# The Indirect Impact of Long-Term Overbrowsing on Insects in the Allegheny National Forest Region of Pennsylvania

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**Abstract** - Overbrowsing has created depauperate plant communities throughout the eastern deciduous forest. We hypothesized these low-diversity plant communities are associated with lower insect diversity. We compared insects inside and outside a 60-year-old fenced deer exclosure where plant species richness is 5x higher inside versus outside. We sampled aboveground and litter insects using sweep nets and pitfall traps and identified specimens to family. Aboveground insect abundance, richness, and diversity were up to 50% higher inside the fenced exclosure versus outside. Conversely, litter insect abundance and diversity were consistently higher outside the exclosure. Community composition of aboveground insects differed throughout the summer ($P < 0.05$), but litter insects differed only in late summer. Our results demonstrate that the indirect effects of long-term overbrowsing can reduce aboveground insect diversity and abundance, and change composition even when plant communities are in close proximity.

## Introduction

The extirpation of *Canis lupus* L. (Gray Wolf) and *Puma concolor* L. (Cougar) combined with lax deer management have caused *Odocoileus virginianus* (Zimmermann) (White-tailed Deer) to become overabundant throughout the eastern deciduous forest, often creating structurally simple and depauperate understory plant communities (Côté et al. 2004, McCabe and McCabe 1997, Ripple et al. 2010). This scenario is particularly true in the Allegheny National Forest region of Pennsylvania where decades of overbrowsing have reduced understory plant diversity by as much as 50–75% (Banta et al. 2005, Carson et al. 2014, Goetsch et al. 2011, Kain et al. 2011, Rooney and Dress 1997) and caused the formation of recalcitrant understory layers (sensu Royo and Carson 2006) dominated by a few unpalatable species that are inimical to biodiversity recovery (Royo and Carson 2006, Royo et al. 2010).

While the deleterious impact of overbrowsing on forest understories is well known (Côté et al. 2004, Rooney and Waller 2003, Waller 2014), the cascading

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effects that browsing has on arthropod communities are less clear. It is predicted that depauperate understories dominated by browse-tolerant plant species will cascade up trophic levels to lower the abundance and diversity of arthropod groups (Hunter and Price 1992, Siemann et al. 1998, Stewart 2001). This cascade may be driven by losses of both structural complexity and food-resource diversity (Stewart 2001). Alternatively, arthropods may simply track plant abundance and thus be somewhat buffered from declines in host-plant diversity (Siemann 1998, Siemann et al. 1998).

To date, studies within the eastern deciduous forest have focused almost entirely on arthropods in the litter layer and have found that overbrowsing indirectly decreases arthropod abundance with variable effects on diversity (Bressette et al. 2012, Brousseau et al. 2013, Christopher and Cameron 2012, Greenwald et al. 2008, Lessard et al. 2012). Oddly, these studies have overlooked aboveground arthropod communities inhabiting the understory (but see Brousseau et al. 2013) or were hampered by small sample sizes (e.g., Bressette et al. 2012). Studies within other forest types in the southwestern United States (Huffman et al. 2009), on islands in the Pacific Northwest (Allombert et al. 2005), and in forests in Europe (Baines et al. 1994, Suominen et al. 2003) have all found that overbrowsing causes decreases in aboveground arthropod richness. If this is a typical response, overbrowsing could be a serious threat to ecosystem services. Arthropods are principal pollinators, seed dispersers, predators, decomposers, and herbivores, and account for the majority of the animal biomass in ecosystems throughout the world (Handel et al. 1981, Wilson 1987, Wise 1993).

Here, we compared arthropod communities within a 60-year-old deer exclosure to an adjacent reference site in the Allegheny National Forest region of Pennsylvania. This is the oldest known deer fence in the eastern deciduous forest. The understory vegetation inside the fenced plot is composed of a diverse layer of forbs, shrubs, and saplings, while the vegetation directly outside, and in much of this region, is depauperate, structurally simple, and often dominated by a single, highly productive fern species, *Dennstaedtia punctilobula* (Michx.) T. Moore (Hay-Scented Fern; Carson et al. 2014, Goetsch et al. 2011, Kain et al. 2011). We tested the hypothesis that long-term deer overbrowsing indirectly decreases the diversity and richness of insects as well as changes insect community composition.

