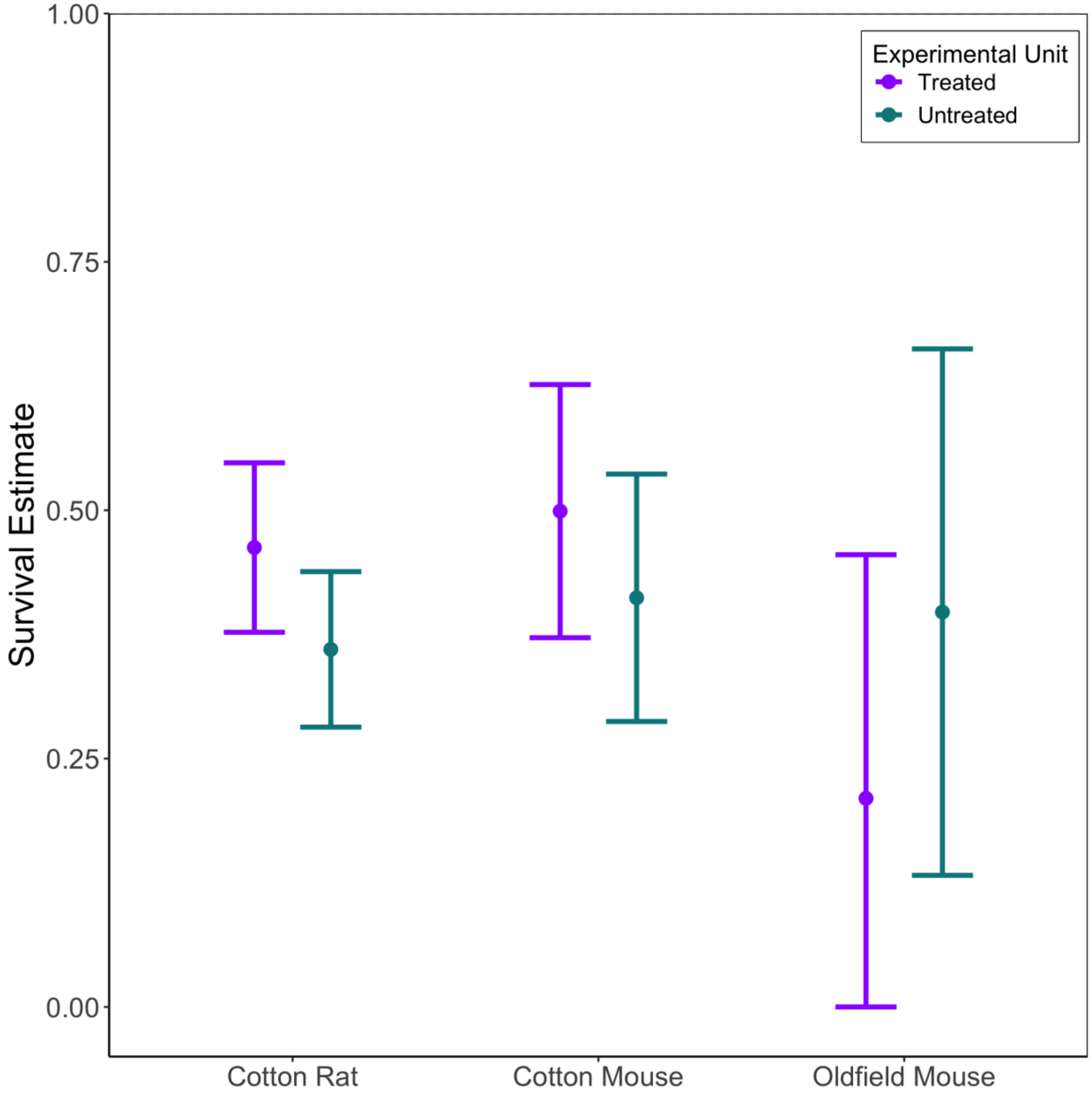


Figure 2.6 Overall average survival estimates of cotton rats, cotton mice, and oldfield mice from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. Estimates are from the model averaged results of models presented in Table 2.1. Error bars show 95% confidence limits.

