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Eagan, Timothy S. II; Beasley, James C.; Olson, Zachary H.; and Rhodes, Olin E. Jr., "Impacts of generalist mesopredators on the demography of small-mammal populations in fragmented landscapes" (2011). *USDA National Wildlife Research Center - Staff Publications*. 1357.

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Impacts of generalist mesopredators on the demography of small-mammal populations in fragmented landscapes

Timothy S. Eagan II, James C. Beasley, Zachary H. Olson, and Olin E. Rhodes, Jr.

Abstract: A consequence of the reduction and subsequent fragmentation of native habitats has been the loss or severe reduction of specialist predator populations from these altered ecosystems, resulting in a “release” of generalist predators. Demographic aspects of small-rodent populations, especially predator-driven density cycles, have been extensively studied. However, the majority of studies examining predator–prey dynamics have been conducted in relatively undisturbed ecosystems, while more limited data are available for regions that have been greatly modified by human settlement. Using raccoons (*Procyon lotor* (L., 1758)) and white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) as focal species, we used an experimental framework to evaluate the hypothesis that generalist mesopredators limit small-mammal abundance in landscapes that have been significantly altered by human land use. Both parametric and nonparametric analyses indicated that populations of white-footed mice exhibited a significant increase (32%) in density where raccoon abundance was reduced when compared with control populations. Our study highlights an important role that superabundant mesopredators can play in ecosystems through the limitation of secondary prey populations. This research suggests that further investigation of the trophic dynamics of agricultural ecosystems is critical if we are to elucidate the fundamental ecological mechanisms associated with the persistence of species in disturbed environments.

Résumé : Une conséquence de la réduction et de la fragmentation subséquente des habitats indigènes est la perte ou la réduction sévère des populations de prédateurs spécialisés dans ces écosystèmes modifiés, ce qui provoque une « libération » des prédateurs généralistes. Les aspects démographiques des populations de petits rongeurs, particulièrement les cycles de densité causés par les prédateurs, ont été très bien étudiés. Cependant, la majorité des études de la dynamique prédateur–proie ont été réalisées dans des écosystèmes relativement peu perturbés, alors qu’il existe moins de données sur les régions qui ont été fortement modifiées par l’établissement humain. Utilisant les ratons laveurs (*Procyon lotor* (L., 1758)) et les souris à pieds blancs (*Peromyscus leucopus* (Rafinesque, 1818)) comme espèces cibles, nous employons un cadre expérimental pour évaluer l’hypothèse selon laquelle les mésoprédateurs généralistes limitent l’abondance des petits mammifères dans les paysages qui ont été significativement altérés par l’utilisation des terres par les humains. Des analyses paramétriques et non paramétriques indiquent toutes deux que les populations de souris à pieds blancs connaissent une augmentation significative (32 %) de densité lorsque l’abondance des ratons laveurs est réduite par rapport aux populations témoins. Notre étude souligne le rôle important que les mésoprédateurs en surabondance peuvent jouer dans les écosystèmes en limitant les populations de proies secondaires. Notre recherche indique qu’une étude plus poussée de la dynamique trophique des écosystèmes agricoles est essentielle pour pouvoir élucider les mécanismes écologiques fondamentaux associés à la persistance des espèces dans les environnements perturbés.

[Traduit par la Rédaction]

Introduction

Changes in landscape structure owing to human land-use practices can have cascading effects on the distribution of species and composition of communities. One consequence of the reduction and subsequent fragmentation of native habitats has been the loss or severe reduction of specialist predator populations from these altered ecosystems, resulting in a “release” of generalist mesopredators (Rogers and Caro 1998;

Crooks and Soulé 1999; Johnson et al. 2007; Letnic et al. 2009). Such increases in mesopredator abundance present a major ecological concern because of the integral role these species play in avian nest predation (Donovan et al. 1997), disease transmission (Page et al. 1999; Smith et al. 2002; Raizman et al. 2009), scavenging dynamics (DeVault et al. 2011), and numerous human–wildlife conflict issues (Ratnaswamy et al. 1997; Beasley and Rhodes 2008). Many of these species also have the potential to negatively impact

Received 19 October 2010. Accepted 24 March 2011. Published at www.nrcresearchpress.com/cjz on 30 July 2011.