## Field-Site Description

We conducted this study within the Allegheny high plateau region of north-central Pennsylvania on State Game Lands #30 (McKean County, 41°38'N, 78°19'W), which is part of the Hemlock–Northern Hardwood Association (Whitney 1990). Further descriptions of the region's natural history can be found in Bjorkbom and Larson (1977) and Hough and Forbes (1943). Deer have overbrowsed this region, as well as much of Pennsylvania, since the 1930s (Carson et al. 2014, Horsley et al. 2003, Redding 1995).

## Methods

We compared insect communities between a 0.4-ha plot surrounded by a well-maintained deer fence (height: 2.1 m, mesh size: 15 cm x 20 cm) versus a nearby reference site (~75 m x 55 m). The fence was erected in the late 1940s and excludes White-tailed Deer, but the mesh is likely large enough to allow in smaller vertebrates such as *Marmota monax* (L.) (Woodchuck; Chips et al. 2014). The exclosure and reference site were exactly the same ones used by Goetsch et al. (2011) and Kain et al. (2011) to evaluate the long-term impact of browsing on the understory and overstory, respectively (see Stout 1998 for further details). The overstory of each site was 60–80 years old and characterized in decreasing order of abundance by *Prunus serotina* Ehrh. (Black Cherry), *Acer saccharum* Marshall (Sugar Maple), *Fagus grandifolia* Ehrh. (American Beech), *Acer rubrum* L. (Red Maple), and *Betula* spp. (birch) (Kain et al. 2011).

A diverse and abundant group of wildflowers and shrubs characterized the understory vegetation inside the fenced plot versus the adjacent reference site (percent plant cover: inside exclosure = 63.42 ± 6.10; reference site = 9.28 ± 1.55, $P < 0.05$; mean species richness: inside exclosure = 6.2; reference site = 1.1, $P < 0.05$; Goetsch et al. 2011). Many of these wildflowers peak in abundance in May prior to canopy closure in late spring. A single species, Hay-scented Fern, dominated the reference site and also dominates understories throughout much of the entire region (Carson et al. 2014, Goetsch et al. 2011, Hill and Silander 2001, Rooney and Dress 1997, Royo et al. 2010). Hay-scented Fern is an unpalatable and fairly shade-tolerant species that peaks in biomass in mid- to late June (Hill and Silander 2001, Horsley and Marquis 1983, Horsley et al. 2003, Rooney and Dress 1997, Royo and Carson 2006).

### Insect sampling

We sampled insects on 12 May, 29 June, and 26 August 2011 within the exclosure and in the unfenced reference site 200 m away of the same size, elevation, and slope. We sampled litter insects with pitfall traps and aboveground insects with sweep nets. On each date and throughout each site, we collected 20 sweep-net and 20 pitfall-trap samples. Sweep nets were made of fine mesh with a hoop 30 cm in diameter with a 1-m handle. We swept the top 10–30 cm of all vegetation within reach along 10-m transects starting every 10 m with respect to the 75 m edge of the plot and from random locations with respect to the 55 m edge. All sweep-net transects were at least 3 m from the fence or edge of the reference plot and at least 10 m from each other. All pitfall traps were placed within random locations at least 3 m from the fence and at least 10 m away from each other to minimize edge effects. Pitfall traps were half-liter plastic containers, 8 cm diameter x 10 cm height, filled with 2 cm of 95% ethanol. We placed the rim of the pitfall trap flush with the soil surface and collected them after 24 hours (House and Stinner 1983, Williams 1958). With the help of commonly used identification guides (Borror and White 1970, BugGuide.net, Marshall 2007), we identified all insects larger than 5 mm to family. In addition, identifications were verified at the Carnegie Museum of Natural History.

**Statistical analyses**

We used univariate repeated-measures analysis of variance (RM-ANOVA; Von Ende 2001) with SAS (PROC GLIMMIX, version 9.3.1; SAS Institute, Inc., Cary, NC) to examine differences in insect abundance, richness, and exponential Shannon diversity ($e^{H'}$) throughout the spring and summer. We used this diversity index because it scales Shannon diversity to a comparable measure of species richness (e.g., number of species; see Jost 2006, 2007). The month of sampling was the repeated measure and the treatment was the deer fence. We treated pitfall and sweep-net sampling techniques as independent measures of arthropod communities and analyzed them separately. To assess differences in arthropod community composition, we performed permutational multivariate analysis of variance (PERMANOVA) via ADONIS using the Vegan Package (R core development team; Anderson 2001). Our experimental treatment (fenced exclosure) was not replicated and our analyses were based upon subsamples (pseudoreplicates sensu Hurlburt 1984), thus our results should be interpreted with appropriate caution (see Oksanen 2001 for a wider discussion on this issue). Nonetheless, because deer have been excluded for 60+ years, this study is quite unique.