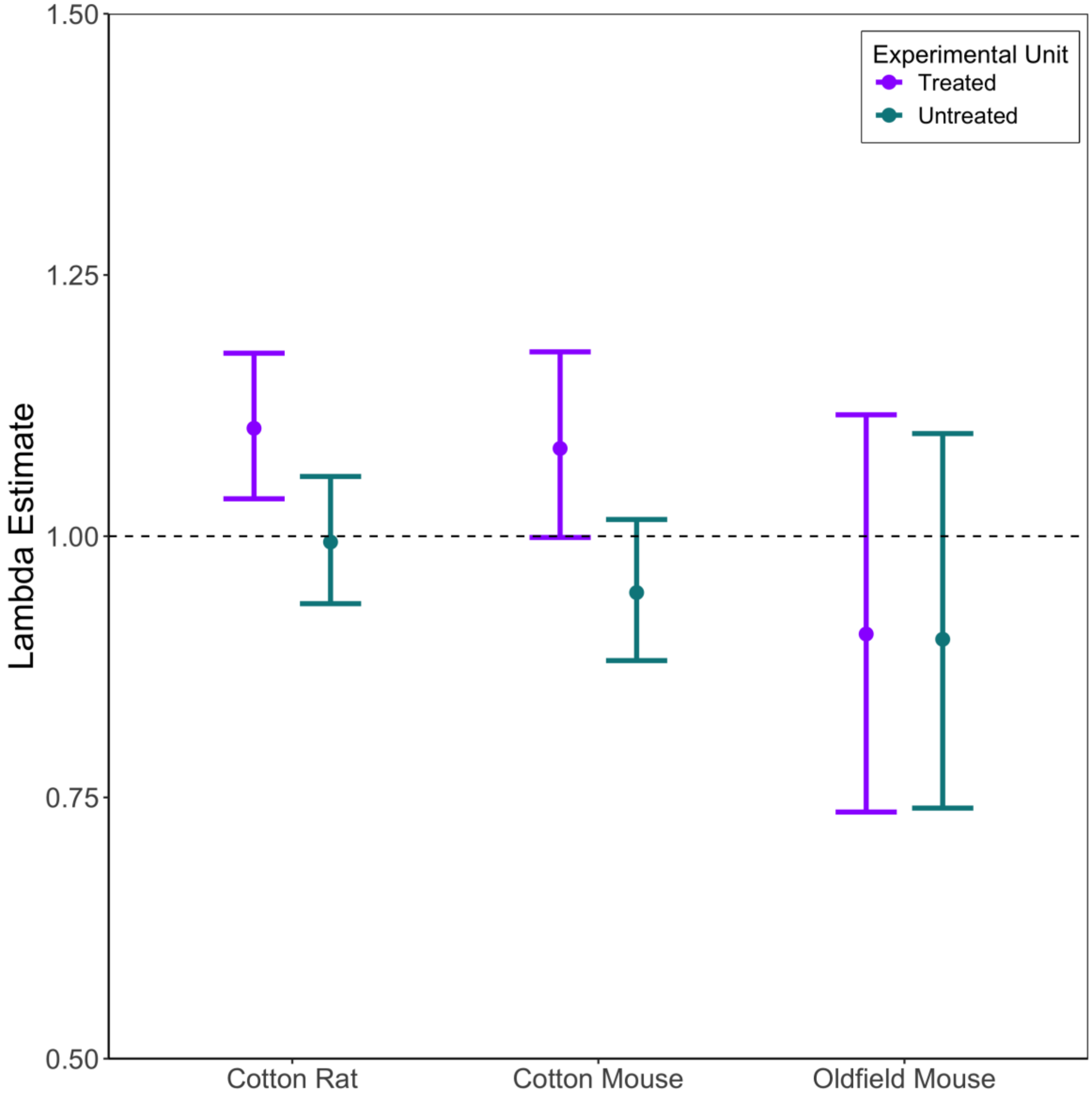


Figure 2.7 Overall average λ estimates of cotton rats, cotton mice, and oldfield mice from April 2018 – December 2019 from a study of response to RIFA removal in southwest Georgia. Estimates are from the model averaged results of models presented in Table 2.2. Error bars show 95% confidence limits. The dashed line indicates no population growth.

