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ORIGINAL PAPER

Effect of forest removal on the abundance of the endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae)

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Abstract We test the hypothesis that the decline of the endangered American burying beetle (*Nicrophorus americanus*) from over 90% of its original range is the result of habitat loss and fragmentation of eastern North America. Forest removal at a site in southeastern Oklahoma known to have a significant population of *N. americanus* gave us a unique opportunity to test this hypothesis. At the local scale of this experiment, *N. americanus* declined significantly after forest removal while beetle numbers at adjacent forested plots did not change. Our results indicate that local disturbances such as forest removal, if occurring across relatively broad spatial scales, can cause wholesale geographic range collapse in this species.

Keywords Habitat loss · Forest fragmentation · Endangered species · American burying beetle · *Nicrophorus americanus* · Silphidae

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Introduction

The American burying beetle (*Nicrophorus americanus* Olivier), once widespread over much of eastern North America, has disappeared from over 90% of its historic range and currently is restricted to the extreme eastern and western limits of its historic range (Fig. 1). In 1989, *N. americanus* was listed as an endangered species by the US Fish and Wildlife Service (1991). Several explanations have been proposed for the decline of the species (see Sikes and Raithel 2002 for a review of major hypotheses), but, as described below, it is likely that two of the primary factors leading to its decline are its relatively large size and its specialized breeding behavior.

Within most guilds, larger species tend to depend on larger prey, occupy a greater diversity of habitats, and dominate in interference competition (Rosenzweig 1966, 1968; Ashmole 1968; Wilson 1975; Schluter and Grant 1984; Polis and McCormick 1986; du Toit and Owen-Smith 1989). Larger guild members also require larger home ranges because the large prey they require are less abundant than smaller prey (Peters 1983; Brown and Maurer 1987; Lawton 1990; Damuth 1991). It is likely that these important implications of body size combine to account for the scarcity and extinction proneness of the vertebrate megafauna. While larger size alone does not necessarily confer endangerment, rarity and extinction tends to be higher for larger members of trophic guilds, in part because they are more vulnerable to disturbances such as habitat loss and fragmentation (Diamond 1984; Martin and Klein 1984; Vrba 1984; Owen-Smith 1988; Stevens 1992; Rosenzweig and Lomolino 1997).

The nocturnal *N. americanus* is the largest North American member of the genus *Nicrophorus*. All members of the genus *Nicrophorus* breed on small vertebrate

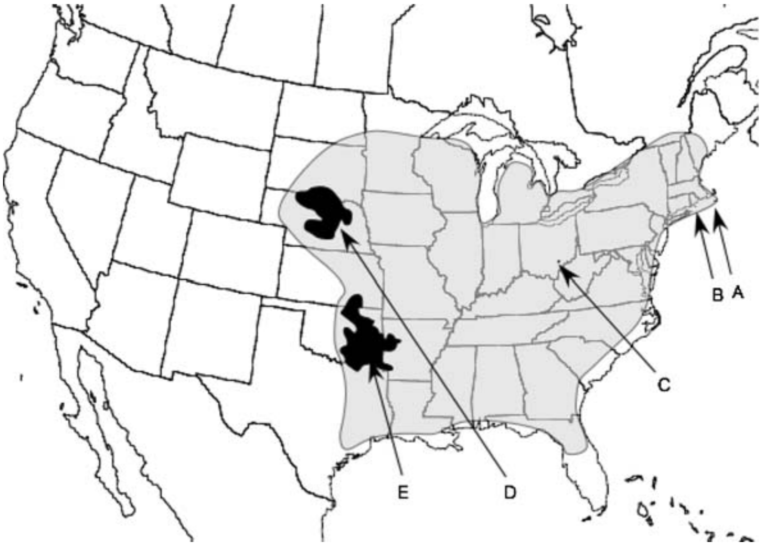

Fig. 1 Current and historical range of *N. americanus*. Populations labeled A and C represent sites where re-introduction attempts are ongoing. Populations B, D, and E are extant populations, and E is site where study reported on here was conducted. Map based on Lomolino et al. (1995) and US Fish and Wildlife web site (http://www.fws.gov/southwest/es/oklahoma/beetle1.htm)

carcasses (size range 5–300 g; Trumbo 1992), a resource that is relatively rare and unpredictable in time and space (Hanski and Cambefort 1991; Eggert and Müller 1997). In contrast to smaller *Nicrophorus* species, *N. americanus* requires larger carcasses for reproduction (80–100 g preferred; Kozol et al. 1988; Trumbo 1992; Raithel, personal communication), making it dependent on a resource that is even more rare and unpredictable than that used by its smaller congeners. In addition, larger carcasses are harder to bury than smaller ones. Thus, *N. americanus*' dependence on larger carcasses and its larger body size may, in part, explain why *N. americanus* has declined dramatically while smaller members of the genus remain relatively abundant and widespread. Thus, at less than two grams, *N. americanus* shares many of the same qualities as the vertebrate megafauna.

