SPATIAL AND TEMPORAL DISTRIBUTION OF WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS)* RELATIVE TO ACORN PRODUCTION

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Abstract. Abundant acorn production by multiple oaks has important ecological ramifications in Northeastern forests. Previous studies have shown that fall production of acorns strongly influences white-footed mouse (*Peromyscus leucopus*) densities the following summer. Mice are important hosts for the bacteria causing Lyme disease, and significant predators of pupae of the exotic, defoliating gypsy moth, and of songbird eggs and nestlings. Recent research has shown hot and cold spots of summer mouse activity density (as measured by track plates) at scales less than ca. 50 m throughout the forest, potentially creating heterogeneous predation risk for gypsy moth pupae and ground nesting birds, and altering local Lyme disease risk. Using acorn production and mouse trapping data collected on six 2.25 hectare grids over the past nine years, I carried out statistical analysis to address two questions: How does mean acorn production and mean mouse density vary at different spatial scales across years? At what spatial and temporal scales is there a significant correlation between acorn production and mouse density the following year?

The abundance of red group oak acorns (subgenus *Erythrobalanus*) the prior fall was strongly correlated with mouse density the following summer at the ≥ 2.25 ha. scale. However, within a 2.25 hectare grid (i.e., at smaller spatial scales), local sites of acorn production were not correlated with the location of mice in late spring or late summer the following year. The results indicate that the distribution of mouse hot and cold spots, and therefore local disease and predation risk, are not influenced by local red oak group acorn production the previous fall, despite the fact that acorns are a major source of overwinter food and a larger scale determinant of mouse density.

INTRODUCTION

Understanding the spatial structure and temporal variation in resource distribution is critical for understanding many ecological processes (Fortin and Dale 2005), informs management decisions (Brown et al. 1995), and can be used to predict disease risk in humans (Ostfeld et al. 2001). Masting, generally defined as high seed production by many individuals followed by one to many years of little or no seed production, is a phenomenon that has important implications in many ecosystems (Ostfeld and Keesing 2000; Koenig and Haddock 1999). In Northeastern forests, *Quercus* masting and the resulting variance in acorn availability influences interspecific relationships and population dynamics of a range of species (Ostfeld 2002) (Fig. 1). Acorn production by oaks the previous fall is strongly positively correlated with the size of the mouse population the following summer (Jones et al. 1998; Wolff 1996; Scarlett 2004). Mice in turn regulate gypsy moths (Jones et al.1998, Elkinton et al. 1996), prey on ground-nesting bird eggs and nestlings (Schmidt 2003), and are the most competent reservoir in the Lyme disease cycle (Ostfeld et al. 2001).

Recent research suggests that there are mouse “hotspots” (i.e., areas with significantly greater individual density and greater foraging activity as measured by track plates) generally at a scale less than ca. 50 m (Schauber et al. 2009). Some areas of the forest have hotspots only briefly (i.e., for a single month or for a single summer), while other hotspots persist across years. This creates a heterogeneous landscape for predation risk to gypsy moths and ground nesting birds as well as the opportunity for ticks to attach to a mouse carrying Lyme disease. What causes these hotspots remains unknown. Because acorns are such an important determinant of mouse density the following summer at the 2 hectare and greater scale (Jones et al. 1998), these analyses sought to explore at what scale that relationship is visible and at what scale there appears to be no effect. This study also sought to understand whether the local site of acorn production the previous fall is a determinant of the location of hotspots the following summer.

When averaged across larger areas, oak acorn production, at least to a certain degree, appears to follow a bimodal pattern of widespread crop failure or success. When observed at smaller spatial scales, however, it becomes clear that study sites and individual trees vary in their absolute and relative abundance of acorn production over time (Koenig et al. 1991; Sork and Bramble 1993; Greenberg et al. 2000). This study examined the affect of spatial scale on the population response of the white-footed mouse (*Peromyscus leucopus*) to acorn production, and explored the affect of acorn production on mouse density the following summer.

Analyses were performed using data from 1999-2007 collected at the Cary Institute of Ecosystem Studies located in Millbrook, New York (140 km north of New York City). This region is appropriate as a study location because it has high density tick populations, high lyme disease risk, and has experienced gypsy moth outbreaks in the past.

All these phenomena are intimately linked to the white-footed mouse population.

METHODS

Study Site

The data used in this study were collected on the grounds of the Cary Institute of Ecosystem Studies located in Dutchess County in Southeastern New York. Six 2.25 hectare (150 m x 150 m) grids were established in second growth forests formerly used as wood lots and agricultural fields. Oaks dominate the canopy—specifically northern red oak (*Quercus rubra*), chestnut oak (*Quercus prinus*), white oak (*Quercus alba*), black oak (*Quercus velutina*), and scarlet oak (*Quercus coccinea*) are present. The understory is characterized by sugar maple saplings (*Accer sacharum*), maple-leaf viburnum (*Virburnum acerfolium*), and witch hazel (*Hammamelis virginiana*) (Schmidt et al. 2001). The six paired grids are part of an ongoing study, with grids within a pair being about 0.5km from one another (Fig. 2). Each grid had 121 trapping stations evenly dispersed every 15 meters, with two Sherman traps associated with a given station (a total of 242 traps per grid) (Ostfeld et al. 2001). Every other row and column of traps had an associated 1 m^2 mesh seedbasket for a total of 25 per grid, evenly spaced every 30 meters (Fig. 3). These seedbaskets were designed to catch average seed rain per square meter and were not positioned with regard to proximity of the trees in the area.

