Artículo de investigación

EVALUATING SMALL MAMMAL RESPONSE TO NATURAL DISTURBANCE AND RESTORATION IN OAK ECOSYSTEMS IN THE MISSISSIPPI ALLUVIAL VALLEY.[1]

Evaluación de la respuesta de pequeños mamíferos a disturbios naturales y a la restauración de robledales y ecosistemas asociados en el valle aluvial de Mississippi.

Key words: disturbance, population estimation, sampling methods, *Peromyscus*, disturbance, program capture, *Quercus*.

Palabras clave: disturbio, estimación poblacional, métodos de muestreo, *Peromyscus*, perturbación, programa de captura, *Quercus*.

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ABSTRACT

Oak species form a conspicuous and often dominant component of bottomland forests of the Mississippi Alluvial Valley. The extent of these forests has been drastically reduced as a result of clearing for agriculture in the past two centuries. Patterns of clearing have reduced the distribution of remaining forest patches to a much more flood-prone subset of the landscape than was historically the case, reducing the diversity of oak species currently present on the landscape. Intensive harvesting has further changed the composition of the remaining stands. Small remnant patches of primary forest continue to exist as Research Natural Areas on the Delta National Forest in Sharkey County, Mississippi. In particular, the Overcup Oak (*Quercus lyrata*) and Redgum (*Liquidambar styraciflua*) Research Natural Areas present substantial components of the trees for which the areas were named, as well as *Quercus nuttallii* and smaller components of other species. Recent interest in afforestation has produced a resurgence of interest in restoration of oak forest to abandoned farmland in the region. We have studied small mammal response to restoration on an extensive experiment near the Delta National Forest since 1995. We have also examined small mammal response to a tornado that disturbed approximately half of the Overcup Oak Research Natural Area in 2008. We use these studies to demonstrate how population estimates of small mammals can be obtained from capture-recapture studies, employing different designs, and utilizing Program Capture for population estimation. Small mammal communities in these stands are more species-rich in early succession than in primary forest. The study of response to tornado damage to the Overcup Oak Research Natural Area is complicated by the fact that this particular forest type is very flood-prone, creating obstacles to colonization by small mammals. Analysis of capture-recapture data with robust methods illustrated in this study permits extraction of more information from the same field effort expended in time-consuming small mammal trapping studies that have been subjected to less detailed analysis. Our work may prove useful to others interested in study of small mammals in oak forest systems in Central and South America.

RESUMEN

Las especies de roble constituyen un componente evidente y frecuentemente dominante de los bosques de tierras bajas del Valle Aluvial de Mississippi. Durante los últimos dos siglos, la extensión de

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estos bosques se ha reducido drásticamente como resultado del corte de árboles para el uso agrícola de tierras. Los patrones de tala han reducido la distribución de los parches de bosque restantes a un subconjunto del paisaje mucho más propenso a inundaciones que nunca antes se habían conocido en la historia, reduciendo la diversidad de especies de roble que actualmente existen en el paisaje. Talas intensivas han cambiado adicionalmente la composición de los rodales restantes. Pequeños parches restantes de los bosques primarios siguen existiendo como áreas naturales de investigación en el bosque denominado Delta National Forest ubicado en el Condado de Sharkey, Mississippi. En particular, las áreas naturales de investigación denominadas Roble Overcup (*Quercus lyrata*) y Liquidámbar Americano (*Liquidambar styraciflua*) tienen componentes importantes de los árboles con que fueron nombradas, así como *Quercus nuttallii* y componentes más pequeños de otras especies. Un reciente interés en forestación ha causado el resurgimiento del interés en la restauración de bosques de roble en las tierras agrícolas abandonadas de la región. Hemos estudiado la respuesta de pequeños mamíferos a esta restauración utilizando un experimento extensivo cerca del Bosque Nacional Delta (Delta National Forest) desde 1995. También examinamos la respuesta de pequeños mamíferos a un tornado que afectó aproximadamente la mitad del Área Natural de Investigación de Roble Overcup (Overcup Oak Research Natural Area) en 2008. Utilizamos estos estudios para demostrar la manera cómo se pueden obtener estas estimaciones de población de pequeños mamíferos con base en estudios de captura-recaptura, empleando diferentes diseños y utilizando el programa denominado Program Capture para calcular la población. Las comunidades de pequeños mamíferos que habitan en estos rodales son más especiosas en la sucesión temprana que en el bosque primario. El estudio de las respuestas a los daños que fueron causados por el tornado al área natural de investigación de roble Overcup es complicado por el hecho de que este tipo de bosque en particular es muy propenso a inundaciones, lo cual crea obstáculos a su colonización por pequeños mamíferos. El análisis de los datos de captura-recaptura con métodos robustos como se ilustró en este artículo permite la extracción de más información que el análisis menos detallado por el mismo esfuerzo de campo en capturar pequeños mamíferos. Nuestro trabajo puede ser útil para otros interesados en el estudio de pequeños mamíferos en sistemas de bosques de roble en Centroamérica y Suramérica.