Anderson (1982) was the first to hypothesize that *N. americanus'* dependence on relatively large carcasses for reproduction limited the beetle to habitats with deep, loose soil where it could more easily bury carcasses. Such soils were found across much of the presettlement eastern deciduous forest; thus Anderson attributed the decline of the species to the coincident pattern of deforestation and fragmentation in North America.

Lomolino and Creighton (1996) provided support for this hypothesis at a regional scale (i.e., across the forested, eastern one-third of Oklahoma). At this scale, *N. americanus* was found predominantly in forests or woodlands with moderate undergrowth and deep soils. In addition, Lomolino and Creighton (1996) demonstrated experimentally that breeding success of *N. americanus* was higher in forest than in grassland habitat.

On a more local scale (Fort Chaffee, AR, 29,000 ha and Camp Gruber, OK, 20,000 ha), *N. americanus* exhibited a relatively wide niche breadth, and individuals were collected at baited pitfall traps in habitats ranging from open grassland to bottomland forest (Creighton et al. 1993; Lomolino et al. 1995). In addition, individually marked beetles were observed moving between diverse habitat types (including grassland and woodland habitats and upland and bottomland forests; Creighton and Schnell 1998). One exception to this local pattern of occurrence was observed in the Tiak District of the Ouachita National Forest (approximately 20,000 ha) in southeastern Oklahoma. Here, *N. americanus* were significantly more likely to be collected in mature forest than in either second-growth or clear-cut sites (Lomolino and Creighton 1996).

Previous studies have focused on the distribution of *N. americanus* across habitats at a single point in time. As a result, they did not test directly the hypothesis that deforestation has lead to the decline of the beetle. In 1995, the United States Forest Service removed trees from an area of the Ouachita National Forest, including a site where we had previously surveyed for *N. americanus* and found them to be relatively abundant (Lomolino and Creighton 1996). The tree removal allowed us to test the deforestation hypothesis directly.

Materials and methods

Description of study site

Field surveys for *N. americanus* were conducted from 1993 through 1996 and in 1998 in the Tiak District of the Ouachita National Forest in McCurtain County, OK (Fig. 1). The habitat consisted of mature oak-pine forest with moderate undergrowth and sandy soil, a habitat type preferred by *N. americanus* (Lomolino et al. 1995; Lomolino and Creighton 1996). Two survey plots were sampled each year of the study (plots one and two). A third plot (plot three) was added in 1995 and was sampled each year thereafter.

After the 1995 survey was completed, the United States Forest Service harvested trees in areas we had previously sampled. Forest age at the time of cutting was 66 years. Plot one was located within a 16.2 ha stand where the majority of trees were removed (seed-tree treatment). Tree density at seed-tree harvest sites ranged from 2.3 to 4.6 m^2/ha after tree removal (Baker 1994). Plots two and three were located in 80.1 ha stands where a small number of trees were removed (single-tree selection treatment); however, the forest remained intact at these two plots. Tree density at single-tree harvest sites ranges from 10.3 to 15.0 m^2/ha after tree removal (Baker 1994). For a detailed description of harvest specifications within the Ouachita National Forest see Baker (1994).

Survey methods

The plots were surveyed each year during the month of June. They were located 1.6 km apart along a gravel road and consisted of eight pitfall traps set at 20 m intervals along a transect line. The traps were set for three nights, baited with aged chicken, and covered with an elevated plastic dome to protect the beetles from rain and excess heat. We checked the traps daily before 1000 h (Daylight Savings Time), rebaited them as necessary, and identified all captured burying beetles to species.

All captured *N. americanus* were permanently marked by cutting a 3 mm triangular notch in the posterior portion of their left elytron. They were also individually marked with numbered bee tags (3 mm in diameter; tags distributed by Graze Beinenzucht Gerate Weinstadt, Germany) affixed with gel super glue to the anterio-central portion of each beetle's right elytron. Marked individuals were held in plastic boxes at the field site until the glue dried, and they were able to fly; all marked beetles were released at the plot where they were captured.