## Results

We found that decades of overbrowsing indirectly reduced aboveground insect abundance ~40%, richness ~45%, and diversity ~50% throughout spring and summer, but this effect was particularly strong in August (fence x time interaction: $P < 0.001$; Fig. 1A, B, C; Table 1). In addition, overbrowsing shifted aboveground

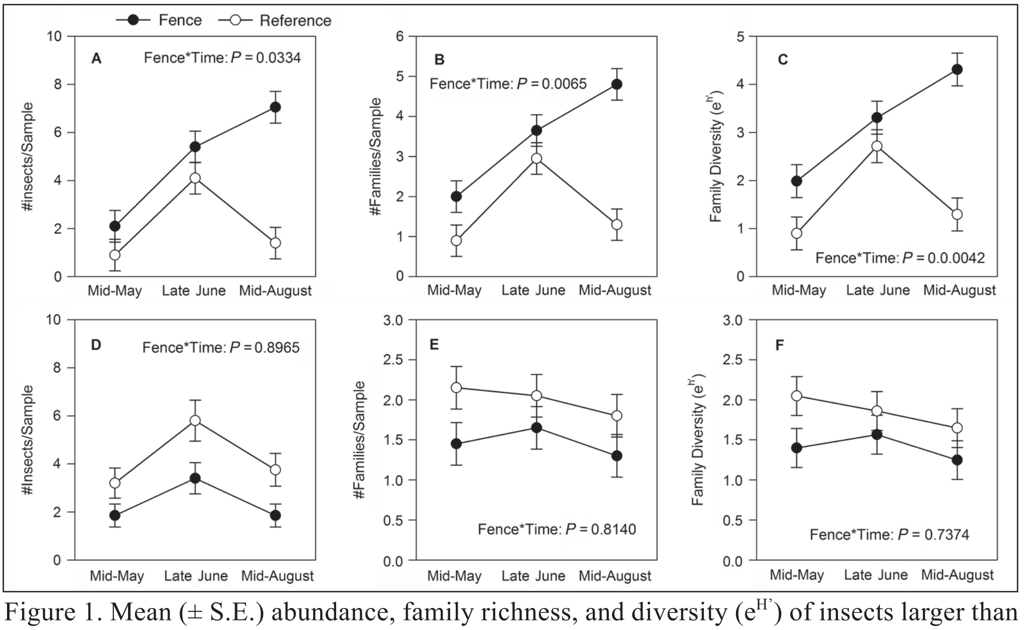


Figure 1. Mean (± S.E.) abundance, family richness, and diversity ($e^{H'}$) of insects larger than 5 mm collected in the spring and summer of 2011 in the Allegheny National Forest region of north-central Pennsylvania in sweep nets (A–C) and pitfall traps (D–F) inside a 60-year-old fenced exclosure and in a nearby reference site.

insect composition over the entire sampling period, particularly in June (Fig. 2A, B, C; Table 2). This shift was primarily driven by higher counts of elaterid beetles in the reference site (19 vs. 6) and more mirid bugs inside of the fenced exclosure (2 vs. 30) (Appendix 1). In contrast, overbrowsing increased litter insect abundance by ~85%, richness by ~30%, and diversity by ~30% throughout spring and summer (Fig. 1D, E, F; Table 1). However, only in August did community composition of litter insects differ between the 2 sites (Fig. 2D, E, F; Table 2). Specifically, browsing increased the abundance of carabid beetles, chrysomelid beetles, and litter ants particularly in August (Appendix 2).