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small-mammal populations, either directly through predation (Sinclair et al. 1998; Hanski et al. 2001), or indirectly through disease (Page et al. 1999, 2001). However, few empirical data are available to suggest the magnitude to which elevated densities of generalist mesopredators can impact the demography of small-mammal populations.

Demographic aspects of small-rodent populations, especially predator-driven “boom and bust” density cycles, have been extensively studied (for reviews see Andersson and Erlinge 1977 and Hanski et al. 2001). Many studies point to specialist predators as the primary driver of rodent cyclic dynamics, while generalist predators serve to stabilize populations (Andersson and Erlinge 1977; Steen et al. 1990; Hanski et al. 1991). However, the majority of studies examining predator–prey dynamics have been conducted in relatively undisturbed landscapes, while more limited data are available for regions that have been greatly modified by humans. Previous studies of small-mammal populations in less-pristine landscapes have documented population density cycles, although food availability, rather than predator abundance, appears to drive cycles of small-mammal populations in these landscapes (Ostfeld et al. 1996; Wolff 1996; Schnurr et al. 2002; Elias et al. 2004).

Within North America, the agricultural ecosystems of the midwestern United States have been dramatically altered to facilitate the production of crops, experiencing as much as an 88% decrease in the amount of forest land since European settlement (Moore and Swihart 2005). As a consequence of the widespread conversion of forest to cropland that characterizes this region, specialist species, particularly specialist mammalian predators, are rare or have been extirpated owing to the reduction and fragmentation of native habitats, while generalist predator and prey species tend to thrive because of their mobility and niche breadth (Gehring and Swihart 2003). Of those species able to persist in the agriculturally dominated environments of the midwestern United States, white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) undoubtedly are one of the most successful, owing to their extreme behavioral plasticity (Adler and Wilson 1987; Bender et al. 1998). Certainly mast resources contribute to the ubiquity of white-footed mice in this region (McShea 2000; Schnurr et al. 2002), although some of their success in agricultural landscapes also must be related to their ability to exploit the superabundant food resources associated with crops. Raccoons (*Procyon lotor* (L., 1758)) are generalist mesopredators that also are ubiquitous in fragmented agricultural landscapes, where they maintain higher densities than populations occurring in more heavily forested landscapes (Crooks 2002; Rosatte et al. 2010; Beasley et al. 2011).

Increased density, along with a disproportionate use of forest patches and corridors by raccoons (Beasley et al. 2007a; Beasley and Rhodes 2010), creates a scenario in which the rate of raccoon predation on avian and small-mammal prey within a forest patch could be quite high. Although mice have been documented in raccoon diets, they rarely occur as a main component (Giles 1939; Schoonover and Marshall 1951; Greenwood 1981; Tyler et al. 2000). Nonetheless, raccoons clearly utilize white-footed mice as a food source (either through predation or by scavenging carcasses) because mice also have a demonstrated role as an intermediate host in the transmission of raccoon roundworm (*Baylisascaris*

procyonis); a parasite for which raccoons are the definitive host and must consume infected mice to complete the parasites’ life cycle (Tiner 1953; Sheppard and Kazacos 1997; Page et al. 2001). Despite the high prevalence of *B. procyonis* in agricultural landscapes (28%; Page et al. 2001), only 5% of natural infections in mice directly result in mortality (Tiner 1953). Thus, it is likely that if raccoons limit mouse abundance, it is primarily via predation rather than through disease transmission. However, we are not aware of any studies that have specifically evaluated mouse predation by raccoons.