Data analysis

The removal of trees from previously surveyed plots gave us a unique opportunity to test Anderson's deforestation hypothesis. However, the scale of the question addressed (effect of deforestation) limits the sample size for statistical analysis. *Nicrophorus americanus* is endangered, and it would be unethical to intentionally cut forest at multiple plots merely to increase sample sizes for statistical analysis. To accommodate the small sample size and the unplanned nature of the experiment we used a statistical resampling procedure to determine the response of *N. americanus* to forest removal.

Beetle density was calculated as the number of individuals captured per functional trap-night at each plot. A functional trap-night was defined as the number of night traps placed in the field minus the number of disturbed traps, minus 0.5 times the number of traps missing bait.

To answer the question of whether deforestation affects density of *N. americanus* we performed three comparisons. First, we used data from the plot that was logged (plot one) only, and compared catch rate before and after tree removal. This comparison tests the idea that within plot one, *N. americanus* densities differed before and after the tree removal. Second, we used data from all locations and all years and compared catch rate from the two post-tree removal years at plot one (deforested) to catch rate from all other years and locations (not deforested). This comparison tests the idea that *N. americanus* densities observed after the tree removal in plot one were different from year to year and plot to plot variability in unlogged locations. Third, we restricted comparisons to post-tree removal years and compared catch rates between deforested and non-deforested plots. This comparison tests the idea that *N. americanus* densities observed after the tree removal in plot one were different from unmanipulated plots during the same years. The three analyses allowed us to determine whether variation observed across years at the tree removal plot was due to tree removal or to random variation in population numbers across sites and study periods.

Comparisons were done as follows. First we calculated the observed difference in catch rate between the post-tree removal plots and years and other plots and years. Second, we used a bootstrap method (resampling with replacement) resampled 1000 times to estimate how often the observed difference would be expected by chance. Finally we calculated the statistical probability of obtaining the observed difference as the proportion of randomizations that yielded results at least as extreme (difference ≥) as those observed. All recaptures were excluded from analyses, and all analyses were done using Resampling Stats version 5.1 (Simon 1999).

Results

A total of 626 burying beetles of four species were captured during the study. The majority were *N. orbicollis* ($n = 380$) followed by *N. americanus* ($n = 185$), *N. tomentosus* ($n = 58$), and *N. pustulatus* ($n = 3$). Total trapping effort was 329 trap-nights. Of the seven *N. americanus* that were recaptured, only one was recaptured at a plot (plot three) different than the original capture plot (plot two), moving a distance of 1.6 km in a

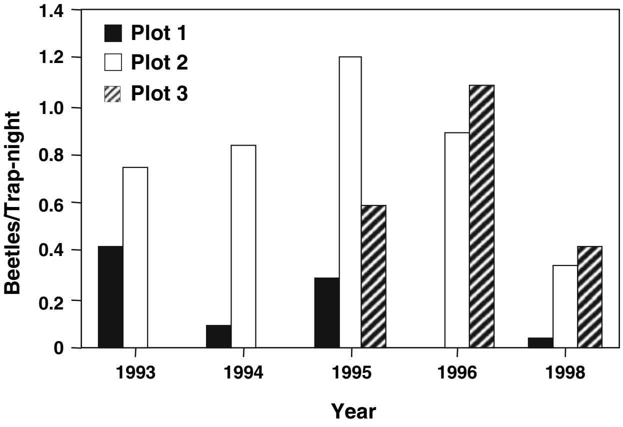

Fig. 2 *Nicrophorus americanus* captured per trap-night for each plot. Trees removed from Plot one after the 1995 survey. Plot one and Plot two surveyed each year of study. Plot three surveyed in 1995, 1996 and 1998

single night. All recaptured beetles were found the same year as their original capture.

Figure 2 illustrates capture data for all years and sites for *N. americanus*. The difference in mean catch rate of *N. americanus* at plot one for the three years prior to tree removal compared to the two years after removal was 0.246 beetles/trap-night, which represents a 92% reduction in beetle numbers. Randomization tests indicated that the probability of obtaining a difference at least this extreme is 0.045. The difference in mean catch rate at all plots and across all years with no tree removal compared to the two years at plot one after trees were removed was 0.61 beetles/trap-night ($P = 0.011$). The difference in mean catch rate at all other plots during the two years after tree removal compared to the two years in plot one after trees were removed was 0.66 beetles/trap-night ($P = 0.020$). Taken together, these analyses indicate that the removal of trees from plot one resulted in a significant decline in densities of *N. americanus*.