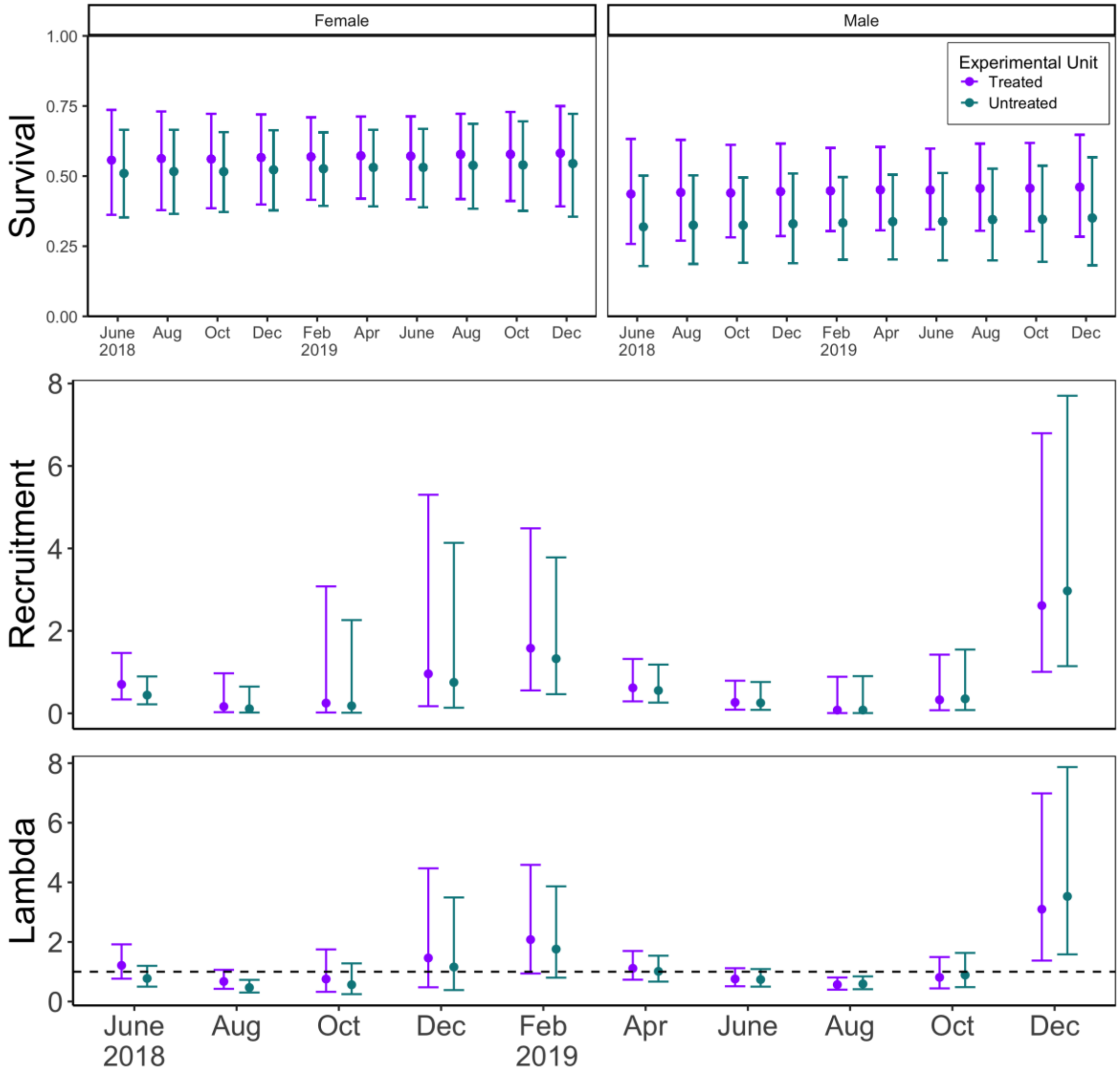


Figure 2.8 Model averaged survival, recruitment, and λ estimates of cotton mice from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. Error bars show 95% confidence limits. The model set for survival is from model averaged results of models presented in Table 2.1. Survival results are separated by sex due to a sex × treatment interaction in the top model. The recruitment results are derived from the model averaged results of the model set in Table 2.2. The dashed line on the λ plot indicates no population growth. The labeled month indicates the end of the 2-month period for which the parameter is estimated.