Data Collection

Small mammal trapping was carried out between 2000 and 2007 on each grid for two trap-nights every three weeks from mid-May to mid-November. Individuals were ear-tagged and released each day (Ostfeld et al. 2001). Seed basket data was collected from 1999 to 2006. The contents of each basket were removed every 3 to 6 weeks usually beginning in July and ending in December. The collected seeds were separated and counted by species. Damaged or predated seeds were not included in final tallies (personal communication—K. Oggenfuss).

Data Organization

Data were analyzed at three spatial scales: the site, the individual grid, and the neighborhood. A site was composed of the two associated grids separated by ca. 0.5 km, combined as a single unit. At the spatial scale of the individual grid, all grids were treated as being independent of one another in space. The "neighborhood" consisted of the trapping station associated with a given seed basket and the four closest trap stations at right angles creating a 21 m x 21 m square with the seed basket at the center (Fig. 4).

Seed counts from different time periods within a season were summed to give a yearly total. Acorns were divided into their two subgenera with the White Oak Group (subgenus *Lepidobalanus*) including acorns from chestnut oaks (*Quercus prinus)* and white oaks (*Quercus alba)*, and the Red Oak Group (subgenus *Erythrobalanus*) including acorns from the red oaks (*Quercus rubra)*, black oaks (*Quercus coccinea)*, and scarlet oaks (*Quercus coccinea)*. Separating species by subgenera (i.e., white oak group (*Lepidoblanus)* and red oak group (*Erythrobalanus*)) was done to address their differing acorn germination biology. Red oak group acorns germinate the following spring, but white oak group acorns germinate the same autumn they fall from the canopy (Fowells 1965). Thus from the prospective of a mouse only red oak group acorns are a reliable source of overwinter food. Immature acorns and those with insect damage were not included in the final count because it is unlikely they would have been a viable source of food for mice. Seed basket data from 1999 to 2006 were analyzed across the six grids for a total of 150 seed baskets per year.

For analyses of the relationship between mouse density and acorn production that relied on grid-wide estimates of mouse density, a Jolly-Seber mark recapture procedure (Ostfeld et al. 2006) was used to estimate the number of mice per grid. The Jolly-Seber procedure was used because it likely provided a more accurate estimate by integrating data from multiple trapping sessions over time. For analyses that relied on estimates of the local population around a trapping station (for which there was no Jolly-Seber estimation available), individuals caught over the two-day trap session were counted. This was conducted for a trapping session in late spring (as defined by the first three weeks of June) and late summer (as defined by the first three weeks of August). Mouse data used was taken between 2000 and 2007 across the six grids for a total of 1452 traps generating population estimates at each time step (i.e., early summer and late summer of each year).

Statistical Analysis

In order to assess whether there was a significant site and grid effect on the total production of acorns and mice across all sample years (i.e., removing the affect of inter annual variation), total acorn production of a given seed basket and total individual mouse count for a trap station were summed for all years. An analysis of variance (ANOVA, Systat 12) was conducted on both the mouse data and the log10 transformed acorn data with nested main effects at the grid and site scales. Where there were significant differences among sites and grids in average acorn production per seed basket and average individual mouse count per trap station, a Tukey pairwise comparison was used as a post-hoc test.

Regression and correlation analyses were carried out at three spatial scales to determine at what spatial scales the relationship between acorn production and mouse density was statistically significant. At the site scale (i.e., the two paired grids separated by ca. 0.5 km) and grid scale (i.e., each grid treated individually) the Jolly-Seber midsummer mouse population estimate was regressed against the total number of acorns collected at the site or the grid the previous fall. Red oak and white oak groups were analyzed separately, but all sites and grids were combined. This potentially ignored significant variation in the response of the mouse population to acorn production between grids and sites. To address this issue, a maximum likelihood analysis was carried out in R 2.8 to determine whether analyzing the grids separately, rather than combined together, resulted in a more parsimonious model (i.e., lowest Aikake Information Criterion (AIC) value). In this analysis simulated annealing (a global optimization procedure) with 15000 iterations was used to establish most likely parameters.

To examine the mouse-acorn relationship at the neighborhood scale (i.e., the five mouse trapping stations closest to a seed basket), a Spearman rank correlation (data were not normally distributed) was carried out using the acorn production of the seed basket the previous fall (independent variable) and the total number of individual mice caught at each trapping station within an associated neighborhood (dependent variable). Correlations were analyzed for the number of individual mice caught in June and August (separately) against total acorns, red oak group acorns, and white oak group acorns, for each year and for each grid.

To further explore the relationship between acorns and mice at spatial scales less than the grid, but not strictly limited to the neighborhood, interpolation of the mouse and acorn data was carried out using ArcGIS 9.2. Inverse distance weighting was used with a search radius of 50 m using the 8 closest known values for mouse trapping stations from June and August trapping sessions, and a search radius of 70 m for the 8 closest known values for seed baskets. Inverse distance weighting was used as it requires less neighboring points than kriging (which requires 15-20 for accuracy; Fortin and Dale 2005), and grids had only 25 seed baskets from which to derive the neighboring points. Search radii were determined by calculating the minimum distance needed to incorporate 8 neighboring points. These maps were then visually compared for correlations between the distribution of acorns the prior fall and mouse captures the following summer.

RESULTS

Do average acorn production and average mouse density vary by location?

Average acorn output of the white oak group 1999-2006 did not significantly vary among grids (F = 1.71, p = 0.14 , df = 5) or sites (F = 0.088, p = 0.92, df = 2). Average acorn output of the red oak group 1999-2006 did not significantly vary among sites (F = 1.29 , p = 0.28 , df = 2), but did significantly vary among grids (F = 2.405, p = 0.044, df = 5, Fig. 4). Henry Experimental grid had significantly less average acorn production than all other grids.