The same three comparisons were performed with the other two common burying beetle species captured during the study (*N. orbicollis* and *N. tomentosus*; results for all three species are summarized in Table 1). Both species were affected by tree removal, although only for *N. orbicollis* were all three randomization tests significant.

Discussion

Our data support Anderson's (1982) hypothesis that the decline in *N. americanus* was the result of anthropogenic disturbance, in this case habitat loss and fragmentation of relatively continuous stands of deciduous forests across the presettlement range of this species. At the local scale that this study was conducted, *N. americanus* disappeared from the site where trees were removed but remained common at nearby sites that were subjected to minimal disturbance. In addition, Lomolino and Creighton (1996) demonstrated that at a regional scale (eastern one-third of Oklahoma), *N. americanus* distribution was biased towards forested sites with deep soils. Taken together, these data suggest that habitat loss and fragmentation across larger areas has resulted in the decline of *N. americanus* to a fraction of its historical range.

There are at least two explanations as to why *N. americanus* disappeared from the disturbed site. First, pre-emergent beetles could have been killed as a result of soil disturbance during the process of tree removal, and new individuals had not had the opportunity to repopulate the site within the three year period after trees were removed. Second, adult beetles could be actively avoiding the disturbed site. All three sites sampled in this study were within 3.2 km of each other, well under the distance individuals have been observed moving in previous studies (at least 2.9 km in one night and 10 km over a several night period, Creighton and Schnell 1998). We also observed one beetle movement between the two select cut sites. Furthermore, previous studies have shown that *N. americanus* are readily captured in pitfall traps set in undisturbed grassland areas (Creighton et al. 1993; Lomolino et al. 1995), suggesting it was the disturbed nature of the tree removal site and not the fact that it was open. Thus, our

Table 1 Results of randomization tests for *N. americanus*, *N. orbicollis* and *N. tomentosus*

Randomization test	*N. americanus*		*N. orbicollis*		*N. tomentosus*	
	Diff.[a]	*P*-value	Diff.	*P*-value	Diff.	*P*-value
1[b]	0.246	0.045	1.90	0.046	0.210	0.033
2[c]	0.610	0.011	1.30	0.021	0.210	0.021
3[d]	0.660	0.020	1.39	0.027	0.20	0.077

[a] Difference in catch rates as measured by beetles/trap-night

[b] Comparison between three years prior to tree removal and two years after removal at plot one

[c] Comparison between all plots and across all years with no tree removal and the two years after trees at plot one

[d] Comparison for only years after tree removal between plots two and three (no tree removal) and plot one (trees removed)

data support the idea that disappearance of *N. americanus* was due to avoidance of the disturbed site. Consistent with this idea, Bedick et al. (1999) noted that *N. americanus* numbers in Nebraska were greatly reduced in areas near recently cleared, agricultural fields compared to less disturbed areas.

Tree removal also negatively impacted the other two common burying beetle species (*N. orbicollis* and *N. tomentosus*), although the support for *N. tomentosus* is not as strong. It is not surprising that *N. orbicollis* was negatively impacted: it is a forest specialist (Lomolino et al. 1995; Lomolino and Creighton 1996) and is rarely captured in open habitat, even a few meters from forested areas (Creighton personal observation). In contrast, *N. tomentosus* is a habitat generalist (Lomolino et al. 1995; Lomolino and Creighton 1996), but at local scale of this study, it may be negatively impacted by disturbance, regardless of habitat type. Given these results, the question as to why *N. americanus* has declined precipitously while smaller species like *N. orbicollis* and *N. tomentosus* have not is an important question to answer. Ultimately, as discussed previously and below, the answer may be related to *N. americanus'* larger body size and concomitant dependence on larger carcasses. However, gaining a deeper understanding of how individuals of all these species perceive and move across the landscape could potentially give valuable insight into this question and should be a research priority for the future.