INTRODUCTION

Oak forests are important habitats for small mammals (Dickson 2001, Saitoh *et al*. 2008, Tioli *et al*. 2009) throughout the range of *Quercus* and presumably other genera in the family Fagaceae as well. Small mammals in mature and old-growth stands of temperate oak forests often are associated with coarse woody debris (Harmon *et al*. 1986, McMinn & Crossley 1996, Loeb 1999, Bowman *et al*. 2000, McCay 2000, Osbourne & Anderson 2002, Osbourne *et al*. 2005). Studies of small mammals in upland oak forests in North America are numerous (e.g. Greenberg 2002, Fantz & Renken 2005,Tietje *et al*. 2008); Hammond & Anthony (2006) evaluated 1535 data sets from a variety of habitats. Those in Central and South America are fewer (Sánchez-Cordero 2001, Otalora Ardila 2003, Navarro Arquez 2005, Lopez-Barrera & Manson 2006, van den Bergh & Kappelle 2006, Ramirez & Perez 2007, Aragon *et al*. 2009, Corredor Prado & Bejarano Bonilla 2009). Like investigations of larger mammals in these systems (Walker & Cardenas 2004, Cujar-Tovar 2006, Tobler *et al*. 2006), these studies have depended upon indices of activity rather than population size estimations to assess habitat relationships and community dynamics. Attempts to determine population size or relative abundance often have used less precise estimation methods such as Minimum Number Left Alive (Vazquez *et al*. 2000), Lincoln Index (Fleming 1974), or Jolly-Seber methods (Rojas Rojas & Barboza Rodriguez 2007). Recent work using more robust population estimation methods such as available in Program Capture (Rexstad & Burnham 1991) or Program Mark (White & Burnham 1999) has proved to be very useful and informative comparing small mammal use of different habitats (e.g. Shanker 2000, Hadley & Wilson 2004). Wiewel *et al*. (2009) further show that the robust methods are ultimately more time efficient than less precise ones.

Oak species form a conspicuous and often dominant component of bottomland forests of the Mississippi Alluvial Valley in North America (Hodges 1997). Clearing for agriculture in the past two centuries (MacDonald *et al*. 1979) has reduced the distribution of remaining forest patches to a more flood-prone subset of the landscape than previously, lowering the diversity of oak species currently present on the landscape. Intensive harvesting has further changed the composition of the remaining stands. Small remnant patches of primary forest such as the Overcup Oak (*Quercus lyrata*) and Redgum (*Liquidambar styraciflua*) Research Natural Areas (RNA) on the Delta National Forest in Sharkey County, Mississippi, present substantial components of the trees for which the areas were named, as well as *Quercus nuttallii* and smaller components of other species (Devall & Ramp 1992). Small mammal communities of the old-growth stands have been little studied.

Recent efforts in afforestation have produced a resurgence of interest in restoration of oak forest to abandoned farmland in the region (Gardiner *et al*. this symposium). Concomitant with that increased interest have been questions concerning rehabilitation of wildlife communities associated with oak forests, and the restoration of this aspect of ecosystem function in the process of restoration. Particularly limited in this respect has been long-term study of small mammal community development in afforestation areas (Savage *et al*. 1996). Long-term study of small mammals in afforestation situations can extend our knowledge of the development of these communities and their functioning. Illustration of techniques of study of populations of small mammals in these ecosystems, existing in a matrix of agricultural lands, may form a useful reference situation for those contemplating conservation and restoration of oak ecosystems in mixed landscapes in South America.

In this report we present study designs and some results from studies of small mammal communities we have conducted in oak forests in Mississippi. In each of these studies we have used a capture-mark-recapture design with robust population estimation using Program Capture. We describe two such studies, (a) small mammal response to restoration on an extensive, long-term experiment near the Delta National Forest, and small mammal population response to a tornado that disturbed approximately half of the Overcup Oak RNA in 2008. This work allowed us to test the null hypotheses (a) that responses of small mammals to different techniques of afforestation are similar among species, and (b) that tornado damage to an old-growth stand of oak forest growing in a floodplain situation has no effect on small mammal populations in the area. In addition to providing useful data on small mammal communities and populations for these North American habitats, we suggest the techniques are applicable to similar questions in oak forests in Central and South America as well.

MATERIALS AND METHODS

STUDY AREAS

Delta National Forest (DNF) is located east of Rolling Fork, in the southern portion of Sharkey County, Mississippi, 32º 46' N, 90º 47' W, elevation 25-29 m above mean sea level. The DNF is the sole unit composed entirely of bottomland hardwood forests in the US National Forest System. Managed by the U.S. Forest Service to produce multiple-use outputs of wood, water, forage, wildlife, and recreation, the DNF comprises 63000 acres in a single contiguous block, long the largest such tract of bottomland forest in the Yazoo River tributary basin of the Mississippi Alluvial Valley. Soils are predominantly heavy clay in composition, reflecting the low, flood-prone position of this landscape. Forest composition reflects the low position of the forest in the floodplain, with stands dominated by species characteristic of the more flood-prone sites. Within the DNF, three RNAS were set aside from commercial harvest activity, the Redgum, Overcup Oak, and Green Ash RNAS (Devall & Ramp 1992). We have worked in two of these RNAS. Redgum RNA (32º 54' N, 90º 42' W, elevation 28 m) lies on a relatively higher site representative of stands dominated by sweetgum (*Liquidambar styraciflua*; large old, individuals with distinctive red heartwood are called "Redgum" trees) and Nuttall Oak (*Quercus nuttallii*). Reflective of the higher site position, understories of this RNA are continuous and dominated by *Sabal minor*. The Overcup Oak RNA (32º 54' N, 90º 44' W, 27-28 m elevation) is situated on a lower site position, and dominated by a stand of the flood tolerant Overcup Oak (*Quercus lyrata*) and Water Hickory (*Carya aquatica*). Understory communities here are depauperate, presumably because the frequent and prolonged flooding in the site is too severe for many understory species. Each of these RNAS is approximately 16 ha in extent. On March 3, 2008, a tornado damaged some forest stands in the DNF extensively, including approximately half of the Overcup Oak RNA (National Weather Service 2008).