## Discussion

### Aboveground insects

We found that overbrowsing caused a reduction in the abundance, richness, and diversity of aboveground insects and also changed the composition of these insect

Table 1. Mixed-model ANOVA results to test for differences in abundance, family richness, and diversity ($e^{H'}$) of insects larger than 5 mm caught in sweep nets and pitfall traps in the spring and summer of 2011 within a 60-year-old fenced exclosure and a nearby reference site in the Allegheny National Forest Region in north-central Pennsylvania. * indicates significant *P*-values. See Figure 1 for all fence x time interactions.

| | Abundance | | | Richness | | | Diversity ($e^{H'}$) | | |
|---|---|---|---|---|---|---|---|---|---|
| | df | *F* | *P* | df | *F* | *P* | df | *F* | *P* |
| Fence | | | | | | | | | |
| Sweep Net | 1, 114 | 8.23 | 0.0049* | 1, 114 | 14.77 | 0.0002* | 1, 114 | 16.26 | 0.0001* |
| Pitfall Trap | 1, 114 | 10.73 | 0.0014* | 1, 114 | 4.82 | 0.0301* | 1, 114 | 3.95 | 0.0492* |
| Time | | | | | | | | | |
| Sweep Net | 2, 114 | 5.43 | 0.0056* | 2, 114 | 7.14 | 0.0012* | 2, 114 | 7.46 | 0.0009* |
| Pitfall Trap | 2, 114 | 6.68 | 0.0018* | 2, 114 | 0.75 | 0.4768 | 2, 114 | 0.79 | 0.4564 |
| Fence x time | | | | | | | | | |
| Sweep Net | 2, 114 | 3.50 | 0.0334* | 2, 114 | 5.27 | 0.0065* | 2, 114 | 5.74 | 0.0042* |
| Pitfall Trap | 2, 114 | 0.11 | 0.8965 | 2, 114 | 0.21 | 0.8140 | 2, 114 | 0.31 | 0.7374 |

Table 2. PERMANOVA results to test for compositional differences of insects larger than 5 mm caught in sweep nets and pitfall traps in the spring and summer of 2011 in a 60-year-old deer fence and an adjacent reference site in the Allegheny National Forest region in north-central Pennsylvania. * indicates significant *P*-values. See Appendices 1 and 2 as well as Figure 2 for a breakdown of insect orders and families.

| | Sweep net | | | | Pitfall trap | | | |
|---|---|---|---|---|---|---|---|---|
| | df | $R^2$ | *F* | *P* | df | $R^2$ | *F* | *P* |
| May | 1, 26 | 0.03 | 0.65 | 0.8335 | 1, 33 | 0.05 | 1.66 | 0.1265 |
| June | 1, 36 | 0.11 | 4.17 | 0.0010* | 1, 36 | 0.04 | 1.40 | 0.2170 |
| August | 1, 34 | 0.05 | 1.65 | 0.0815 | 1, 31 | 0.10 | 3.50 | 0.0145* |
| Overall | 1, 98 | 0.03 | 2.89 | 0.0005* | 1, 102 | 0.02 | 1.83 | 0.1045 |

communities. These reductions and changes were likely caused by the depauperate nature of the understory vegetation that occurred in the reference site versus the rich understory layer that occurred inside the exclosure. Indeed, the general reduction of herbivorous hemipteran insects (Miridae) drove much of this decline across the sampling period (Appendix 1). Our results may apply broadly because overbrowsing has caused the formation of a depauperate understory plant community throughout the region (Carson et al. 2014) and elsewhere (Royo and Carson 2006, Waller 2014). Our findings are consistent with the impact of ungulate browsers on aboveground insects in lowland rainforests in the Pacific Northwest, European woodlands, boreal forests, and Ponderosa forests (Allombert et al. 2005, Baines et al. 1994, Brousseau et al. 2013, Huffman et al. 2009). While results varied throughout spring and summer (Fig. 1A, B, and C), the overall signal was that long-term deer overabundance caused a decline in the diversity, richness, and abundance of aboveground insects and significantly changed arthropod community composition.