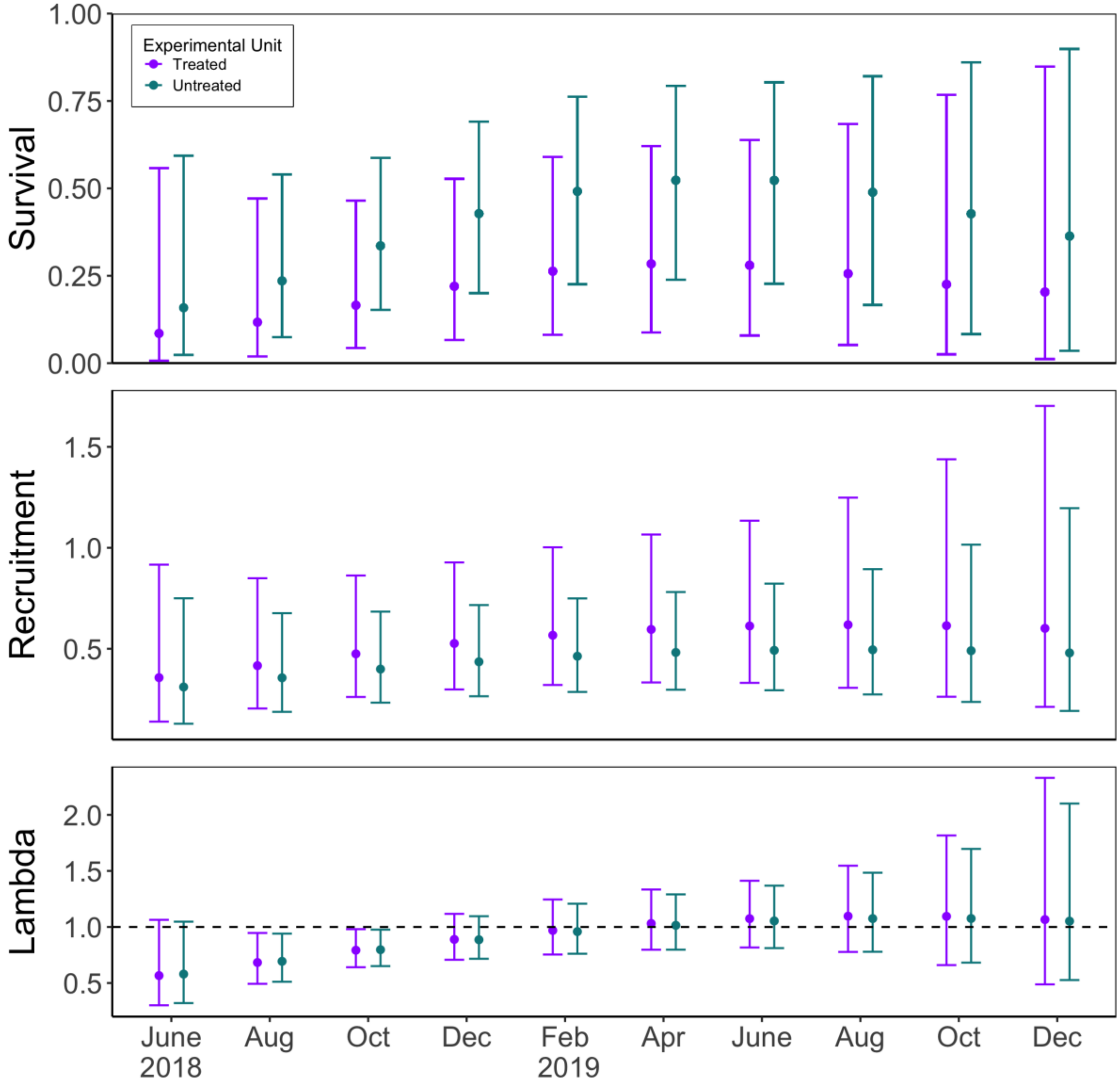


Figure 2.9 Model averaged survival, recruitment, and λ estimates of oldfield mice from April 2018 – December 2019 from a study of small mammal response to RIFA removal in southwest Georgia. Error bars show 95% confidence limits. The model set for survival is from model averaged results of models presented in Table 2.1. The recruitment results are derived from the model averaged results of the model set in Table 2.2. The dashed line on the λ plot indicates no population growth. The labeled month indicates the end of the 2-month period for which the parameter is estimated.

Appendix 1. Ant Species

Appendix Table 1.1 Taxonomic list of ant species found in collection vials in a study on RIFA reinvasion in southwest Georgia from April 2018 – December 2019.

Genus	Species
Brachymyrmex	*obscurior*
Brachymyrmex	*patagonicus*
Camponotus	*casteneus*
Camponotus	*floridanus*
Camponotus	*pennsylvanicus*
Dorymyrmex	*bossutus*
Dorymyrmex	*bureni*
Dorymyrmex	*flavopectus*
Dorymyrmex	*flavus*
Dorymyrmex	*reginicula*
Dorymyrmex	*smithi*
Forelius	*mccooki*
Forelius	*pruinosus*
Forelius	*spp*
Formica	*biophilica*
Formica	*dolosa*
Formica	*pallidefulva*
Nylanderia	*arenivaga*
Nylanderia	*faisonensis*
Nylanderia	*fulva*
Nylanderia	*parvula*
Nylanderia	*phantasma*
Nylanderia	*spp*
Nylanderia	*vividula*

Nylanderia	*wojciki*
Pheidole	*bilimeki*
Pheidole	*davisi*
Pheidole	*dentata*
Pheidole	*dentigula*
Pheidole	*metallescens*
Pheidole	*morrisii*
Pheidole	*navigans*
Pheidole	*obscurithorax*
Pheidole	*soritis*
Pheidole	*spp*
Pheidole	*tetra*
Pheidole	*tysoni*
Prenolepis	*imparis*
Pseudomyrmex	*pallidus*
Solenopsis	*invicta*
Solenopsis	*molesta*

Appendix 2: Detectability Models

Appendix Table 2.1 Variables included in my detectability model suites for cotton rats, cotton mice, and oldfield mice for a study from April 2018 – December 2019 on response to RIFA removal in southwest Georgia.

Variable	**Description**
ageclass	A juvenile or adult designation based on weight at initial capture and changing to adult for the next capture period if caught again
c	A recapture effect indicating an animal's likelihood of detection depending on whether it has been captured before
capture count	A count of unique individuals of species other than that species captured in a session
session	The primary sampling period that occurred every 2 months from April 2018 - December 2019
sex	Female or male designation
time	Variation by the three nights of trapping within a secondary session
trap group	A subset of traps within a session that were trapped on the same days. There were 2 trap groups per session, 3 days each, with one trap group opening after the previous had closed on the third day

Appendix Table 2.2 Detectability model set used for cotton rats from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. The top model was used in subsequent modeling.

Model	**AICc**	**ΔAICc**	***w***	**npar**
~trapgroup * session + session * time + c + ageclass + sex + capture count	6535.31	0.00	0.89	48
~trapgroup * session + session * time + c + ageclass + sex	6539.57	4.25	0.11	47
~trapgroup * session + session * time + ageclass + sex + capture count	6553.00	17.69	0.00	47
~trapgroup * session + session * time + c + sex	6553.55	18.24	0.00	46
~trapgroup * session + time + c + ageclass + sex + capture count	6555.51	20.20	0.00	28
~session + session * time + c + ageclass + sex + capture count	6556.56	21.25	0.00	38
~session + session * time + c + ageclass + sex	6556.74	21.43	0.00	37
~trapgroup * session + c + ageclass + sex + capture count	6556.84	21.53	0.00	26
~trapgroup * session + session * time + ageclass + sex	6557.06	21.75	0.00	46
~trapgroup * session + time + c + ageclass + sex	6559.67	24.36	0.00	27
~trapgroup * session + c + ageclass + sex	6561.00	25.69	0.00	25
~session + session * time + c + sex	6568.89	33.58	0.00	36
~trapgroup * session + session * time + c + ageclass	6569.08	33.77	0.00	46
~trapgroup * session + time + ageclass + sex + capture count	6571.61	36.29	0.00	27
~trapgroup * session + session * time + sex	6571.66	36.35	0.00	45
~trapgroup * session + time + c + sex	6573.93	38.62	0.00	26
~trapgroup * session + c + sex	6575.15	39.83	0.00	24
~trapgroup * session + time + ageclass + sex	6575.47	40.16	0.00	26
~session + time + c + ageclass + sex + capture count	6577.28	41.97	0.00	18
~session + time + c + ageclass + sex	6577.39	42.08	0.00	17
~session + c + ageclass + sex + capture count	6577.65	42.34	0.00	16
~session + c + ageclass + sex	6577.83	42.52	0.00	15
~trapgroup * session + session * time + ageclass	6578.85	43.54	0.00	45
~session + session * time + ageclass + sex	6579.61	44.30	0.00	36
~session + session * time + ageclass + sex + capture count	6580.19	44.88	0.00	37
~trapgroup * session + session * time + c + capture count	6580.27	44.96	0.00	46
~trapgroup * session + session * time + c	6583.43	48.12	0.00	45
~session + session * time + c + ageclass	6588.31	53.00	0.00	36
~trapgroup * session + time + c + ageclass	6588.87	53.56	0.00	26
~session + time + c + sex	6589.75	54.43	0.00	16