Average mouse density 2000-2007 varied significantly among grids and among sites for both early summer (June) and late summer (August) trapping sessions. June average mouse density significantly varied among all three sites (F = 30.31, $p < 0.001$, df = 2, Fig. 5a). In August, Green site had significantly greater average mouse density than the other two sites (F = 17.5, $p < 0.001$, df = 2, Fig. 5b). At the grid level for the June trapping session, Green Control grid had greater average mouse density than all other grids, and Tea Control grid had significantly lower average mouse density than all others with the exception of Tea Experimental grid (F = 16.36 , $p<0.001$, df = 5, Fig. 6a). At the grid level for the August trapping session, Green control grid had significantly greater average mouse density than all other grids (F = 17.52, $p < 0.001$, df = 5, Fig. 6b).

At what spatial scale(s) does mouse density correlate with acorn density?

Regression analysis using Jolly-Seber individual mouse estimates against the total number of red oak group acorns and white oak group acorns was similar at both the site and grid spatial scales. White oak group acorns the prior fall had no significant affect on the mouse population the following summer at either the site (p = 0.34, r^2 = 0.26, n = 24) or grid (p = 0.55, r^2 = 0.006, n = 48) scales. Red oak group acorns, however, were significantly correlated with mouse density at the site (p = 0.025, r^2 = 0.73, n = 24) and grid ($p < 0.001$, r^2 = 0.504, n = 48) scales (Fig. 7). Regression analysis between mouse population and red oak group acorn production was also carried out for each grid. The results of a likelihood analysis suggested that the model that best fit the data was one that combined all individual grids using the untransformed acorn data (Table 1). Since the relationship between acorns and mice did not vary significantly between the individual grids, further analysis of differences in intercepts and slopes of the regression lines was not justified.

At the neighborhood scale, of the 288 correlations conducted (6 combinations of acorn type [red oak group, white oak group, and total acorns] and mouse trapping sessions [i.e., June or August] x 8 years x 6 grids), only 20 were significant. Many of these significant correlations were implausible; such as acorns being negatively correlated with the size mouse population the following summer, or acorns affecting the August mouse population, but not the June mouse population. Twenty significant correlations out of 288 (6.9%), is not much higher than the 5% one would statistically expect to occur by chance. The twenty significant correlations were therefore assumed to be spurious.

Results of visual comparison of interpolated data of all grids and all years suggested that the distribution of fall acorns had no relationship to the distribution of individual mice the following summer at any spatial scale less than ca. 2.25 hectares (Fig. 8).

DISCUSSION

Mouse density and acorn production

While red oak group acorns are an important determinant of the mouse population at the >2.25 hectare scale (Fig. 7), there is no discernable relationship between the specific location of acorn production and local (i.e. <2.25 hectare scale) mouse density the following summer. A strong relationship between oak masting and *P. leucopus* population density at larger scales has already been demonstrated (Wolff 1996, Jones et al. 1998, Ostfeld et al. 1996). Red oak group acorns are a major source of winter food, and although rodent caches are typically consumed as early as January (Wolff 1996), they have a very large influence on the summer population by increasing the survivorship of the spring/early summer breeding population. The results of this study suggest that local summer mouse activity density is not influenced by the fall location of their most important overwinter food source.

There are several possible reasons for the deterioration of the large scale positive relationship between acorns and mice when examined at smaller scales. Studies suggest that a typical mouse home range is generally small (500 m^2) (Wolff 1985) and that they will forage beyond that during oak masting events (McShea and Giles 1992). Given that mice cache acorns (Johnson et al. 2002), they could presumably be removing them to locations with more suitable habitat or other, less ephemeral, food resources. Territoriality can also influence the foraging behavior of mice (Vessey 1987). Thus it is possible that local summer activity density, and by extension trap success, is shaped by conflict over existing resources or access to mates. If interspecific competition causes mice to relocate during the summer it seems unlikely that acorn production the previous year would have a major affect on where they dispersed. Analysis of the average mouse and acorn production across all years also suggests there are other factors influencing the mouse population. Although the grids significantly varied in average acorn production, grids with significantly higher acorn production did not have significantly greater average mouse density. Thus it appears that while the relationship between acorn production and mouse density in a given year did not significantly vary among grids (Table 1), there are likely differences (i.e., other food resources, vegetative cover, etc.) that influence these averages over time.

Implications for heterogeneous predation risk

Acorns are not an important determinant of summer mouse density at scales <2.25 hectares and therefore are very unlikely to influence the location of mouse activity hot and cold spots which typically occur at scales <50m. These hot and cold spots may be ecologically significant if they create a heterogeneous predation risk landscape for gypsy moth and ground nesting songbirds (Schauber et al. 2009). The existence of cold spots of mouse activity permits the gypsy moth to persist at low levels throughout the forest even though the existing mouse population, if evenly distributed, would otherwise be capable of causing extinction (Goodwin et al. 2005, Schauber et al. 2007). Likewise, ground-nesting birds will expose their eggs and nestlings to lower predation risk if they establish a nest in an area with lower mouse activity (Schmidt et al. 2001). The existence of hot spots is also of particular interest from a human perspective because higher local mouse density may increase the likelihood of ticks finding a reservoir-competent host and thus acquiring the bacteria that, if passed to humans, causes Lyme disease. This study rules out acorns as a predictor of the location of hot and cold spots; suggesting that further research into what creates and maintains mouse activity hot and cold spots should focus on different factors such as vegetative coverage, other food resources, spatial fidelity and territoriality.