Peaks in arthropod abundance and richness later in the season in the reference site may be attributed to high percent cover of Hay-scented Fern, which reaches peak frond density in June and July followed by senesce in August (Hill and Silander 2001). Though we know very little about insect associations with Hay-scented Fern (Balick et al. 1978), high frond density may create a favorable habitat for understory insects in June (e.g., Elaterid beetles; Fig. 2B, Appendix 1). Arthropod abundance is known to track plant abundance rather than plant diversity

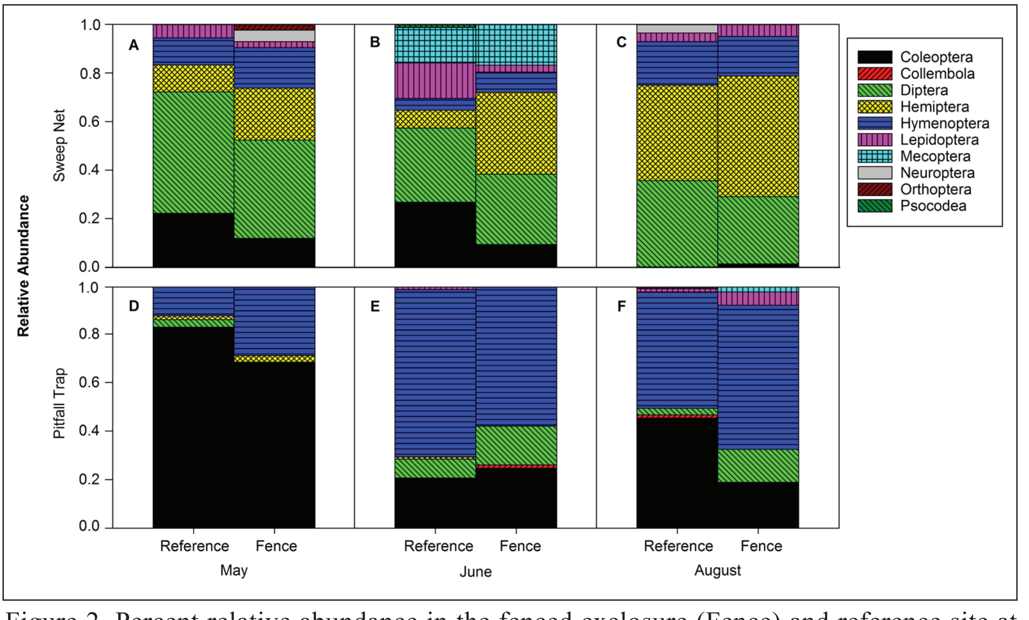


Figure 2. Percent relative abundance in the fenced exclosure (Fence) and reference site at each sampling date in 2011 for both sweep nets in (A) May, (B) June, and (C) August, and pitfall trap samples for (D) May, (E) June, and (F) August. Aboveground insect communities were significantly different throughout the summer, but particularly in June and litter insect communities were significantly different only in August (see Table 2). See Appendices 1 and 2 for the relative abundance of each insect family.

in other community types, particularly grasslands (Siemann 1998, Siemann et al. 1998), and dense host concentrations cause increases in insect herbivore abundance (Long et al. 2003, Root 1973).

**Litter insects**

Overbrowsing increased litter insect richness, abundance, and diversity throughout the sampling period and led to changes in insect community composition only in late summer. Increases in the absolute abundance of predatory ground beetles as well as ants likely drive these changes. Our findings build upon previous studies in North America and Europe, which documented that the indirect effects of overbrowsing led to increases in the absolute abundance of predatory ground beetles (Brousseau et al. 2013, Melis et al. 2006). The mechanism by which browsing increases the abundance of particular litter insects is unclear, but is likely caused by increased temperatures and lower humidity in the litter layer because of decreased plant cover (Stewart 2001). Specifically, browsers likely create environments favorable to arthropods adapted for high-light, dry environments (Gonzalez-Megias et al. 2004, Melis et al. 2006, Suominem et al. 2003). In contrast, some studies found that overbrowsing causes declines in litter arthropod abundance and diversity via an increase in vulnerability to avian predators and changes in soil nutrients (Bressette et al. 2012, Wardle et al. 2001).

## Conclusions

We found that aboveground insect richness, abundance, and diversity were higher and insect species composition different inside a >60-year-old deer exclosure versus a nearby reference site. The sharply contrasting understory plant communities that occurred in each site likely caused these differences. In contrast, we found higher abundance, richness and diversity of litter insects in an area exposed to browsing. Our results, and the results of others, call for large-scale, well-replicated experiments that evaluate not only the impact of overbrowsing on arthropod abundance but also how these may subsequently alter entire food webs in the understory as well as in forest canopies over long time scales. We are aware of only one White-tailed Deer exclosure of this advanced age; therefore deer refugia (e.g., tall boulders) could substitute for very old deer exclosures in this approach (Banta et al. 2005, Chollet et al. 2013, Comisky et al. 2005, Rooney 1997). We suggest that differences in the arthropod communities could cascade further up the food chain and impact the abundance and diversity of higher trophic levels, particularly avian insectivores (e.g., Nuttle et al. 2011).