The Sharkey Large-Scale Afforestation Experiment is an approximately 800 ha area of abandoned farmland immediately to the north of the DNF (32º 58 N, 90º 54 W, elevation 28-30 m above mean sea level). Extensive growing-season flooding of parts of the site made it unprofitable for farming. The land was acquired in the 1990s by the U.S. Fish and Wildlife Service, and is managed as forestland for wildlife populations it might support. In 1995, staff of the US Forest Service Center for Bottomland Hardwoods Research and representatives of a number of other agencies and academic institutions established an experiment on the area, in order to investigate alternative methods of restoring marginally productive farmland to forest in the Mississippi Alluvial Valley. Four afforestation practices reflective of thinking at that time were chosen. The experiment was established as a randomized, complete block design of three blocks each consisting of four 8-ha plots to which the treatments were randomly assigned. The treatments, in order of intensity of labor effort and of initial cost of establishment, were Natural Regeneration (NAT) involving no direct intervention; Direct Seeding (SOW) of acorns of the site-appropriate Nuttall Oak, planted mechanically using specially modified agricultural planting equipment; Hand Planted (PLN) seedlings of Nuttall Oak; and a two-stage interplanting (NUR) of a) a cottonwood (*Populus deltoides*) plantation designed to simulate succession and for early harvest and b) followed by hand planted Nuttall Oak seedlings two years later. Details of the treatments are available in Schweitzer *et al*. (1997). A ten-year rotation of the cottonwood plantation was anticipated at initiation of the experiment, during which additional treatments would be applied to smaller subportions of the treatment plots. These additional treatments were installed during harvest operations of the cottonwood stands in March 2008, and include four intensities of harvest of the cottonwood trees, a complete harvest, a harvest followed by coppice regrowth of the cut cottonwood stems, a thinning removal of half of the cottonwood stems, and an uncut control.

SMALL MAMMAL SAMPLING

We conducted small mammal sampling using Sherman live traps and capture-recapture methodology. We set a single trap on the ground at each predetermined location. We baited the traps with whole oats moistened with imitation vanilla flavoring, and mixed in an approximate ratio of 65ml vanilla flavoring per kg of oats (1 oz. of vanilla flavoring to 1 lb of oats). A small amount of polyester fiberfill was added to the trap as thermal insulation for animals captured on cool nights (< 10 ºC).

Traps were arrayed in the field in square grids, with trap spacing held constant for each study. At the Sharkey Large-Scale Afforestation Experiment we conducted a preliminary study of two plots with a grid of 100 traps spaced in a 10 x 10 array with individual traps 20 m apart, sampling an area of 3.2 ha. High density of captures and low numbers of recaptures in this study caused us to reduce the distance between traps to 10 x 10 m and to reduce the number of traps to 64, sampling an area of 0.49 ha. We have used the same trapping array in all subsequent work on that experiment. This effort involves 448 traps in seven grids of 64 traps in each experimental block. The sampling unit is the trapping grid.

On the Overcup Oak RNA, we arranged the traps in two scales. At the larger scale of the entire 16-ha RNA, we sampled at each of the 20 vegetation sampling plots were established on a grid consisting of 4 rows of plots 90 m apart with five plots spaced 70 m apart in each row, covering an area of 12.6 ha. Ten of these sampling plots were located in the portion of the RNA damaged by the tornado and ten in the undamaged portion. At each of the vegetation plots, the smaller scale of sampling, we arranged six traps at 20 m intervals around the periphery of the 0.08-ha vegetation sampling plots. A total of 120 traps was used in this study, 60 each in the undamaged and tornado damaged portions of the RNA.

Our trapping sessions extended for one week per location. In the Sharkey Large-scale Afforestation Experiment we randomly assigned our sampling blocks to weeks in the trapping season to account for potential confounding effects during the analysis. We set the traps on the first day of the session, and checked them once per day for five days. We did not disinfect our traps, a practice suggested to be followed in areas where hantavirus is endemic (Mills *et al*. 1995). Traps were checked once per day, during the morning hours. When traps contained animals, we shook the animal into a plastic bag for handling. We then cleaned, rebaited, and reset the trap at the original location.

Individual captures were identified to species, sex, and reproductive condition when possible, and their body mass, body length, tail length, hind foot length, and ear length measured. The specific location of the trap in which the capture occurred was noted, and each animal was given a numbered metal ear tag. Recaptured animals were weighed, their tag number, species, sex, and reproductive condition noted. Because of the difficulty of identifying *Peromyscus* species, we remeasured all individual *Peromyscus* on each capture. Animals were released at the capture site.