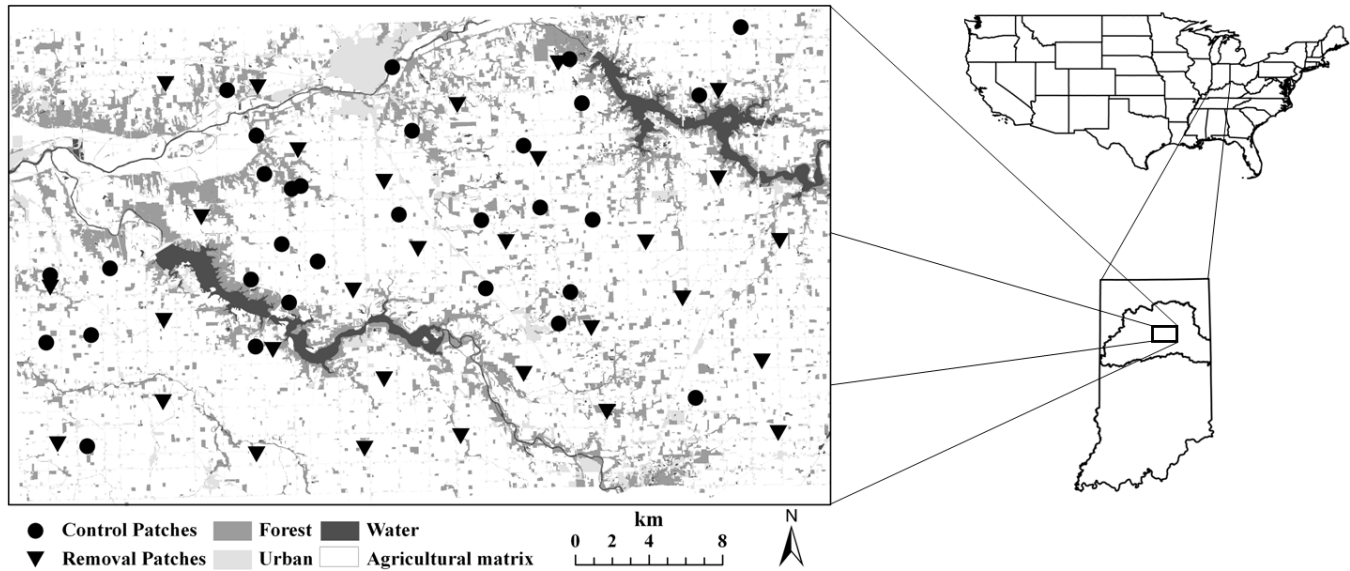
Given evidence for strong population responses of small mammals to the removal of specialist predators in relatively undisturbed landscapes, and a paucity of empirical data regarding manipulations of generalist predator communities in regions with limited specialist predator communities (e.g., agricultural ecosystems), there is a clear need for additional experimental research to elucidate the role of generalist predators, particularly raccoons, in limiting small-mammal populations in disturbed environments. Thus, our primary objective in this research was to test the hypothesis that elevated densities of generalist mesopredators created by anthropogenic changes in land use limit the abundance of small-mammal populations in highly modified landscapes. Specifically, we used raccoon eradication experiments with appropriate controls to evaluate changes in density of white-footed mice within habitat patches prior to and subsequent to raccoon removal, as well as concurrently between patches from which raccoons had been removed versus control (nonremoval) patches within a fragmented agricultural ecosystem.

Materials and methods

Study area

This study took place in portions of the Upper Wabash River Basin (UWB) in north-central Indiana. The UWB is a highly deforested region of heavy agricultural production—only 8% of the region is forested compared with the state of Indiana that currently has around 19% forest cover, and had approximately 87% forest cover before European settlement (Moore and Swihart 2005). Seventy-one percent of the land area of the UWB is used for agricultural production, with the main crops consisting of corn and soybeans (Beasley et al. 2007a). Remaining forest land (mainly oak (*Quercus* L.) – hickory (*Carya* Nutt.) – maple (*Acer* L.) forest) is highly fragmented; with the only contiguous tracts reserved to areas unfit for cultivation, such as floodplains and steeply sloped terrain. Beasley et al. (2007a) classified the land cover of our 1100 km² study area as 66% agriculture, 15% forest, 6% anthropogenic, 3% water, 2% shrub land, 1% roads, and 1% corridors. The majority of study sites used in this research were privately owned, isolated woodlots surrounded by a matrix of lands used for agricultural production, with a few sites located in larger tracts of more contiguous forest (Fig. 1). Trapping sites included 30 forest patches also trapped for raccoons using live capture–mark–recapture as part of ongoing studies in our laboratory to monitor raccoon abundance (hereafter referred to as control patches), and 30 patches in which a comprehensive raccoon eradication experiment was undertaken in 2007 (hereafter referred to as removal patches). Both control and removal patches were