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**Appendix 1.** Mean relative abundance (± S.E.) and total count of insects larger than 5 mm caught in sweep nets in the spring and summer of 2011 in a 60-year-old deer fence and adjacent reference site in the Allegheny National Forest Region in northcentral Pennsylvania. All insects were identified to family.

| | | Sweep-net samples | | |
|---|---|---|---|---|
| Order/family | Treatment | May | June | August |
| Coleoptera | | | | |
| Canthandae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Cerembycidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Chrysomelidae | Reference | 0.11 (0.08) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.07 (0.04) | 0.01 (0.01) | 0.01 (0.01) |
| Curculionidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| Elateridae | Reference | 0.00 (0.00) | 0.23 (0.05) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.01 (0.04) | 0.00 (0.00) |
| Lucanidae | Reference | 0.11 (0.08) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Staphylinidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.01 (0.01) | 0.01 (0.01) |
| Diptera | | | | |
| Anthomyiidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.11 (0.06) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.05 (0.02) |
| Anthomyzidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Calliphoridae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| Chironomidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Dolichopodidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.05 (0.03) |
| Drosophilidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.05 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Empididae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.05 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Heleomyzidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.04 (0.04) |
| | Fence | 0.00 (0.00) | 0.03 (0.02) | 0.02 (0.01) |
| Lauxaniidae | Reference | 0.00 (0.00) | 0.18 (0.09) | 0.11 (0.08) |
| | Fence | 0.00 (0.00) | 0.05 (0.02) | 0.08 (0.03) |
| Lonchaeidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| Micropezidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| Muscidae | Reference | 0.00 (0.00) | 0.04 (0.04) | 0.04 (0.04) |
| | Fence | 0.00 (0.00) | 0.04 (0.02) | 0.04 (0.01) |
| Mycetophilidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.04 (0.04) |
| | Fence | 0.00 (0.00) | 0.04 (0.02) | 0.00 (0.00) |
| Phoridae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.07 (0.04) | 0.00 (0.00) | 0.00 (0.00) |
| Rhagionidae | Reference | 0.06 (0.06) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |

| Order/family | Treatment | Sweep-net samples May | June | August |
|---|---|---|---|---|
| Simuliidae | Reference | 0.11 (0.08) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.05 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Stratiomyidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Syrphidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.02 (0.02) |
| Tachinidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.04 (0.04) |
| | Fence | 0.07 (0.04) | 0.00 (0.00) | 0.00 (0.00) |
| Tipulidae | Reference | 0.00 (0.00) | 0.05 (0.03) | 0.00 (0.00) |
| | Fence | 0.05 (0.03) | 0.12 (0.04) | 0.01 (0.01) |
| Hemiptera | | | | |
| Aphididae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| Berytidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| Cercopidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| Cicadellidae | Reference | 0.11 (0.08) | 0.01 (0.01) | 0.14 (0.07) |
| | Fence | 0.07 (0.04) | 0.03 (0.02) | 0.09 (0.02) |
| Membracidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.02 (0.01) | 0.04 (0.02) |
| Miridae | Reference | 0.00 (0.00) | 0.02 (0.02) | 0.11 (0.06) |
| Nabidae | Reference | 0.00 (0.00) | 0.02 (0.02) | 0.14 (0.08) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.16 (0.05) |
| Pentatomidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.04 (0.01) |
| Hymenoptera | | | | |
| Braconidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.04 (0.04) |
| | Fence | 0.02 (0.02) | 0.01 (0.01) | 0.01 (0.01) |
| Formicidae | Reference | 0.11 (0.08) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.10 (0.04) | 0.00 (0.00) | 0.00 (0.00) |
| Ichneumonidae | Reference | 0.00 (0.00) | 0.05 (0.02) | 0.14 (0.07) |
| | Fence | 0.00 (0.00) | 0.03 (0.02) | 0.09 (0.03) |
| Pteromalidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| Tenthredinidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.05 (0.03) | 0.05 (0.04) | 0.05 (0.02) |
| Lepidoptera | | | | |
| Arctiidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Galechiidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| Geometridae | Reference | 0.06 (0.06) | 0.06 (0.02) | 0.04 (0.04) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.01 (0.01) |
| Noctuidae | Reference | 0.00 (0.00) | 0.04 (0.02) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.02 (0.01) | 0.02 (0.01) |
| Notodontidae | Reference | 0.00 (0.00) | 0.04 (0.02) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.02 (0.02) |
| Mecoptera | | | | |
| Panorpidae | Reference | 0.00 (0.00) | 0.15 (0.04) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.18 (0.05) | 0.00 (0.00) |