Capture data resulting from each trapping session were summarized for each animal as a vector of day-location combinations for each capture grid. All capture data for each species from each grid in each session were analyzed in a single run of Program Capture. Analysis of the resulting population estimates has been conducted using SAS. We accepted statistical significance at P = 0.05 in the work on the Sharkey Large-scale Afforestation Experiment, and at P = 0.10 in the Overcup Oak RNA study with its more limited sample sizes.

RESULTS

We have conducted 18 trapping sessions on the Sharkey Large-Scale Afforestation Experiment, 1995-2009 (264 days; 106,136 trap-nights; 13,623 captures); and one on the Overcup Oak RNA, 2009

Table 1. Small mammal species captured on Sharkey Large-scale Afforestation Experiment

Species	Year First Encountered	Frequency[1]		Comparison[2]
		1995-1998	2003-2009	
N, grids sampled		62	180	
Sigmodon hispidus	1995	0.89	0.76	*
Oryzomys palustris	1995	0.66	0.65	ns
Peromyscus leucopus	1995	0.35	0.54	*
Mus musculus	1995	0.24	0.11	*
Reithrodontomys humulis	1996	0.37	0.01	*
Sylvilagus aquaticus	1996	0.00	0.01	-
Peromyscus nuttallii	1997	0.02	0.00	-
Cryptotis parva	2004	-	0.00	-
Neotoma floridana	2004	0.00	0.06	*
Glaucomys volans	2008	-	0.01	-

1. Frequency is the proportion of grids sampled from which the species was reported.

2. A grid was an array of 64 traps sampled for at least 5 consecutive nights.

Asterisks indicate that the two frequencies differ, by binomial test, at experiment-wide P=0.05.

(5 days, 600 trap-nights, 32 captures). Small mammal communities in these oak ecosystems in bottomland hardwood forests of the Mississippi Alluvial Valley are more species-rich in early succession than in primary forest. We have captured nine species in the Sharkey Large-Scale Afforestation Experiment (Table 1); and three on DNF, *Neotoma floridana*, and *Peromyscus leucopus* in Overcup Oak RNA during this work We also captured *Peromyscus gossypinus* in the Redgum RNA in unrelated work in both 2008 and 2009 (P. B. Hamel & C. G. Smith, III, *personal observations*).

Colonizing communities of small mammals in the Sharkey Large-scale Afforestation Experiment are characterized primarily by *Sigmodon hispidus* and *Oryzomys palustris*, with smaller numbers of *Peromyscus leucopus*, *Reithrodontomys humulis*, and *Mus musculus*. Sampling conducted after ten years of succession on the site captured primarily the same species, at different frequencies of occurrence. *O. palustris* and *S. hispidus* are still the dominant species. *P. leucopus* has increased significantly in frequency, while *S. hispidus* has declined, and *R. humulis* has virtually disappeared. *Mus musculus* is significantly less frequent than in the initial stage of colonization as well. *Neotoma floridana* has appeared in the fauna, as have *Glaucomys volans* and *Cryptotis parva*. *Sylvilagus aquaticus*, which we have captured only incidentally, became frequent and abundant enough to hunt early in the development of the stands; these rabbits are generally distributed on the site. The species occurs within the Delta National Forest as well. The tree squirrels, *Sciurus carolinensis* and *S. niger,* occur in the forest but are not yet present in the afforestation site as no hard mast is yet produced. Like the rabbits, these animals are difficult to capture with the trapping scheme we have employed. We have captured only one *Peromyscus nuttallii* in this work; this animal characteristic of bottomlands is one we have expected to capture regularly. The scarcity of this animal is noteworthy (Barrett & Feldhamer 2008).

We encountered two small rodents in the trapping on the Overcup Oak RNA in 2009 (Table 2). Two *Neotoma floridana*, one of them a juvenile, indicate that this species is present on the RNA in numbers too low to estimate populations separately for the tornado-damaged and undamaged portions of the RNA. We were able to estimate populations of *P. leucopus* for the entire area and for the tornado-damaged and undamaged portions of the area separately. Two growing seasons after the tornado, populations of this species are uniformly distributed across the RNA (Table 2).

Populations of *Peromyscus leucopus* on the Sharkey Site in November 2008 (Table 3) reflect the difficulty of estimating populations of small mammals in capture-recapture studies without analysis using robust methods as exemplified in Program Capture. Three different models were necessary to estimate populations of these animals on the site, that involving heterogeneity among animals in capture probability [M(h)], heterogeneity among days and individuals in capture probability [M(th)], as well as the null model of uniform capture probability among days and individuals [M(o)]. Analysis of variance of population estimates using block and treatment as main effects yields a significant result ($F_{8.12} = 4.05$, $P < 0.02$, $R^2 = 0.73$), in which block is a significant effect ($F = 9.2$, $P < 0.01$), but

Table 2. Small mammal populations in Overcup Oak Research Natural Area, October 2009

Species	Treatment	Population Size +/- S.E.	95% C.I.	P (capture)	Model
Peromyscus leucopus	Entire RNA	23 ± 3.8	20 - 36	0.25	M(o)
Peromyscus leucopus	Tornado Damaged Portion	11 ± 3.0	9 - 23	0.23	M(o)
Peromyscus leucopus	Undamaged Portion	13 ± 4.5	11 - 34	0.29	M(th)
Neotoma floridana	Entire RNA	2?		inestimable	

Neotoma floridana population inestimable because no recaptures were made treatment is not (F = 2.3, P = 0.1). The inference from this result is that the species is generally distributed among the treatments in this experiment after 13 growing seasons, but that significant variations in population distribution exist, external to those factors controlled in the experimental design.