Fig. 1. The spatial dispersion of 30 control (circles) and 30 removal patches (triangles) in our study area in northern Indiana, USA. In 2007 we depopulated raccoons (*Procyon lotor*) from removal patches and estimated the density of populations of white-footed mice (*Peromyscus leucopus*) in all patches in 2007 and 2008.



manually selected to represent the distribution of woodlot sizes and degrees of isolation present in our study landscape (Beasley et al. 2007a).

Raccoon removal

Raccoon removal took place in 30 of the 60 study sites in March–June of 2007. Raccoons were live-trapped with box traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA) baited with commercial cat food and then subsequently euthanized in accordance with the guidelines of the American Society of Mammalogists (ASM) (Gannon and Sikes 2007) and authorized under Purdue Animal Care and Use Committee (PACUC) protocol (07-018). To accomplish the removal, each forest patch was saturated with box traps and trapped continuously until no raccoons were caught or tracks observed for 4 consecutive days. This resulted in a minimum of 14 trapping days, and trapping was capped at a maximum of 25 days. A 25-day maximum was believed to be a period sufficient to remove all resident raccoons so that only immigrating individuals constituted new captures. The removal was a one-time event for each patch (i.e., raccoons were trapped to extirpation and then allowed to recolonize without manipulation).

Trapping and mark–recapture of white-footed mice

We live-trapped mice from all 60 habitat patches during the late spring through summer of both 2007 (shortly following raccoon removal) and 2008 in accordance with ASM guidelines (Gannon and Sikes 2007) and authorized under PACUC protocol (07-024). In 2007, mouse trapping commenced immediately subsequent to raccoon removal, resulting in a mean of <2 months (mean = 57.9 days, SE = 4.425 days) between the raccoon removal and the mouse trapping. We captured mice using Sherman live-traps (H.B. Sherman Traps, Tallahassee, Florida, USA) distributed in a grid, with traps spaced 20 m apart. The standard trapping grid consisted of 30 traps placed in 5 rows of 6 traps each.

In some cases the size and shape of woodlots dictated that the shape of the standard grid be altered; however, 30 traps were used in each grid regardless of shape.

We also placed two raccoon-size Tomahawk live-traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA), baited with commercial cat food, at opposite corners of each grid to curtail predator damage to small-mammal traps. Predators captured in live-traps were released at the conclusion of daily trap checks. We marked the corners of each trapping grid with a GPS to ensure that subsequent grids were set in the same spatial locations. A trapping round consisted of 1 day of prebaiting followed by 5 days of trapping. Small-mammal traps were baited with a mixture of rolled-oats and peanut butter. We affixed a uniquely numbered ear tag to each white-footed mouse (National Band and Tag Co., Newport, Kentucky, USA) and recorded gender, age, and mass. All animals were released at the point of capture.

Statistical analysis

We derived patch-specific abundance estimates for white-footed mice separately for the preremoval and postremoval years using the Huggins closed capture model (Huggins 1989, 1991) in the program MARK (White and Burnham 1999). Within each year, individuals from all patches were combined into a single input file, but each patch was delineated as a unique attribute group in MARK. This allowed us to overcome problems associated with populations with few individuals by estimating capture (p) and recapture (c) probabilities for the combined data set, but still derive patch-specific estimates of N . By constraining the p and c parameters to be constant across years a more precise estimate of N is obtained, but assumes that capture and recapture rates are constant among patches. Given the general trappability of mice, and that we used identical trapping methodology for all sites, we believe that the assumption of similar capture and recapture rates among patches is valid.