~session + c + sex	6590.11	54.80	0.00	14
~trapgroup * session + time + sex	6590.31	55.00	0.00	25
~trapgroup * session + session * time + capture count	6590.41	55.10	0.00	45
~session + session * time + sex	6592.22	56.91	0.00	35
~trapgroup * session + c + ageclass	6592.24	56.93	0.00	24
~trapgroup * session + session * time	6593.73	58.42	0.00	44
~trapgroup * session + time + ageclass	6597.54	62.23	0.00	25
~session + time + ageclass + sex	6598.33	63.02	0.00	16
~session + time + ageclass + sex + capture count	6598.98	63.67	0.00	17
~session + session * time + c	6600.28	64.97	0.00	35
~trapgroup * session + time + c + capture count	6600.38	65.07	0.00	26
~session + session * time + c + capture count	6601.29	65.98	0.00	36
~session + session * time + ageclass	6602.62	67.30	0.00	35
~trapgroup * session + time + c	6603.51	68.19	0.00	25
~trapgroup * session + c + capture count	6603.65	68.33	0.00	24
~trapgroup * session + c	6606.65	71.34	0.00	23
~session + time + c + ageclass	6608.64	73.33	0.00	16
~trapgroup * session + time + capture count	6609.50	74.19	0.00	25
~session + c + ageclass	6610.38	75.07	0.00	14
~session + time + sex	6611.13	75.82	0.00	15
~trapgroup * session + time	6612.69	77.38	0.00	24
~session + session * time	6614.94	79.63	0.00	34
~session + session * time + capture count	6616.18	80.87	0.00	35
~trapgroup * session + ageclass + sex + capture count	6619.15	83.84	0.00	25
~session + time + c	6620.84	85.53	0.00	15
~session + time + ageclass	6621.62	86.31	0.00	15
~session + time + c + capture count	6621.87	86.56	0.00	16
~session + c	6622.48	87.17	0.00	13
~trapgroup * session + ageclass + sex	6623.02	87.70	0.00	24
~session + c + capture count	6623.47	88.16	0.00	14
~session + time	6634.15	98.84	0.00	14
~session + time + capture count	6635.41	100.10	0.00	15
~trapgroup * session + sex	6637.87	102.56	0.00	23
~trapgroup * session + ageclass	6645.20	109.89	0.00	23
~session + ageclass + sex	6645.28	109.97	0.00	14
~session + ageclass + sex + capture count	6645.91	110.60	0.00	15
~trapgroup * session + capture count	6657.22	121.91	0.00	23

~session + sex	6658.14	122.83	0.00	13
~trapgroup * session	6660.36	125.05	0.00	22
~session + ageclass	6668.68	133.37	0.00	13
~session	6681.26	145.95	0.00	12
~session + capture count	6682.53	147.22	0.00	13

Appendix Table 2.3 Detectability model set used for cotton mice from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. The top model was used in subsequent modeling. For cotton mice, a modified session variable of session was used in which detectability for October 2018 was set equal to October 2019, due to only one capture of a cotton mouse in October 2018.

Model	**AICc**	**ΔAICc**	***w***	**npar**
~trapgroup * session + c + capture count	1500.90	0.00	0.37	23
~trapgroup * session + c + ageclass + sex + capture count	1501.55	0.64	0.27	25
~session + c + ageclass + sex + capture count	1503.49	2.58	0.10	15
~trapgroup * session + time + c + capture count	1504.22	3.32	0.07	25
~session + c + capture count	1504.31	3.41	0.07	13
~trapgroup * session + time + c + ageclass + sex + capture count	1504.78	3.88	0.05	27
~session + time + c + ageclass + sex + capture count	1505.38	4.48	0.04	17
~session + time + c + capture count	1506.42	5.52	0.02	15
~trapgroup * session + c + ageclass	1511.91	11.01	0.00	23
~trapgroup * session + c	1512.28	11.38	0.00	22
~trapgroup * session + c + ageclass + sex	1512.72	11.82	0.00	24
~trapgroup * session + c + sex	1513.08	12.18	0.00	23
~trapgroup * session + time + c + ageclass	1515.90	15.00	0.00	25
~trapgroup * session + time + c	1516.27	15.37	0.00	24
~trapgroup * session + time + c + ageclass + sex	1516.71	15.81	0.00	26
~trapgroup * session + time + c + sex	1517.06	16.15	0.00	25
~session + c + ageclass	1517.12	16.22	0.00	13
~session + c + ageclass + sex	1518.43	17.53	0.00	14
~session + c	1520.13	19.23	0.00	12
~session + time + c + ageclass	1520.40	19.50	0.00	15
~session + session2 * time + c + ageclass + sex + capture count	1520.45	19.55	0.00	35
~trapgroup * session + session * time + c + capture count	1521.06	20.16	0.00	43
~session + session * time + c + capture count	1521.30	20.40	0.00	33
~session + c + sex	1521.46	20.56	0.00	13
~session + time + c + ageclass + sex	1521.67	20.76	0.00	16
~trapgroup * session + session * time + c + ageclass + sex + capture count	1521.88	20.98	0.00	45
~session + time + c	1523.43	22.53	0.00	14