Importance of spatial scale

What emerges as a strong relationship at the ≥2.25 ha. scale is not apparent when looking at smaller scales. Other studies on small mammal distribution also suggest that prediction accuracy changes with scale (Orrock et al. 2000). This study highlights the importance of conducting studies on a diversity of temporally and spatially different scales in order to gain a more complete picture of causality. It also clearly shows that scale can influence what conclusions are reached in a study, and that findings at one spatial scale are not necessarily applicable at others.

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APPENDIX

TABLE 1. Maximum likelihood estimates of the relationship between mice and red oak group acorns. * : Model with the lowest Akaike Information Criterion (AIC) value and therefore the best fit.

Grid Organization	Model	No. Observations	No. Parameters	AIC	Slope	R^2
Combined	Mean	48	2	535.63	n/a	n/a
Combined	Linear	48	3	518.34	0.999	0.333
Combined*	Power	48	3	504.09	1.01	0.505
Separate	Mean	48	7	545.93	n/a	n/a
Separate	Linear	48	13	519.63	0.994	0.636
Separate	Power	48	13	542.59	1.053	0.414

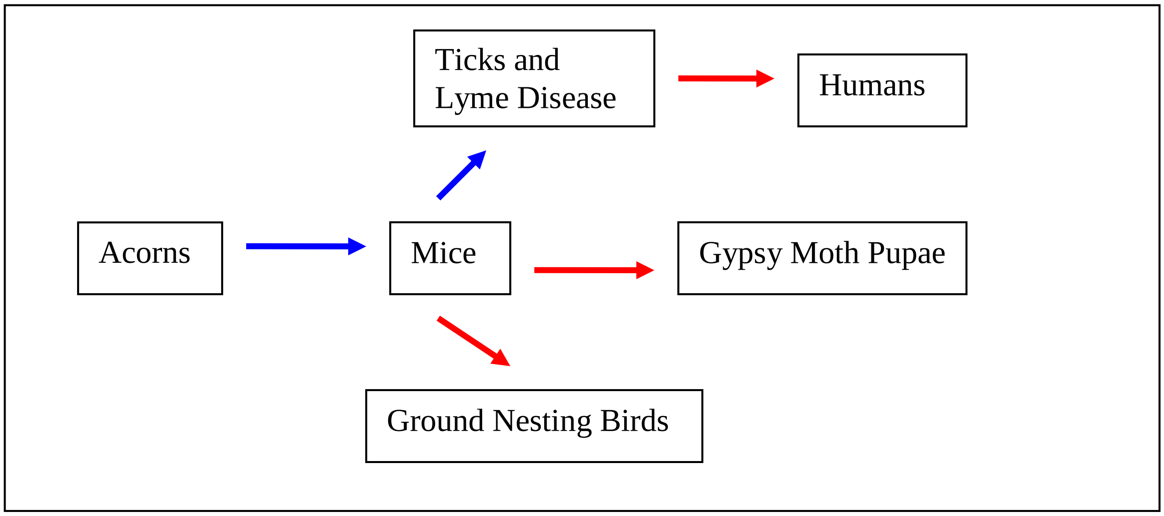


FIGURE 1. A simplified flow chart illustrating how acorn production reverberates throughout the system. Blue arrows represent a positive relationship between the arrow's origin and termination. Red arrows represent a negative relationship. Adapted from Ostfeld 2002.

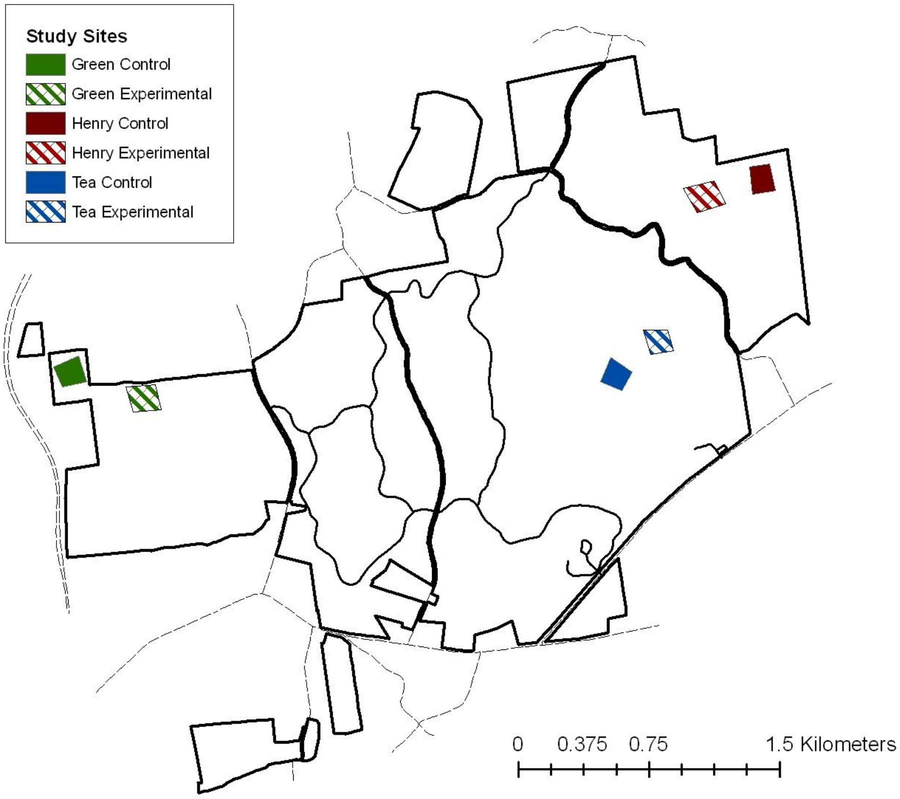


FIGURE 2. Location of the Grids on the Cary Institute property. "Control" and "Experimental" are naming conventions from ongoing experiments. A "site" is the two associated grids (i.e. Henry Experimental and Henry Control) and a "grid" is each grid treated independently.