Huggins models estimate p and c probabilities as real pa-

rameters, but differ from full-likelihood models in that N is a derived parameter from the model—using information only from the number of captured individuals (Huggins 1991). Another advantage of using the Huggins model is that it allows covariates such as sex and age to be incorporated into the models (Huggins 1991). This model does assume closure, but this assumption should be satisfied by the short trapping design utilized in this study.

We developed a suite of models in MARK varying the effects of time on capture and recapture probabilities, and also included the effects of the individual covariates mass and sex. We then used Akaike's information criteria, corrected for small sample size (AIC_c ; Burnham and Anderson 2002), to determine the overall best-fitting model for estimation of the abundance of white-footed mice. Because not all grids were the same size, abundance for each patch was converted to density by dividing abundance by the area of the grid plus a 15.5 m buffer on all sides. This buffer size was selected based on the radius of the mean home-range size reported for white-footed mice inhabiting a fragmented, agricultural landscape similar to our study area (Krohne and Hoch 1999).

All statistical tests used to evaluate responses of white-footed mice to raccoon removal were implemented in SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA). We assessed the normality of the distributions of both the prerule and postremoval densities using a Kolmogorov–Smirnov D test; if deviance from normality was detected, then variables were log-transformed to obtain acceptable normal distribution parameters. We first tested for differences in mean densities between our experimental groups (removal and control) separately by year (prerule and postremoval years) using one-way ANOVA. We also expected a priori that the densities in the removal group would increase between the prerule and postremoval years, while control group densities would remain unchanged. Therefore, we conducted a one-tailed, paired t test to detect an increase in the mean density of mice in the removal group between prerule and postremoval years, as well as a two-tailed, paired t test to determine if mean mouse densities in the control group changed between years.

We tested the hypothesis that the mean postremoval densities of the control and removal groups were equal using analysis of covariance (ANCOVA). We included postremoval densities in the model as the dependent variable, experimental group (control or removal) as an independent variable, and prerule densities as the covariate, log-transforming to meet the assumption of normality where necessary. We used least squares means (LSMEANS option in SAS) to obtain mean density estimates for both treatment groups while correcting for pretreatment density values. We then calculated the significance of the difference in covariate adjusted, mean densities between the treatment groups using the Dunnett–Hsu adjustment. We utilized the Dunnett–Hsu adjustment as a one-tailed test to examine whether there was evidence for a higher mean density in the removal group relative to the control group. This test statistic is considered significant ($P > 0.05$) when the lower confidence interval for the difference in the means is greater than zero.

We also tested the hypothesis that the relative change in

mean ranks between the control and removal groups was zero using a rank ANCOVA test, described by Stokes et al. (2000). First, density values for the pooled set of control and removal patches were ranked from lowest (rank = 1) to highest (rank = 60) within each year, with tied ranks given mean values. Next, residuals were obtained from a linear regression of the paired values of postremoval rank values and prerule rank values for the 60 mouse populations. Finally, the means of the residual values from this regression were compared between the control and the removal groups using Cochran–Mantel–Haenszel statistics. This method uses randomizations to test the null hypothesis of no association between the dependent variable and the treatment, which increases the probability that any differences detected are due more to treatment effects than to imbalances in the covariates between treatments (Koch et al. 1982). This nonparametric approach also allowed us to determine whether there was a change in the mean densities in the control and removal groups relative to each other, without relying on the typical assumptions associated with parametric testing such as normality, equal variance, and linearity.