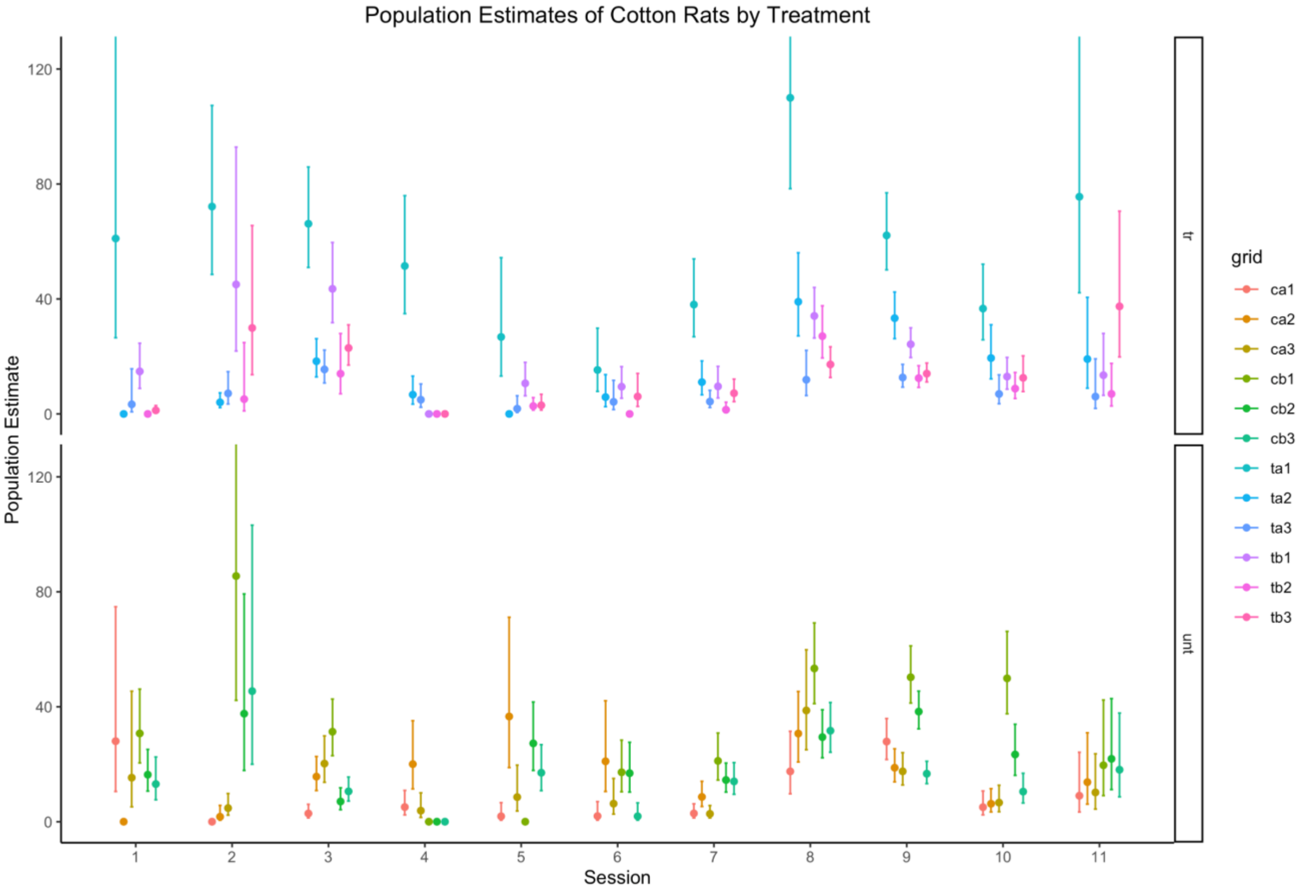
~session + time + c + sex	1524.73	23.82	0.00	15
~trapgroup * session + session * time + c + ageclass	1533.23	32.33	0.00	43
~trapgroup * session + time + capture count	1533.57	32.66	0.00	24
~trapgroup * session + session * time + c	1533.60	32.70	0.00	42
~trapgroup * session + session * time + c + ageclass + sex	1534.30	33.40	0.00	44
~trapgroup * session + time + ageclass + sex + capture count	1534.54	33.64	0.00	26
~trapgroup * session + session * time + c + sex	1534.65	33.74	0.00	43
~session + session * time + c + ageclass	1535.98	35.08	0.00	33
~session + session * time + c + ageclass + sex	1537.44	36.54	0.00	34
~trapgroup * session + time + ageclass	1537.74	36.84	0.00	24
~trapgroup * session + time	1538.32	37.41	0.00	23
~trapgroup * session + time + ageclass + sex	1538.78	37.88	0.00	25
~session + session * time + c	1539.06	38.16	0.00	32
~trapgroup * session + time + sex	1539.41	38.51	0.00	24
~session + session * time + c + sex	1540.56	39.66	0.00	33
~session + time + ageclass + sex + capture count	1542.44	41.54	0.00	16
~session + time + capture count	1542.95	42.05	0.00	14
~session + time + ageclass	1545.48	44.58	0.00	14
~trapgroup * session + capture count	1546.62	45.72	0.00	22
~session + time + ageclass + sex	1547.07	46.16	0.00	15
~trapgroup * session + ageclass + sex + capture count	1547.56	46.66	0.00	24
~session + time	1548.71	47.81	0.00	13
~session + time + sex	1550.34	49.44	0.00	14
~trapgroup * session + ageclass	1550.73	49.83	0.00	22
~trapgroup * session	1551.37	50.46	0.00	21
~trapgroup * session + ageclass + sex	1551.76	50.86	0.00	23
~trapgroup * session + sex	1552.46	51.55	0.00	22
~session + ageclass + sex + capture count	1555.28	54.38	0.00	14
~session + capture count	1555.88	54.98	0.00	12
~trapgroup * session + session * time + capture count	1556.98	56.08	0.00	42
~session + ageclass	1558.34	57.44	0.00	12
~trapgroup * session + session * time + ageclass + sex + capture count	1558.38	57.48	0.00	44
~session + ageclass + sex	1559.94	59.03	0.00	13
~trapgroup * session + session * time + ageclass	1561.14	60.24	0.00	42
~trapgroup * session + session * time	1561.50	60.60	0.00	41
~session	1561.71	60.81	0.00	11