Despite the strong support of Anderson's deforestation hypothesis found in Oklahoma, both the small Block Island, Rhode Island population and the Nebraska population occur in relatively open, treeless areas. However the presence of other factors important to the survival of *N. americanus* may contribute to the persistence of the species in these areas. First, both populations occur predominantly in protected or relatively undisturbed areas with deep, sandy soils (Bedick et al. 1999; Raithel 2002; Sikes and Raithel 2002). Second, the Block Island population occurs on an isolated island with few vertebrate scavengers and relatively high densities of small vertebrates that make up the beetles' carrion base (Kozol 1988; Raithel 2002; Sikes and Raithel 2002). Thus, a combination of other favorable ecological factors may be present in these areas that allow for the persistence of the species, despite the lack of optimal habitat.

Other studies reveal that habitat reduction and fragmentation at broader scales have significant, negative impacts on carrion beetles, including *Nicrophorus* species. In a temperate forest site that did not include *N. americanus*, Gibbs and Stanton (2001) demonstrated that population sizes of forest species of *Nicrophorus* and overall carrion beetle diversity declined in fragmented forests. Trumbo and Bloch (2000) found that *N. marginatus*, a grassland specialist (see Lomolino et al. 1995; Lomolino and Creighton 1996), was never trapped in fields smaller than 5 ha, and the breeding success of forest species was lower in edge habitat and in smaller forest fragments, most likely due to increased competition from vertebrate scavengers.

The species that disappear from fragments often tend to be the larger-bodied species. Klein (1989) has shown in the tropics that carrion and dung beetle communities are negatively impacted by forest fragmentation, and smaller forest fragments contained fewer species mostly because larger bodied species tended to disappear. A similar pattern may be occurring within the temperate zone burying beetle community. Trumbo and Thomas (1998) showed that, on true islands, larger-bodied burying beetle species (burying beetle community did not include *N. americanus*) tend to disappear while smaller species become overrepresented. This general pattern of larger bodied species being more vulnerable to fragmentation may also explain, in part, why species like *N. orbicollis* and *N. tomentosus* can be negatively impacted by forest removal or habitat disturbance at a local scale (as demonstrated in the study reported here) but not decline dramatically across their overall geographic range.

While a pattern of decline with increased disturbance and fragmentation has been shown for a number of carrion beetle species, mechanisms underlying the pattern have not been clearly elucidated. For *N. americanus*, a number of factors may be involved in the species decline. Historically, vertebrate species such as the passenger pigeon (*Ectopistes migratorius*) may have been important reproductive resources, and their loss may have had a significant impact on the beetle. Currently, a number of demonstrated effects of habitat fragmentation could be involved in the local-scale decline of *N. americanus*.

First, habitat loss and fragmentation often affect communities of small mammals. For example, Taulman et al. (1998) demonstrated that southern flying squirrel (*Glaucomys volans*) density declined after even moderate tree removal, and squirrels disappeared completely in areas with heavy tree harvest. Nupp and Swihart (2000) studied small mammal communities in forest fragments within an agriculture matrix in northern Indiana. Larger bodied species declined and disappeared in smaller fragments. These small mammal communities may represent much of the carrion base for burying beetle reproduction. Supporting this idea, Holloway and Schnell (1997) found a positive correlation between biomass of small mammals and the number of *N. americanus* captured on a 29,000 ha site in western Arkansas.

Second, habitat loss and fragmentation may tip the competitive balance in favor of other members of the burying beetle guild. Nupp and Swihart (2000) found that while larger-bodied rodents disappeared from smaller forest fragments, *Peromyscus* numbers increased, possibly as a result of competitive release. *Peromyscus* are too small to be used by *N. americanus*, but are well within the range of *N. americanus'* smaller competitors (see Mathews 1995). Other competitors such as carrion flies and vertebrate scavengers also increase in forest fragments and disturbed habitats (Gibbs and Stanton 2001; Patton 1994). One potentially important competitor in southeastern Oklahoma is the imported fire ant (*Solenopsis invicta*). Very large numbers of this species were observed along the transect line the last two years of our study at plot one where trees were removed, but not at the other two plots (Creighton and Bastarache, personal observations).

The effects of habitat loss and fragmentation on biodiversity have received increased attention in recent years, with the general consensus that both processes can lead to a reduction in biodiversity (Fahrig 2003). Taken together, these results suggest that local disturbance in the form of habitat loss and fragmentation can, if occurring across broad enough areas, have effects that cascade throughout animal communities and ultimately result in wholesale, geographic range collapse. These effects may be particularly severe in species such as *N. americanus*, who depend on relatively ephemeral resources, but simultaneously require conditions (relatively soft soils for burying carcasses) typically limited to late successional and old-growth ecosystems such as the pre-settlement forests of eastern, North America.

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