HABITAT RELATIONSHIPS OF RED-BACKED SALAMANDERS (*PLETHODON CINEREUS*) IN APPALACHIAN GRAZING SYSTEMS

by

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ABSTRACT

Woodland salamanders (*Plethodon* spp.) are important contributors to biodiversity and trophic processes within Appalachian forests. However, altered microclimates and vegetation structure after timber harvest, such as increased soil temperatures and reduced ground cover, can result in long-term population declines of some Appalachian salamanders. If changes in forest structure following harvest alter salamander habitat quality, conversion of forests to pastures or meadows presumably would cause even more severe and permanent impacts. However, woodland salamander responses to Appalachian grazing systems are virtually unknown. Herein, I present results of research measuring responses of red-backed salamanders (*Plethodon cinereus*) to silvopasture and m eadow conversion treatments in southern West Virginia. Artificial coverboards searches within northern red oak (*Quercus rubra*) silvopasture (6.7 m^2/ ha basal area), hay meadow (>5 years after forest conversion), forest edge, and reference forest plots yielded 2,675 salamanders between May 2004 and November 2005. Because abundance differed significantly between years, I conducted analyses of the relationships between salamander presence and abundance and habitat characteristics separately for 2004 and 2005. Models that contained percent herbaceous vegetation and treatment type best predicted salamander presence and abundance in both 2004 and 2005. Salamander presence and abundance was positively associated with percent herbaceous vegetation and negatively associated with increasingly disturbed treatment types, such as grazed meadows and silvopastures. Ungrazed meadows had the highest average percent cover of herbaceous vegetation, followed by woodland edges. Dense herbaceous vegetation may mitigate the loss of canopy cover in habitats that are not regularly grazed by livestock, such as silvopastures and grazed meadows. I found that salamander physiological condition and adult sex ratios did not differ significantly among treatment types, whereas hay meadows had significantly more adults than other treatments. My results indicate that red-backed salamanders may be more resilient to changes in forest cover and structure than previously thought, however populations within meadow habitats may not represent healthy populations in their age structure. My Mark-recapture results indicate that salamanders in both meadows and silvopastures were dispersers from woodland habitats, rather than resident populations. Area-constrained searches showed that silvopasture and meadow habitats were unsuitable for residence of red-backed salamanders, but that salamanders may be able to use these habitats in the presence of artificial cover objects.

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INTRODUCTION

Woodland salamanders of the family Plethodontidae are perhaps the most abundant vertebrates in the moist temperate forests of North America (Petranka 1998). In eastern deciduous forests the density of red-backed salamanders (*Plethodon cinereus*) and other terrestrial plethodontids can exceed 1-2 individuals/m^2 (Burton and Likens 1975, Hairston 1987, Mathis 1991), with the biomass of woodland salamanders regularly surpassing that of birds and mammals combined (Burton and Likens 1975, Hairston 1987). Accordingly, woodland salamanders are considered important components of forest food webs. These species cycle nutrients into higher levels of food webs by feeding on invertebrate detritivores (Jaeger 1972, Burton and Likens 1975, Burton 1976) and in turn serve as prey for larger vertebrates (Pough 1983, Petranka 1998). Thus, woodland salamanders provide an important link in the transfer of trophic energy within forested ecosystems (Burton and Likens 1975, Dunson et al. 1992).

Despite their abundance, most woodland salamanders generally are restricted to a relatively narrow range of environmental conditions. Because plethodontids are lungless and rely entirely on cutaneous respiration, their skin must remain moist to permit efficient gas exchange (Feder 1983). The moist and permeable skin of woodland salamanders makes them vulnerable to desiccation and limits activity on the forest floor to periods when humidity and soil moisture are high (Spotila 1972). Consequently, woodland salamanders spend most of the time in moist and cool environments beneath woody debris and rocks, or in burrows (Feder 1983, Grover 1998, Petranka 1998). Even when conditions are favorable, terrestrial salamanders risk desiccation during periods of surface activity and must periodically retreat to moist microhabitats to rehydrate (Feder 1983).