~trapgroup * session + session * time + ageclass + sex	1562.43	61.53	0.00	43
~trapgroup * session + session * time + sex	1562.85	61.95	0.00	42
~session + sex	1563.35	62.45	0.00	12
~session + session * time + ageclass + sex + capture count	1564.40	63.50	0.00	34
~session + session * time + capture count	1564.51	63.61	0.00	32
~session + session * time + ageclass	1566.99	66.09	0.00	32
~session + session * time + ageclass + sex	1568.78	67.88	0.00	33
~session + session * time	1569.99	69.09	0.00	31
~session + session * time + sex	1571.83	70.92	0.00	32

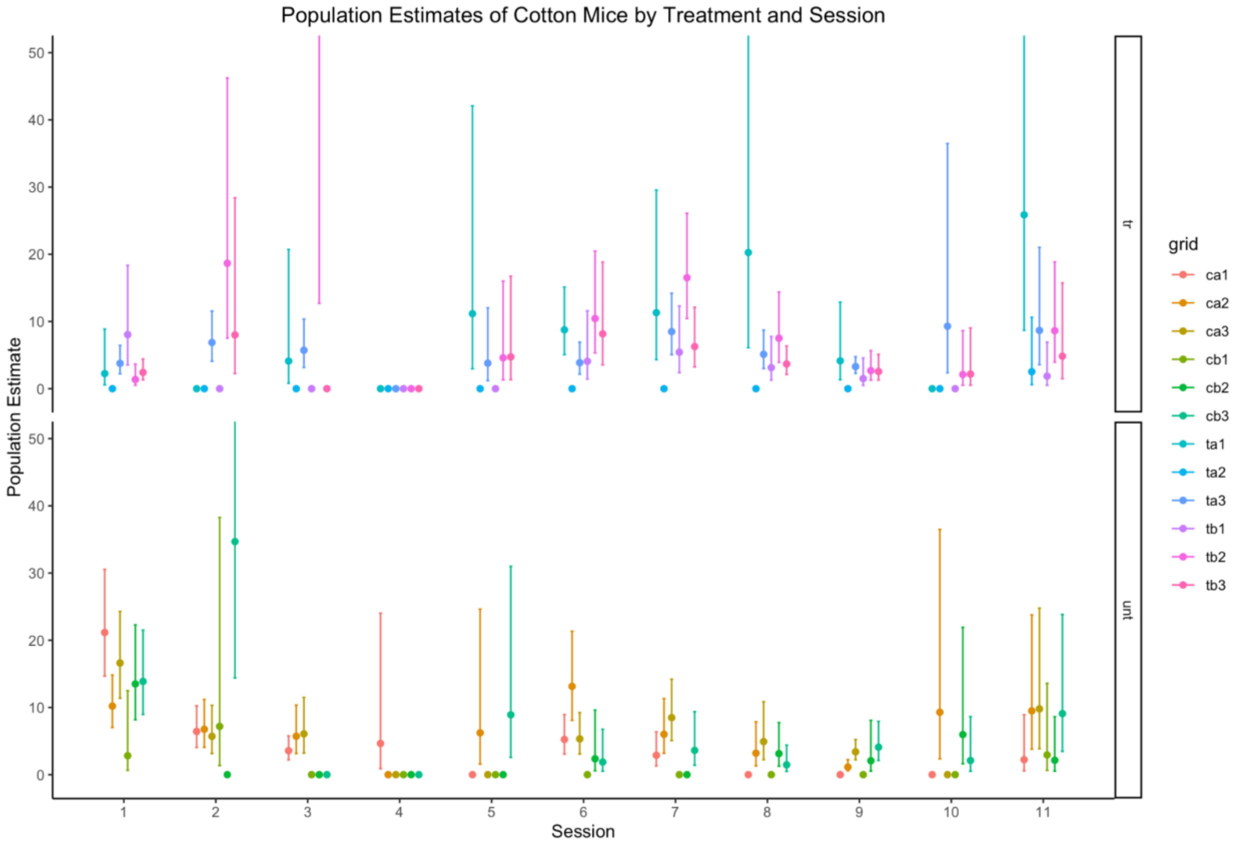
Appendix Table 2.4 Detectability model set used for oldfield mice from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. The top model was used in subsequent modeling.