Results

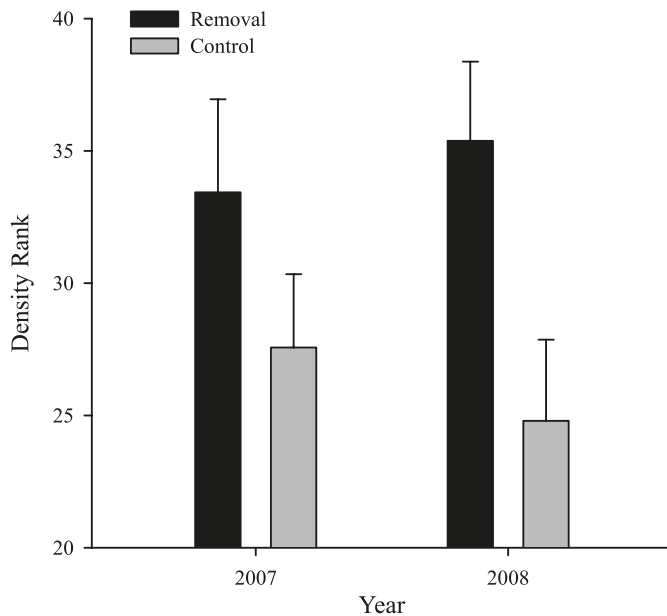
One removal site was excluded from our analysis because in the postremoval year only one mouse was caught and never recaptured; therefore no population estimate was available for this site. Four-hundred and thirty-three raccoons were removed within our 30 experimental woodlots, ranging from 2 to 40 raccoons/woodlot (mean = 14.43 raccoons/woodlot, SE = 1.81 raccoons/woodlot).

The use of predator traps was effective at curtailing damage to small-mammal traps, as we observed minimal trap disturbances owing to predator activity. A total of 1208 mice were captured in the prerule year and 1197 were captured in the postremoval year, with 9000 trap-nights conducted in each year. Only 10 mice from nine sites were recaptured from 2007 to 2008. The Kolmogorov–Smirnov D test revealed that neither the prerule nor the postremoval distributions of population-density values conformed to expectations of a normal distribution (prerule distribution: $D = 0.110$, $P = 0.071$; postremoval distribution: $D = 0.125$, $P = 0.021$). However, after transformation using the natural logarithm of the data values, both variables exhibited conformity to the expectations of a normal distribution (prerule distribution: $D = 0.076$, $P > 0.150$; postremoval distribution: $D = 0.079$, $P > 0.150$) and these transformed values were used in all subsequent analyses.

In both 2007 and 2008, a single (but different) best model was obtained for the estimation of mouse abundance ($\Delta AIC_c > 30$ between the top model and the next best model each year). Patch-specific mouse densities prior to raccoon removal ranged from ~4 to 42 mice/ha (mean = 17.2 mice/ha, SD = 8.7 mice/ha), and means were not significantly different between control (mean = 15.4 mice/ha, SD = 7.0 mice/ha) and removal (mean = 19.1 mice/ha, SD = 10.0 mice/ha) groups ($F_{[1,57]} = 1.05$, $P = 0.311$; supplementary Table S1¹). In contrast, following raccoon removal, patch-specific mouse densities ranged from ~3 to 73 mice/ha (mean = 29.7 mice/ha, SD = 14.3 mice/ha), and we detected

¹Supplementary data are available with the article through the journal Web site (<http://nrcresearchpress.com/doi/suppl/10.1139/z11-045>).

Fig. 2. Comparison of the mean (± 1 SE) rank densities for each treatment group before and after the removal of raccoons (*Procyon lotor*).



significant differences in mouse density among treatment groups ($F_{[1,57]} = 5.61$, $P = 0.021$), with higher mouse densities observed in treatment woodlots (control: mean = 25.6 mice/ha, SD = 12.5 mice/ha; removal: mean = 33.94 mice/ha, SD = 14.9 mice/ha; supplementary Table S1¹). The one-tailed, paired t test for the removal group demonstrated an increase in mouse density from 2007 to 2008 ($t_{[28]} = -2.833$, $P = 0.004$), while the two-tailed, paired t test indicated that mean mouse density was not significantly different between years in the control group ($t_{[29]} = -1.431$, $P = 0.163$).