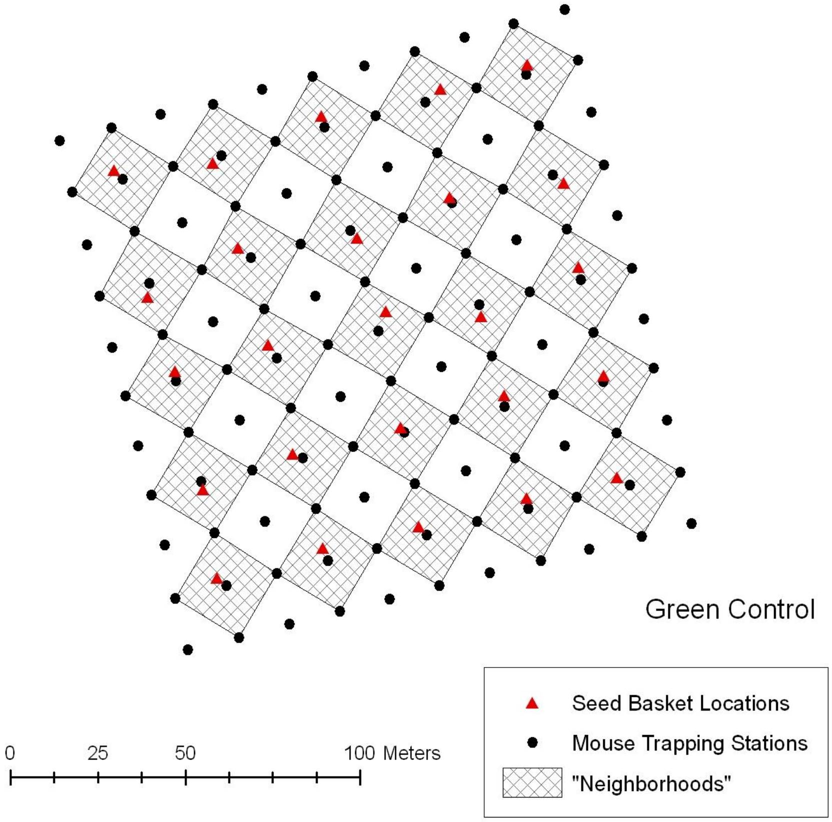


FIGURE 3. Layout of a typical grid, in this case Green Control. The spatial scale of the "neighborhood" is the five closest seed baskets associated with a given mouse trapping station.