DISCUSSION

Small mammal capture-recapture data are time-consuming to obtain, and subject to a variety of confounding variables that make interpretation of the results problematical. Each of these factors affects the likelihood of capture or recapture of individual animals, and affects each species in a particular way (Otis & Burnham 1978, White *et al*. 1982). Hence determination of relationships between species and the sampled oak ecosystems is complicated. Simply expressing the number of captures obtained during a session as a function of the effort expended, while an interesting reflection of the behavior of the animals during the individual trapping session, is insufficient for determining population responses or for comparing species abundances or responses to treatments. Several existing analytical programs are available which can estimate populations, select appropriate mathematical formulations of analysis that account for particular combinations of confounding effects, and provide standard errors of population estimates as well. Two of these are Program Capture (Rexstad & Burnham 1991) and Program Mark (White & Burnham 1999). We began using Program Capture in the initial stages of the Sharkey Large-Scale Afforestation Experiment and continue to do so here. Program Mark is a more recent development which we have not used. (Note: The use of trade or firm names in this publication is for reader information and does not imply endorsement by the United States Department of Agriculture of any product or service.) The robust methods utilized in these analyses are applied to field data similar to those gathered by workers in oak forests in Central and South America (Fleming 1974, Van den Bergh & Kappelle 1998, Vazquez *et al*. 2000, Sánchez-Cordero 2001, and Rojas Rojas & Barboza Rodriguez 2007). We can extract more information from the data after these analyses than can be obtained by analysis of the very same data using less robust methods.

The study of response to tornado damage to the Overcup Oak Research Natural Area is complicated by the fact that this particular forest type is very flood-prone, creating obstacles to colonization by small mammals. Uniform distribution of *P. leucopus* populations across the entire Overcup Oak RNA presumably reflects abundance of downed woody debris in the RNA (Harmon *et al*. 1986, Bowman *et al*. 2000). Upon release, the captured animals ran directly to downed woody debris for cover. Although significantly more abundant on the tornado damaged portion of the area (R. Partelli Feltrin, unpublished results), coarse woody debris is generally distributed in the primary forest of the RNA. We are not certain why *Peromyscus gossypinus* was not encountered on this site. The species occurs in the Redgum RNA 1.6 km east of the Overcup Oak RNA, and is associated characteristically with downed woody debris (Loeb 1999). Overcup Oak RNA experiences substantial flooding, which may reduce dispersal of the one species into it. It is also possible that Delta National Forest harbors only a hybrid population of *P. gossypinus* x *P. leucopus* (Barko & Feldhamer 2002). The animals we captured in the Overcup Oak RNA in 2009 exhibited characteristics of both species. Their feet measured in the range indicated for *P. leucopus*, while their body weights were in the range indicated for *P. gossypinus*. We did not take blood samples to confirm genetic identity as did Barko & Feldhamer (2002).

We are unable to reject the null hypothesis that tornado damage to an old-growth stand of oak forest growing in a floodplain situation has no effect on small mammal populations in the area, as populations of *P. leucopus* were similar in both tornado-damaged and undamaged areas of the Overcup Oak RNA two growing seasons after the storm. Shortly after the sampling reported here, a flood inundated the site completely. We are uncertain of the specific effect of that flood on the populations of small mammals in Overcup Oak RNA without further sampling effort.

We are able to reject the null hypothesis that responses of small mammals to different techniques of afforestation are similar among species, based upon frequency of occurrence data across the 13

Table 3. Populations of *Peromyscus leucopus* on the Sharkey Large-scale Afforestation Experiment, November 2008.

Treatment	Block	Population Size +/- S.E.	95% C.I.	P (capture)	Model
Natural Regeneration	1	24 ± 10.7	15 - 65	0.33	M(th)
Natural Regeneration	2	1 ± 1	1 - 1	0.8	M(h)
Natural Regeneration	3	2 ± 0.15	2 - 2	0.6	M(o)
Average		9.00			
Sowed Acorns	1	11 ± 5.8	7 - 36	0.2	M(th)
Sowed Acorns	2	4 ± 1.2	4 - 11	0.65	M(th)
Sowed Acorns	3	1 ± ?	-		?
Average		5.33			
Planted Oak Seedlings	1	8 ± 0.67	8 - 8	0.39	M(th)
Planted Oak Seedlings	2	7 ± 1.3	7 - 13	0.57	M(th)
Planted Oak Seedlings	3	8 ± 0.25	8 - 8	0.62	M(o)
Average		7.67			
Cottonwood Harvest	1	4 ± 1.2	4 - 12	0.4	M(th)
Cottonwood Harvest	2	0	-		-
Cottonwood Harvest	3	0	-		-
Average		1.33			
Cottonwood Coppice	1	10 ± 7.3	6 - 44	0.12	M(o)
Cottonwood Coppice	2	0	-		-
Cottonwood Coppice	3	1 ± 1	1 - 1	0.8	M(h)
Average		3.67			
Cottonwood Thinned	1	21 ± 5.7	15 - 39	0.14	M(h)
Cottonwood Thinned	2	9 ± 0.93	9 - 15	0.42	M(o)
Cottonwood Thinned	3	9 ± 4.2	7 - 28	0.17	M(o)
Average		13.00			
Cottonwood Control	1	7 ± 1.55	7 - 15	0.3	M(o)
Cottonwood Control	2	6 ± 0.32	6 - 6	0.57	M(o)
Cottonwood Control	3	1 ± 1	1 - 1	0.8	M(h)
Average		4.67			
Sharkey Site Average		6.63			