| Order/family | Treatment | Sweep-net samples May | June | August |
|---|---|---|---|---|
| Neuroptera | | | | |
| Hemerobiidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.04 (0.04) |
| | Fence | 0.05 (0.05) | 0.00 (0.00) | 0.00 (0.00) |
| Orthoptera | | | | |
| Acrididae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| Psocodea | | | | |
| Pseudocaecilidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Total count | Reference | 18 | 82 | 28 |
| | Fence | 42 | 106 | 141 |

**Appendix 2**. Mean relative abundance (± S.E.) and total count of insects larger than 5 mm caught in pitfall traps in the spring and summer of 2011 in a 60-year-old deer fence and adjacent reference site in the Allegheny National Forest Region in north-central Pennsylvania. All insects were identified to family.

| | | Pitfall-trap samples | | |
|---|---|---|---|---|
| Order/family | Treatment | May | June | Aug |
| Coleoptera | | | | |
| Anthribidae | Reference | 0.03 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.03 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Carabidae | Reference | 0.17 (0.10) | 0.05 (0.02) | 0.35 (0.08) |
| | Fence | 0.24 (0.07) | 0.10 (0.04) | 0.11 (0.05) |
| Chrysomelidae | Reference | 0.16 (0.05) | 0.00 (0.00) | 0.05 (0.02) |
| | Fence | 0.11 (0.05) | 0.00 (0.00) | 0.00 (0.00) |
| Curculionidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.03 (0.03) |
| | Fence | 0.03 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Elateridae | Reference | 0.06 (0.05) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Erotylidae | Reference | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.05 (0.04) | 0.00 (0.00) | 0.00 (0.00) |
| Histeridae | Reference | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Lampyridae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Nitidulidae | Reference | 0.09 (0.05) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Scarabacidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Silphidae | Reference | 0.06 (0.04) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Staphylinidae | Reference | 0.20 (0.07) | 0.14 (0.05) | 0.01 (0.01) |
| | Fence | 0.24 (0.09) | 0.15 (0.07) | 0.08 (0.04) |
| Tenebrionidae | Reference | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Collembola | | | | |
| Tomoceridae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| Diptera | | | | |
| Anisopodidae | Reference | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Anthomyiidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.03 (0.03) |
| Calliphoridae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.08 (0.04) |
| Lauxaniidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Muscidae | Reference | 0.00 (0.00) | 0.01 (0.01) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.03 (0.02) | 0.03 (0.03) |
| Nematocera | Reference | 0.02 (0.02) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Tipulidae | Reference | 0.00 (0.00) | 0.06 (0.03) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.12 (0.05) | 0.00 (0.00) |

| Order/family | Treatment | Pitfall-trap samples May | June | Aug |
|---|---|---|---|---|
| Hemiptera | | | | |
| Cicadellidae | Reference | 0.02 (0.02) | 0.01 (0.01) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Pentatomidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.03 (0.03) | 0.00 (0.00) | 0.00 (0.00) |
| Hymenoptera | | | | |
| Formicidae | Reference | 0.13 (0.05) | 0.69 (0.18) | 0.48 (0.10) |
| | Fence | 0.29 (0.11) | 0.59 (0.2) | 0.59 (0.15) |
| Lepidoptera | | | | |
| Geometridae | Reference | 0.00 (0.00) | 0.02 (0.02) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Noctuidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.05 (0.04) |
| Mecoptera | | | | |
| Panorpidae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.03 (0.03) |
| Orthoptera | | | | |
| Gryllaeridae | Reference | 0.00 (0.00) | 0.00 (0.00) | 0.01 (0.01) |
| | Fence | 0.00 (0.00) | 0.00 (0.00) | 0.00 (0.00) |
| Total count | Reference | 64 | 116 | 75 |
| | Fence | 38 | 68 | 37 |