Individuals surface to feed periodically, often at night, and then return to surface cover or burrows where the risks of predation and desiccation are reduced (Smith and Petranka 2000).

Because of requirement for cool, moist environments, many woodland salamanders are associated with characteristics of mature or late successional forests (deMaynadier and Hunter 1995, Petranka 1998, Russell et al. 2004a). Presence and abundance of woodland salamanders have been positively correlated with the volume of coarse woody debris (CWD; Petranka et al. 1994, Brooks 1999, Grover and Wilbur 2002), stand age (Petranka et al. 1993, 1994; Ford et al. 2002a, Hicks and Pearson 2003), canopy cover (DeGraaf and Yamasaki 2002, Duguay and Wood 2002, Morneault et al. 2004), depth and type of leaf litter (Pough et al. 1987, deMaynadier and Hunter 1998), organic soil layer moisture and depth (DeGraaf and Yamasaki 2002), and understory vegetation density (Pough et al. 1987, Brooks 1999, DeGraaf and Yamasaki 2002, Morneault et al. 2004). Because they do not require aquatic habitats for breeding, terrestrial plethodontids are relatively sedentary, with home ranges on the order of tens of square meters or less and limited dispersal ability (Kleeberger and Werner 1982, Mathis 1990, 1991; Marvin 1998). Further, population densities, sex-ratios, and age distributions of woodland salamanders are stable over time, and appear largely unaffected by stochastic events, except for severe habitat disturbance (Hairston 1987, Grover 1998). Therefore, woodland salamanders have been suggested as good indicators of changes in the composition and structure of forest ecosystems (Jung et al. 2000, Hyde and Simons 2001, Welsh and Droege 2001).

Studies in the Appalachians and other eastern forests have reported negative effects of timber harvest on woodland salamanders, with responses related to the intensity of disturbance and consequent changes to forest floor microhabitats (deMaynadier and Hunter 1995, Russell et al. 2004a). Several studies reported that salamanders were extirpated in clearcuts or remained at very low densities where CWD or leaf litter was still present (Pough et al. 1987, Ash 1988, 1997; Petranka et al. 1993, 1994; Harper and Guynn 1999, Ford et al. 2002a, DeGraaf and Yamasaki 2002, Duguay and Wood 2002, Knapp et al. 2003, Morneault et al. 2004) or where this ground cover was completely removed (Wyman 1988, Waldick et al. 1999). In contrast, responses of salamanders to alternative harvest practices including firewood cutting, thinning, shelterwoods, and selective harvests are equivocal, with some studies reporting relatively small reductions in abundance (Pough et al. 1987, Enright 1998, Messere and Ducey 1998, Brooks 1999, Harpole and Haas 1999, Knapp et al. 2003) or no effects (Bartman et al. 2001, Ford et al. 2002b).

Presumably, the microclimatic, vegetation, and structural changes that occur after timber harvest, and clearcutting in particular, create unsuitable conditions for woodland salamanders (deMaynadier and Hunter 1995, Russell et al. 2004a). Canopy removal increases light penetration that results in higher soil temperatures and greater evaporative water losses. Leaf litter, CWD, and understory vegetation, may be reduced following harvest and site preparation. Moreover, harvested areas are subject to greater fluctuations in temperature and humidity, and to increased soil surface disturbance (Russell et al. 2004a). Edge effects produced by the contrast between recently harvested areas and adjacent mature stands also may degrade microclimates of remaining salamander habitats (deMaynadier and Hunter 1998, DeGraaf and Yamasaki 2002). These conditions can force woodland salamanders into fossorial "refuge" habitats to avoid desiccation. Unfortunately, successful foraging is infrequent and long-term physiological condition then declines (Heatwole 1962, Jaeger 1980, Feder 1983, Morneault et al. 2004). Petranka et al. (2003, 2004) suggested that clearcutting and other timber harvesting practices have caused long-term declines and localized extirpation of woodland salamanders from many eastern forests. However, several recent studies indicate that salamander populations in the Appalachians eventually recover from the effects of timber harvest, often within 5-24 years of cutting (Ash 1997, Harper and Guynn 1999, Ford et al. 2002a, b; Morneault et al. 2004).