seasons of the sample. We can further examine the response of one of the species within an individual season, taking advantage of the detailed population estimates provided by the Program Capture analyses. Clearly, *P. leucopus* is more widespread on the site now than in the beginning of the experiment (Table 1). The great variability in distribution of *P. leucopus* populations across the Sharkey Large-Scale Afforestation Experiment as exemplified by the capture data for November 2008 (Table 3) indicates that additional explanations must be sought to explain the variations in distribution, explanations specific to the Sharkey Large-Scale Afforestation Experiment rather than to the distribution of *P. leucopus* in afforested locales in the Mississippi Alluvial Valley. We offer the following as a hypothesis for some of the variability, subject to test in additional work. The explanation reflects specific events that occurred within Block 1 of the experiment, as follows. For reasons external to the design of this experiment, the natural regeneration treatment plot in Block 1, adjacent to the cottonwood nurse crop treatment plot, has a very dense stand of *Cornus* sp., swamp dogwoods, which provide abundant cover, a situation not reflected in the natural regeneration treatment plots in the other blocks in the study. Furthermore, in the fall of 2005 a portion of the stand of cottonwoods in the cottonwood-nurse crop treatment plot, whose trees were already weakened by attack of wood-boring insects (*Saperda calcarata*), was damaged by the passage of a hurricane. By the spring of 2007, we could detect qualitatively a response of *P. leucopus* to the increase in downed woody debris produced by the storm breaking the susceptible trees (Figure 1, where sampling plots are individually identified). All 3 animals in NURM and all 5 animals in NURW were in the NW corner part of plot where the storm damaged the vegetation and one animal moved between the plots during the sampling week. Of two animals captured in NURS, one was a female captured several days in the plot, and the other a male who had been captured in NURM and NURW as well. Harvesting activity took place shortly after and eliminated the potential source of coarse woody debris .

CONCLUSIONS

Capture-mark-recapture methods are in widespread use to sample small mammals in oak forests throughout the range of the *Quercus* and related species. Robust analytical methods have been

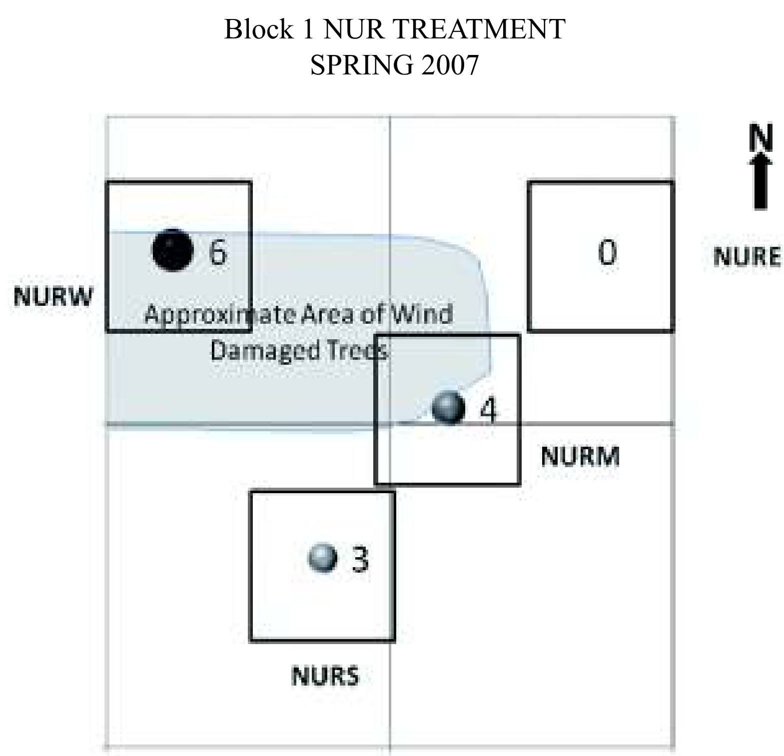

Figure 1. *Peromyscus leucopus* population size estimates for four trapping grids on the Sharkey Site, Block 1, NUR treatment, Spring 2007. Hatched area indicates approximate area damaged by windstorms in Fall 2005. The four small squares indicate replicate small mammal sampling grids within the treatment plot, with their individual designations. Numbers inside the plots indicate the *P. leucopus* population estimate for that sampling grid. All captures in NURW and NURM occurred within the hatched area. One of two animals captured in NURS was also captured in NURM and in NURW. Total area of treatment is 8 ha, that of each sampling grid 0.5 ha

employed in North America, Europe, and Asia, but less so in Central America and South America. These analytical methods permit extraction of more information from the same field data sets than do earlier methods. We document succession in small mammal communities in oak restoration areas, lack of effect of tornado on populations of a small mammal in primary oak forest in Mississippi, and complex responses of the same species to intratreatment variations in environmental conditions within a successional study. Our work may prove useful to others interested in study. of small mammals in oak forest systems in Central and South America.