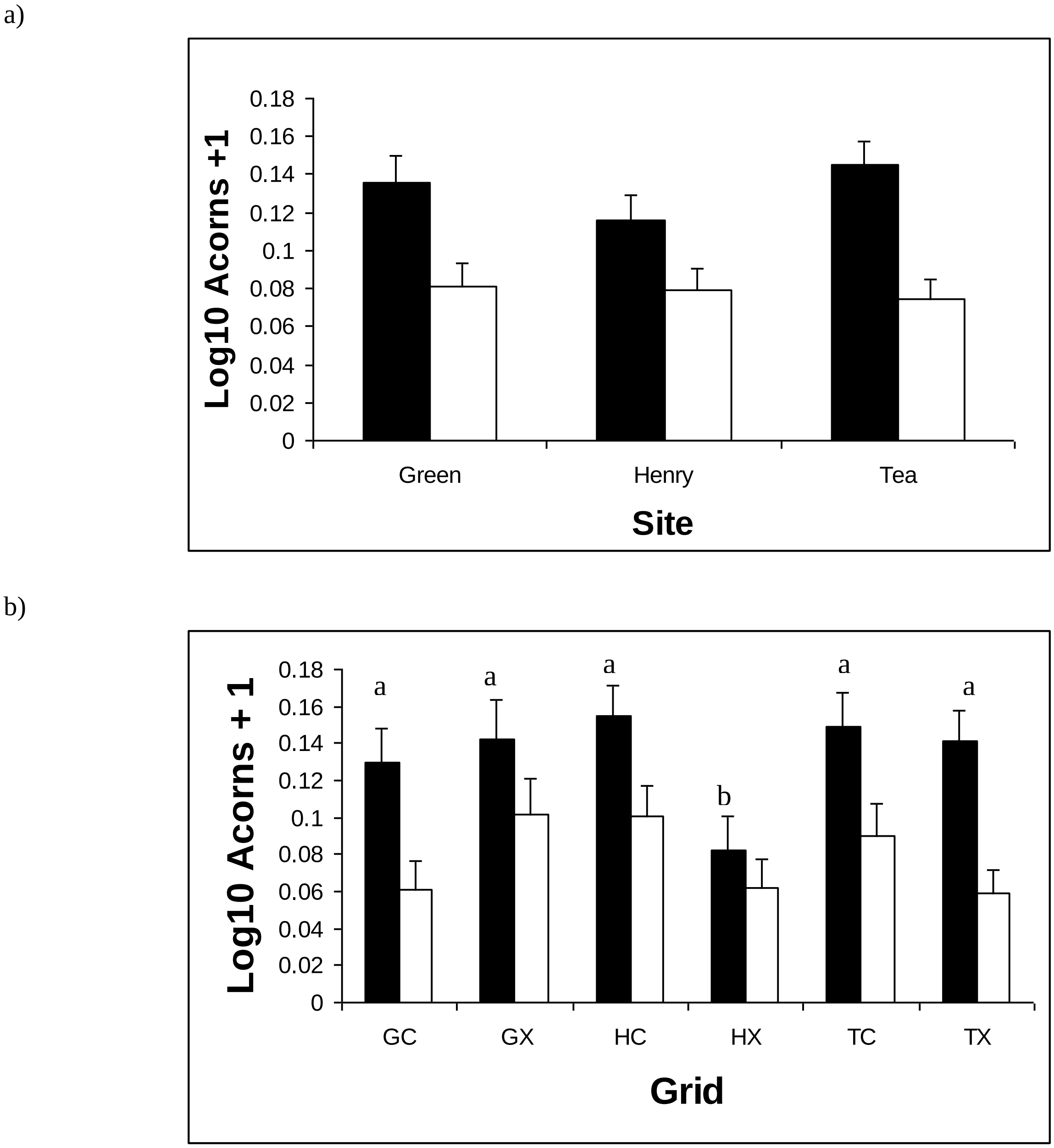


FIGURE 4. Average number of acorns, 2000-2006, per m^2 (log transformed), by (a) site and (b) grid. Black bars are acorns from the red oak group and white bars are acorns from the white oak group. Values are means + 1 SE. Means with different letters differ significantly (Tukey's Post Hoc, $p < 0.05$).

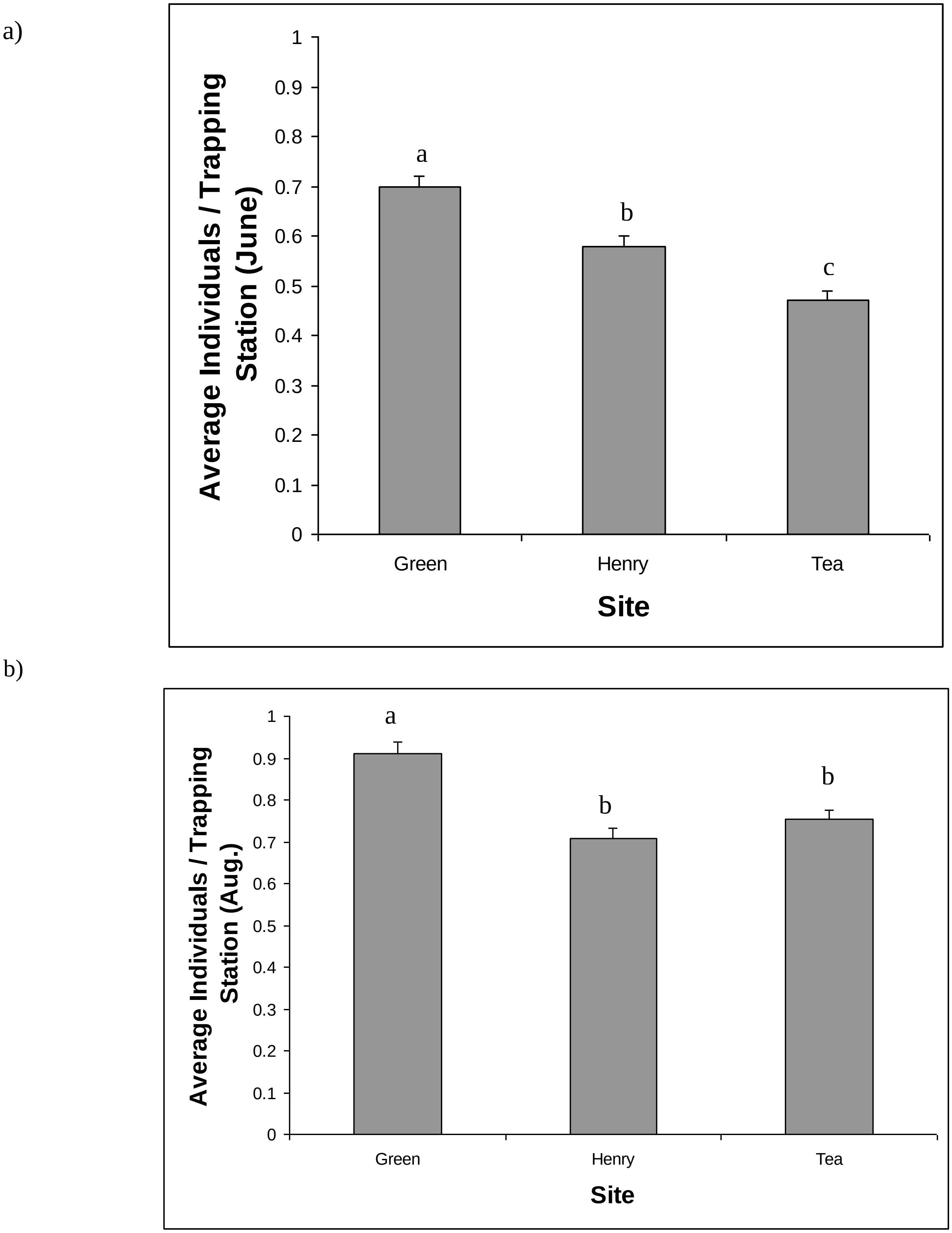


FIGURE 5. Average number of individual mice captured per trapping station by site, 2001-2007, in (a) June and (b) August trapping sessions. Values are means +1 SE. Means with different letters differ significantly (Tukey's Post Hoc, $p < 0.05$).