Model	**AICc**	**ΔAICc**	***w***	**npar**
~session + c + sex	482.29	0.00	0.23	14
~session + time	482.93	0.64	0.17	14
~session + c	483.22	0.93	0.15	13
~session	484.45	2.16	0.08	12
~session + time + sex	484.74	2.45	0.07	15
~session + time + c	484.89	2.60	0.06	15
~session + time + c + sex	484.91	2.62	0.06	16
~session + time + capture count	485.30	3.01	0.05	15
~session + c + capture count	485.67	3.38	0.04	14
~session + sex	486.11	3.82	0.03	13
~session + capture count	486.74	4.45	0.03	13
~session + time + c + capture count	487.44	5.15	0.02	16

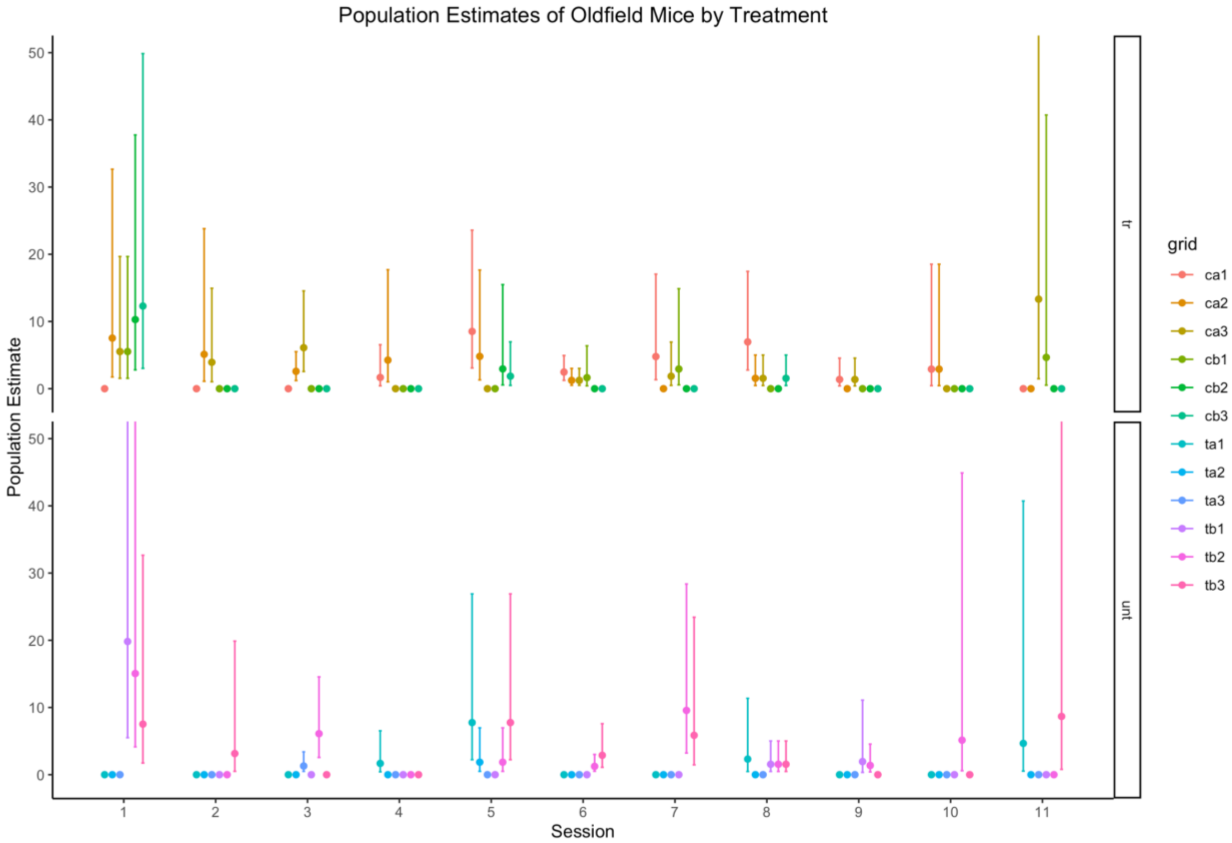
Appendix 3: Abundance Estimates



Appendix Figure 3.1 Model averaged abundance estimates for cotton rats from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. Error bars represent 95% confidence limits. The model set is those presented in Table 1.1.



Appendix Figure 3.2. Model averaged abundance estimates for cotton mice from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. Error bars represent 95% confidence limits. The model set is those presented in Table 1.1.



Appendix Figure 3.3. Model averaged abundance estimates for oldfield mice from April 2018 – December 2019 from study of response to RIFA removal in southwest Georgia. Error bars represent 95% confidence limits. The model set is those presented in Table 1.1.