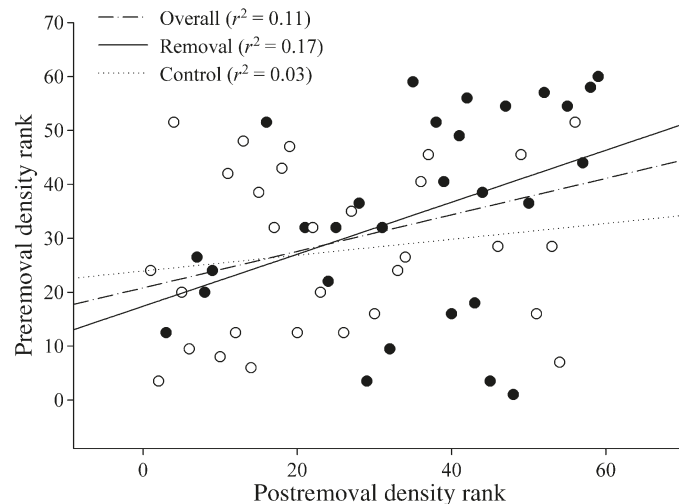
Our ANCOVA indicated that a significant proportion of the variance in 2008 densities was explained by the model ($F_{[2,56]} = 5.06$, $P = 0.0096$), and the effects of both treatment and 2007 densities (covariate) were significant effects ($F = 4.18$, $P = 0.046$ for each). LSMEANS estimation of mean 2008 densities using log-transformed data yielded values of 3.13 mice/ha for the control group and 3.41 mice/ha for the removal group; back-transformed, the densities were 22.87 and 30.27 mice/ha, respectively. The Dunnett–Hsu comparison revealed a positive difference of 0.272 between the log-transformed means with a lower 95% confidence limit of 0.049, indicating that the removal group had a significantly higher mean density than the control group in 2008 ($P = 0.023$).

In 2007, the mean density rank of the control group was 27.57 (SE = 2.77) and the mean density rank of the removal group was 33.43 (SE = 3.52). In 2008, the mean ranks for the control and removal groups were 24.80 (SE = 3.06) and 35.38 (SE = 3.00), respectively (Fig. 2). The Cochran–Mantel–Haenszel statistic for differing row mean scores of residuals (Fig. 3) was 3.85 ($P = 0.0497$), indicating a significant difference in mean ranked densities between the control and the removal groups.

Discussion

Our data demonstrated that white-footed mice exhibited a

Fig. 3. Regressions of the postremoval rank densities on the pre-removal rank densities; a separate regression was performed for the removal group, the control group, and an overall regression pooling both groups. The removal group is represented by solid circles and the control group by open circles.



numerical response to the reduced abundance of a generalist mesopredator, the raccoon, supporting our hypothesis that high densities of generalist mesopredators, facilitated by anthropogenic changes in land use, can limit small-mammal populations. Although the total number of mice caught in both years was approximately the same, both parametric and nonparametric tests revealed a small but significant shift towards higher densities in the removal relative to the control patches. In comparison, many predator removal studies in terrestrial landscapes have demonstrated a 2- to 3-fold increase in small-mammal density after predator exclusion (e.g., Erlinge 1987; Desy and Batzli 1989; Meserve et al. 1993, 1996; Reid et al. 1995). However, these studies focused on the exclusion of specialist predators or entire predator communities, rather than a single generalist mesopredator. Thus, given the highly opportunistic and generalist foraging behavior of raccoons (Gehring and Swihart 2003), it is not surprising that the magnitude of response in mice was weaker than the response observed in previous studies. Nonetheless, the widespread experimental framework of our study design (30 unique forest patches representing a wide diversity of local- and landscape-level habitat characteristics) provides strong empirical support that raccoons can directly limit mouse populations in landscapes with high densities of raccoons.