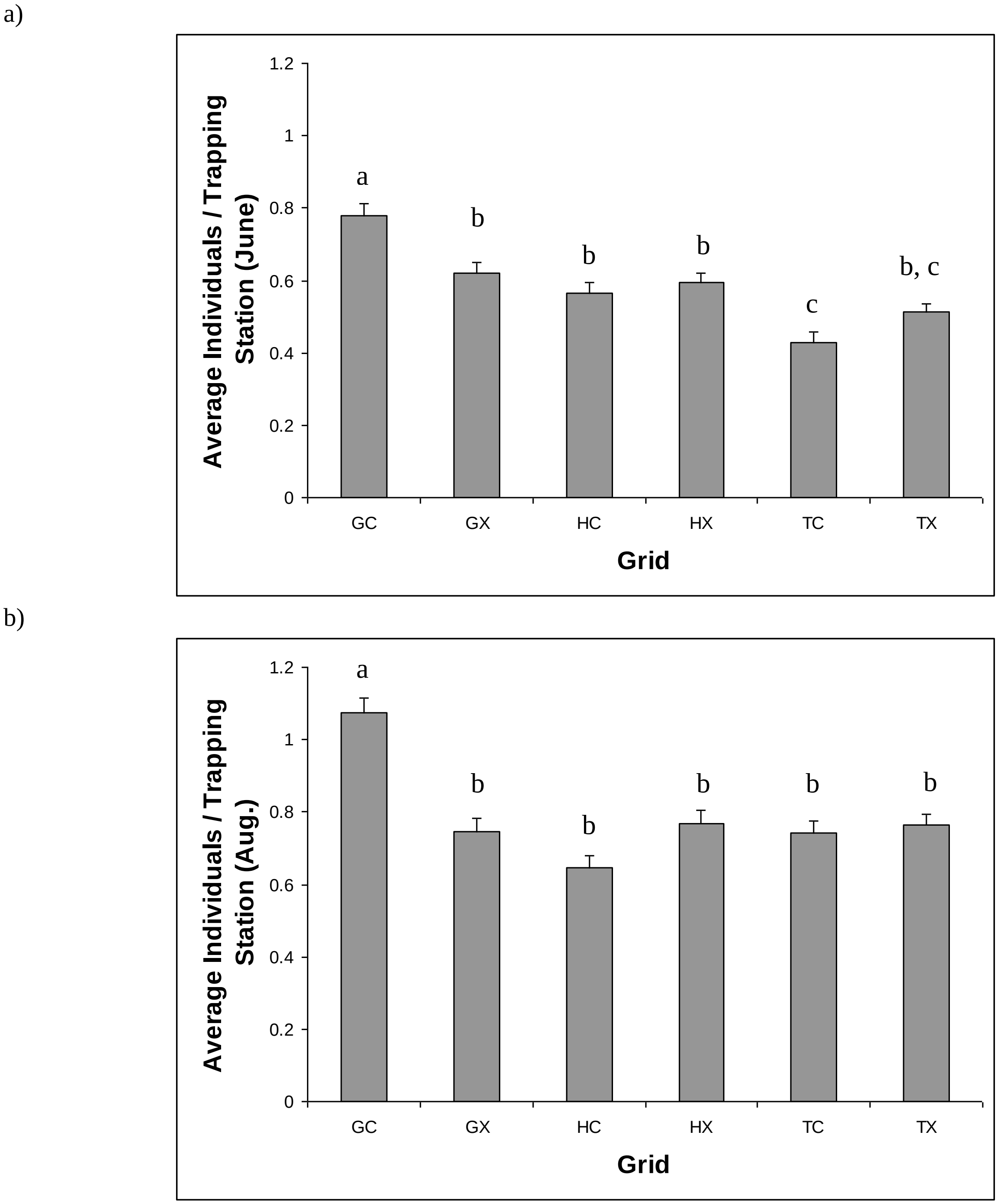
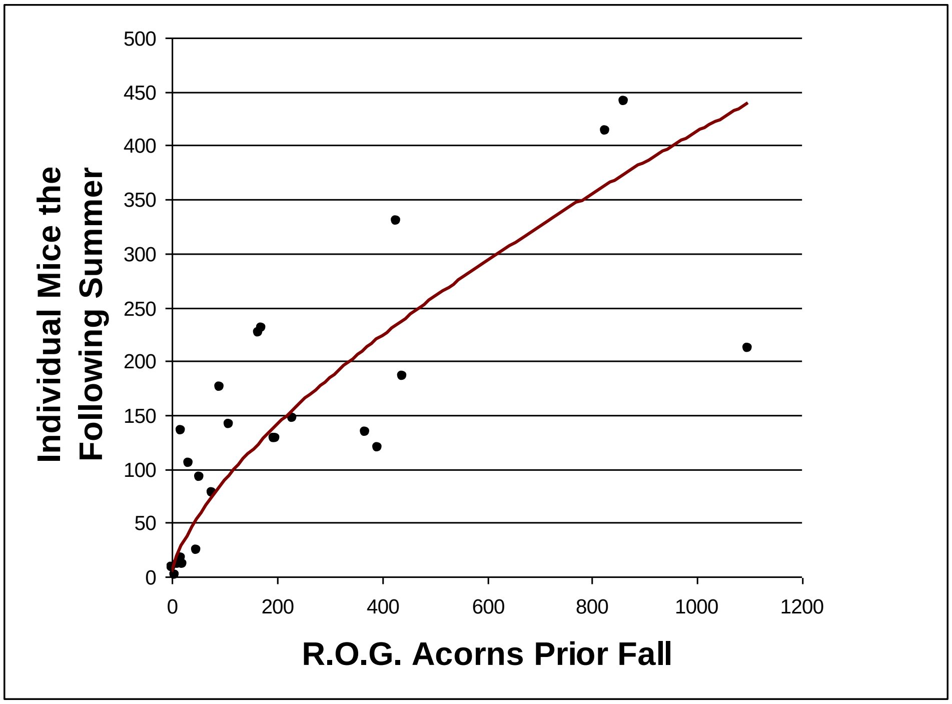