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BIBLIOGRAPHIC REFERENCES

Aragon, E.E., A. Garza, & F.A. Cervantes. 2009. Structure and organization of rodent assembles of a forest of the Sierra Madre Occidental, Durango, Mexico. Revista Chilena de Historia Natural 82:523-542.

Barko, V. A. & G.A. Feldhamer. 2002. Cotton mice (*Peromyscus gossypinus*) in southern Illinois: Evidence for hybridization with white-footed mice (*Peromyscus leucopus*). American Midland Naturalist 147:109-115.

Barrett, G. W., & G. A. Feldhamer. 2008. The golden mouse: ecology and conservation. New York: Springer-Verlag.

Bowman, J. C., D. Sleep, G. J. Forbes, & M. Edwards. 2000. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management 129:119-124.

Corredor Prado, J. P. & D.A. Bejarano Bonilla. 2009. Pequeños mamíferos no voladores de la reserva natural Ibanasca (Tolima, Colombia). Revista Tumbaga 4:121-134.

Cujar-Tovar, A. 2006. Uso del hábitat del venado (*Mazama rufina*) en la Reserva Biológica Cachalú y su área de influencia. pp. 101 – 118. En: C. Solano & N. Vargas (eds.). Memorias del I Simposio Internacional de Robles y Ecosistemas Asociados. Fundacion Natura–Pontificia Universidad Javeriana. Bogotá.

Devall, M. S. & P. F. Ramp. 1992. U.S. Forest Service Research Natural Areas and protection of old growth in the south. Natural Areas Journal 12:75-85.

Dickson, J. G. (ed.). 2001. Wildlife of southern forests: habitat and management. Blaine, Washington: Hancock House Publishers. 480 p.

Fantz, D. K. & R. B. Renken. 2005. Short-term landscape-scale effects of forest management on *Peromyscus* spp. mice within Missouri Ozark Forests. Wildlife Society Bulletin 33:293-301.

Fleming, T. H. 1974. The population ecology of two species of Costa Rican heteromyid rodents. Ecology 55:493-510.

Gardiner, E. S., D.C. Dey, & J.A. Stanturf. 2010. Approaches to restoration of oak forests on farmed lowlands in the eastern U.S. II Simposio Internacional de Robles y Ecosistemas Asociados. Noviembre 12, 13 de 2009. Revista Colombia Forestal Vol. 13 (2): 223-236. Bogotá.

Greenberg, C. H. 2002. Response of white-footed mice (*Peromyscus leucopus*) to coarse woody debris and microsite use in southern Appalachian treefall gaps. Forest Ecology and Management 164:57-66.

Hadley, G. L. & K. R. Wilson. 2004. Patterns of density and survival in small mammals in ski runs and adjacent forest patches. Journal of Wildlife Management 68:288-298.

Hamel, P. B. 2003. Winter bird community differences among methods of bottomland hardwood forest restoration: results after seven growing seasons. Forestry 76(2):189-197.

Hammond, E. L. & R. G. Anthony. 2006. Mark–recapture estimates of population parameters for selected species of small mammals. Journal of Mammalogy 87:618-627.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Hodges, J. D. 1997. Development and ecology of bottomland hardwood sites. Forest Ecology and Management 90:117-125.

Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460-471.

Lopez-Barrera, F. & R. H. Manson. 2006. Ecology of acorn dispersal by small mammals in montane forests of Chiapas, Mexico. pp.165–176. En: M. Kappelle (ed.). Ecology and conservation of Neotropical montane oak forests. Springer-Verlag. Berlin.

McCay, T. S. 2000. Use of woody debris by cotton mice (*Peromyscus gossypinus*) in a southeastern pine forest. Journal of Mammalogy 81:527-535.

MacDonald, P. O., W. E. Frayer, & J. K. Clauser. 1979. Documentation, Chronology and Future Projections of Bottomland Hardwood Habitat Loss in the Lower Mississippi Alluvial Plain. Vol. 1. HRB-Singer. Inc. State College. Pennsylvania.

McMinn, J. W., & D. A. Crossley Jr. (eds.). 1996. Biodiversity and coarse woody debris in southern forests, proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity; 1993 October 18-20; Athens, GA. Gen. Tech. Rep. SE-94. Department of Agriculture, Forest Service, Southern Research Station. Asheville, N.C.: U.S.

Mills, J. N., T.L. Yates, J. E. Childs, R. R. Parmenter, T. G. Ksiazek, P. E. Rollin, & C. J. Peters. 1995. Guidelines for working with rodents potentially infected with Hantavirus. Journal of Mammalogy 76:716-722.