Although the exact causal mechanism driving the suppression of mouse populations was not specifically tested in our study, a contemporaneous field study failed to identify a change in prevalence of *B. procyonis* in our experimental patches subsequent to raccoon removal (Eagan 2009). Thus, there is little evidence to indicate that *B. procyonis* alone could have accounted for the magnitude of response by white-footed mice in our study. Alternatively, given that raccoon movement is primarily concentrated within forest habitat and along forest–agricultural interfaces in agricultural ecosystems (Beasley et al. 2007a; Beasley and Rhodes 2010), reduced search areas for prey created by the fragmentation of forest undoubtedly facilitates increased levels of raccoon predation in these landscapes. Thus, reduced predation

on white-footed mice in removal patches presents a much more likely scenario for the response that we observed. In particular, raccoons have been shown to impact the nesting success of many species (Cote and Sutherland 1997; Hartman et al. 1997; Ratnaswamy and Warren 1998; Barton and Roth 2008) and could limit the abundance of white-footed mice by preying on young. Although mice rarely are reported as a primary food item in raccoon dietary studies (Giles 1939; Schoonover and Marshall 1951; Greenwood 1981; Tyler et al. 2000), none of these dietary studies have been conducted in landscapes with high densities of raccoons. Moreover, we are not aware of any studies that have specifically evaluated raccoon predation upon adult mice.

Mesopredators like the raccoon typically are considered food-resource generalists because they occupy broad trophic positions within ecosystems (Lotze and Anderson 1979). Although raccoons utilize agricultural food resources extensively when available (Rivest and Bergeron 1981; Beasley and Rhodes 2008) given the general abundance of white-footed mice in our study landscape, we suspect raccoons engage in prey-switching behavior by increasing predation pressure on mice when crops are unavailable or when juvenile mice are abundant (Murdoch 1969). Although further research is needed to test this hypothesis in our system, density-dependent prey switching is common among generalist predators and may have important implications for the structure of vertebrate communities in areas where resource specialists are rare (Gehring and Swihart 2003).

Because the removal experiment underlying this study was a one-time event, it is conceivable that immigration of new individuals (both mice and raccoons) into removal patches could have confounded our analysis of population responses of white-footed mice inhabiting those patches. Although immigration events by white-footed mice in our study area probably occurred locally instead of on a broader scale—white-footed mice inhabit very small home ranges (~0.1 ha; Lackey et al. 1985) and experimental trials suggested that mice could not orient towards a forest patch at distances as low as 10 m when released in a crop field (Zollner and Lima 1997)—the immigration of new raccoons into removal patches represents a more-likely bias associated with this experiment. However, despite their size and mobility, home-range data for raccoons within our study area indicate that raccoons maintain relatively small home ranges and utilize a mean of only two forest patches throughout the year (Beasley et al. 2007*b*). Indeed, initial data on the recolonization of experimental patches at 1 year postremoval indicate that, on average, the removal patches had only been recolonized to approximately 25% of the number of individuals removed (data not shown). Given the limited recolonization of removal patches by raccoons, it is most probable that the responses of mouse populations observed in this study were due to the within-patch dynamics rather than to biases associated with immigrating raccoons.

Fragmented habitats often support diversity-poor communities (Tilman 1994), where species that are less adaptable to landscape heterogeneity have been extirpated and those exhibiting broader niche breadth often flourish (Swihart et al. 2003). In particular, mesopredators are highly abundant in agricultural ecosystems (Smyser et al. 2010; Beasley et al. 2011) and there is an extensive literature detailing the various

effects that increased populations of these species have on such ecosystems (Goodrich and Buskirk 1995; Donovan et al. 1997; Crooks and Soulé 1999). Our study highlights an important role that superabundant mesopredators can play in ecosystems through the limitation of populations of white-footed mice and potentially other secondary prey species. This result merits attention as a secondary effect of predator removal experiments (such as those often performed to decrease waterfowl nest predation; Cote and Sutherland 1997) in that the removal of one mesopredator can concomitantly result in the increased density of an alternate nest predator (Brook et al. 2008). This research suggests that further investigation of the trophic dynamics of agricultural ecosystems is critical if we are to elucidate the fundamental ecological mechanisms associated with the persistence of species in disturbed environments.

Acknowledgements

This study would not have been possible without the cooperation of numerous landowners who permitted us access to their land. We thank M. Downey, P. Girgis, B. Griffin, C. Hennessy, K. Kellner, and S. McCord for their assistance in collecting field data. We also thank P. Zollner and K. Page for providing comments on drafts of the manuscript. Funding for this research was provided by the Department of Forestry and Natural Resources at Purdue University.

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