FIGURE 6. Average number of individual mice captured per trapping station by grid, 2000-2006, in (a) June and (b) August trapping sessions. Values are means +1 SE. Means with different letters differ significantly (Tukey's Post Hoc, $p < 0.05$).

a)



b)

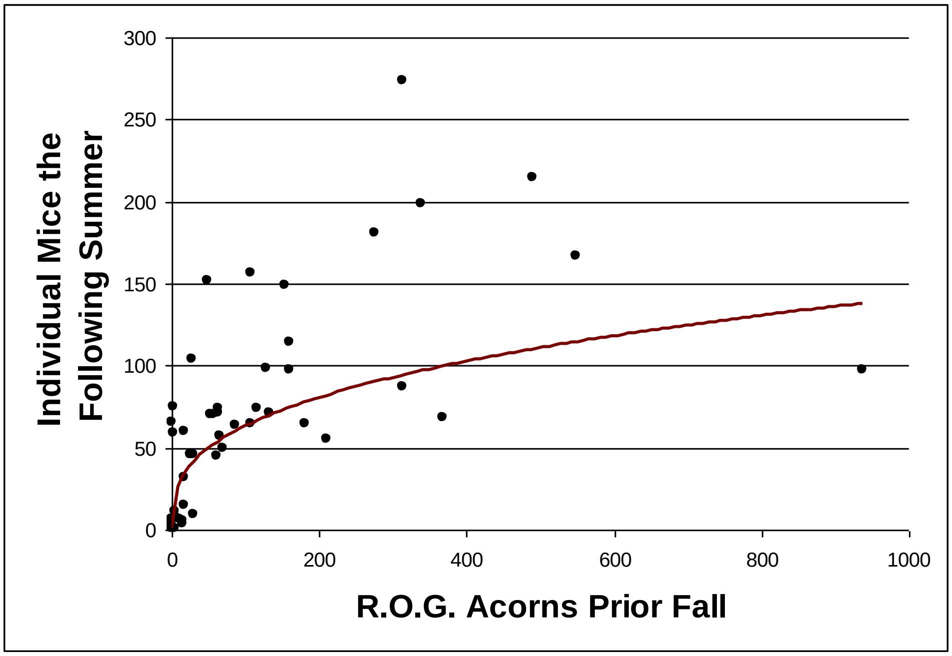


FIGURE 7. Regression between fall production of red oak group acorns and the following summer's mouse population at the (a) site and (b) grid scale.

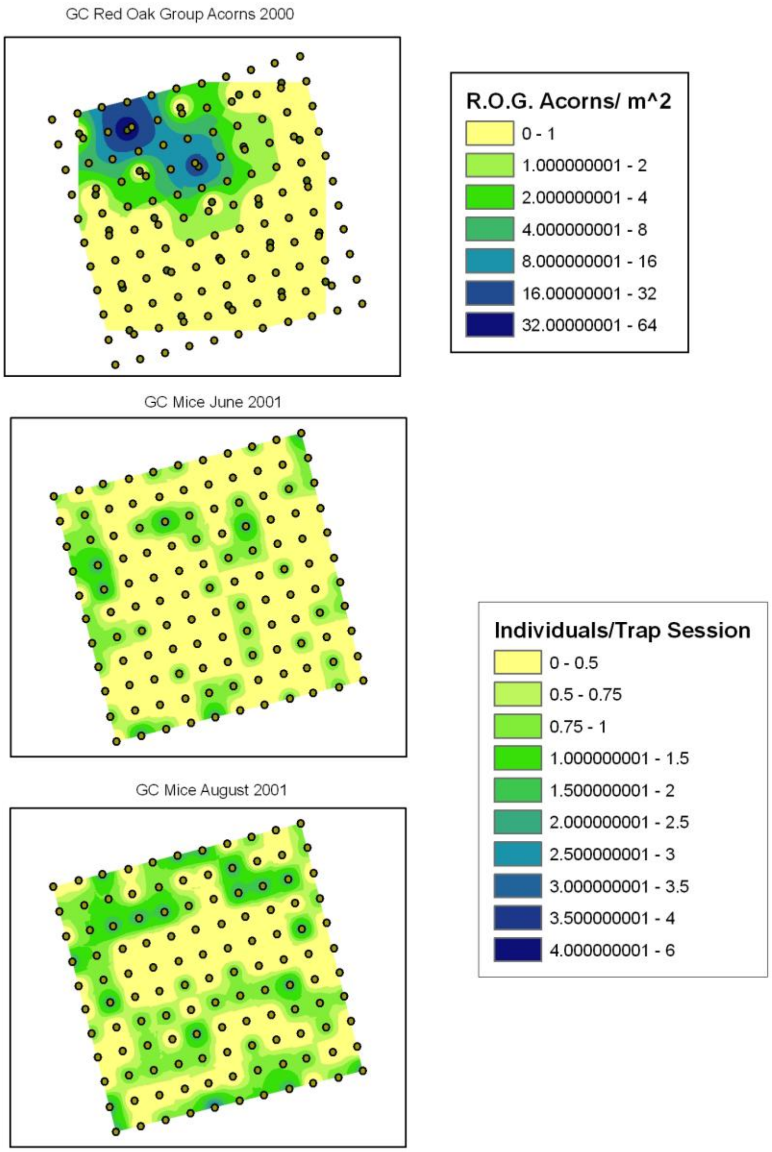


FIGURE 8. An example of the maps used to visually assess correlations between masting and mouse activity/density at scales less than a grid. The first map shows the fall distribution of acorns/m^2 in 2000 on the Green Control Grid, while the second and third maps show the June and August individual mouse distribution/trap session in 2001 for the same location. If there was a relationship in this example, one would expect to see more mice in the upper left corner. Only very rarely did there appear to be a visual correlation in among maps.