National Weather Service. 2008. Storm Data and Unusual Weather Phenomena. Acceso: March 2008. Disponible en:http://www.srh.noaa.gov/jan/stormdata/data/mar2008.pdf

Navarro Arquez, E. 2005. Abundancia relativa y distribución de los indicios de las especies de mamíferos medianos en dos coberturas vegetales en el santuario de flora y fauna Otún Quimbaya, Pereira–Colombia. Trabajo de Grado, Pontificia Universidad Javeriana, Facultad de Ciencias, Bogotá. 78 p.

Osbourne, J. D. & J. T. Anderson. 2002. Small mammal response to coarse woody debris in the central Appalachians. Proceedings of the Southeastern Association of Fish and Wildlife Agencies. 56:198-209.

Osbourne, J. D., J. T. Anderson, & A. B. Spurgeon. 2005. Effects of habitat on small-mammal diversity and abundance in West Virginia. Wildlife Society Bulletin. 33:814-822.

Otálora Ardila, A. 2003. Mamíferos de los bosques de roble. Acta Biologica Colombiana 8:57-71.

Otis, D. L., K. P. Burnham, G. C. White, & D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs: 62: 1-135.

Ramírez, H. E. & W. A. Pérez. 2007. Mamíferos de un fragmento de bosque de roble en el Departamento del Cauca, Colombia. Boletin Cientifico Universidad de Caldas 11: 65-79.

Rexstad, E., & K. P. Burnham. 1991. Users Guide for Interactive Program CAPTURE. Colorado Cooperative Fish & Wildlife Research Unit. Colorado State University. Fort Collins. Colorado.

Rojas Rojas, L. & M. Barboza Rodriguez. 2007. Ecología poblacional del ratón *Peromyscus mexicanus* (Rodentia: Muridae) en el Parque Nacional Volcán Poás, Costa Rica. Revista de Biología Tropical 55:1037-1050.

Saitoh, T., J. O. Vik, N.C. Stenseth, T. Takanishi, S. Hayakashi, N. Ishida, M. Ohmori, T. Morita, S. Uemura, M. Kadomatsu, J. Osawa, K. Maekawa. 2008. Effects of acorn abundance on density dependence in a Japanese wood mouse (*Apodemus speciosus*) population. Population Ecology 50:159-167.

Sánchez-Cordero, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. Global Ecology and Biogeography 10:63-76.

Savage, L., J. Anthony, & R. Buchholz. 1996. Rodent damage to direct seeded willow oak in Louisiana. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 50:340-349.

Schweitzer, C. J., J. A. Stanturf, J. P. Shepard, T. M. Wilkins, C. J. Portwood, & L. C. Dorris, Jr. 1997. Large-scale comparison of reforestation techniques commonly used in the Lower Mississippi Alluvial Valley: first year results. pp. 313-320. En: S. G. Pallardy, R. A. Cecich, H. Garrett & P.S. Johnson (eds). Proceedings of the 11th Central Hardwood Forest Conference; 23-26 March 1997, Columbia, MO. Gen. Tech. Rep. NC-188. US Department of Agriculture, Forest Service, North Central Forest Experiment Station, St Paul, MN.

Shanker, K. 2000. Small mammal trapping in tropical montane forests of the Upper Nilgiris, southern India: an evaluation of capture-recapture models in estimating abundance. Journal of Biosciences 25:99-111.

Tietje, W. D., D.E. Lee, & J.K. Vreeland. 2008. Survival and abundance of three species of mice in relation to density of shrubs and prescribed fire in understory of an oak woodland in California. Southwestern Naturalist 53:357-369.

Tioli, S., F. Cagnacci, A. Stradiotto, & A. Rizzoli. 2009. Edge effect on density estimates of a radiotracked population of yellow-necked mice. Journal of Wildlife Management 73:184-190.

Tobler, M. W., E.J. Naranjo, & I. Lira-Torres. 2006. Habitat preference, feeding habits and conservation of Baird's Tapir in Neotropical montane oak forests. pp. 347 – 362 En: M. Kappelle (ed.). Ecology and conservation of Neotropical montane oak forests. Springer-Verlag. Berlin, Germany.

Van den Bergh, M. B., & M. Kappelle. 1998. Diversity and distribution of small terrestrial rodents along a disturbance gradient in montane Costa Rica. Revista de Biología Tropical 46:331-338.

Van den Bergh, M. B., & M. Kappelle. 2006. Small terrestrial rodents in disturbed and old-growth montane oak forest in Costa Rica. pp. 337 – 345. En: M. Kappelle (ed.). Ecology and conservation of Neotropical montane oak forests. Springer-Verlag. Berlin, Germany.

Vázquez, L. B., R. A. Medellín, & G. N. Cameron. 2000. Population and community ecology of small rodents in montane forest of western Mexico. Journal of Mammalogy 81:77-85.

Walker, R. & E. Cárdenas. 2004. Evaluación del estado de conservación de la fauna en el municipio de Murillo, Tolima. Boletin Cientifico. Universidad de Caldas: 15-29.

Wiewel, A. S., A. A. Yackel Adams, & G. H. Rodda. 2009. Evaluating abundance estimate precision and the assumptions of a count-based index for small mammals. Journal of Wildlife Management 73:761-771.

White, G. C., D. R. Anderson, K. P. Burnham, & D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP. Los Alamos, New México. 235 p.

White, G. C. & K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.