In the fragmented forests of eastern North America, row crops, pasture, and old fields are common matrix habitats (Humphreys 1997, Gibbs 1998, Gustafson et al. 2001). In the Appalachian forest region, grassland and pasture-based livestock production account for approximately 25% of the land use and most of the agricultural acreage (Humphreys 1997). Within the Allegheny Mountains of east-central West Virginia, the Monongahela National Forest coordinates one of the largest grazing allotment programs on public lands in the eastern United States (A. Stump, USDA Forest Service, personal communication). If woodland salamander populations decline, at least temporarily, after timber harvest from changes in forest characteristics such as stand age, soil moisture, and volume of CWD, forests that were converted to and maintained as grasslands, pastures, and other non-forest habitats presumably represents a more severe and permanent disturbance. Non-forested habitats such as open fields and pastures are thought to represent unsuitable habitats for desiccation-prone, poorly dispersing woodland salamanders (Petranka 1998, Marsh et al. 2004). Although a recent experiment demonstrated that red-backed salamanders were capable of dispersing across narrow (e.g., 50 m) bands of non-forest habitat (Marsh et al. 2004), responses of most woodland salamander species to grassland or pasture conversions remain largely unknown.

The hilly topography of much of the Appalachian region does not support intensive crop agriculture, but is favorable for grazing livestock on lands producing long-term forest crops, which is an agroforestry practice called silvopasture (Carlson et al. 1994). Silvopasture, which combines livestock grazing and forest management on the same unit of land (Clason and Sharrow 2000), probably is the most common form of agroforestry in temperate North America (Gold et al. 2000). These silvopasture systems are increasingly being considered as viable multiuse agricultural systems for the Appalachian forested region (Buergler 2004), which are created from existing forest stands by heavy thinning (e.g., reducing basal area to 6 – 7 m^2/ha) to promote growth of herbaceous forage (Buergler 2004). When abundance or nutritive value of existing forage is insufficient, both cool- and warm-season grasses may be sown. Fertilizers and herbicides are often applied to promote growth of desired forage and to control competing vegetation (Buergler 2004). To facilitate forage production and prevent injury to livestock, surface cover including understory vegetation, CWD, and emergent rocks is often completely removed from the stand. As in traditional pastures, livestock are periodically rotated among silvopastures to prevent overgrazing (Buergler 2004).

Productivity, nutritive value, and digestibility of forage are higher in silvopastures than traditional pastures because of improved soil fertility, retention of soil moisture, and moderated soil temperatures (Buergler 2004). Therefore, partial canopy retention in silvopastures may approximate effects of thinning or selective harvest and represent a less severe impact to woodland salamanders than clearcutting or traditional pasture conversion. In contrast with selective harvest methods, however, complete removal of surface cover and direct disturbance from livestock grazing in silvopasture stands may decrease suitability of these habitats for woodland salamanders. Despite the increasing interest in the use of silvopasture systems within Appalachian forests (Buergler 2004), biodiversity responses, especially those of woodland salamanders, to silvopasture systems are currently unknown. The Appalachian region supports high densities of salamanders and high species richness, therefore, woodland salamanders represent a group of interest relative to the use of silvopastural systems.

Pilot work at the USDA Agricultural Research Service's Appalachian Farming System Research Center (AFSRC) in West Virginia during 2002 and 2003 indicated that red-backed salamanders occurred under artificial cover objects in both actively grazed meadow and silvopasture plots (Table 1). Presence of woodland salamanders within these plots contradicts current understanding of plethodontid habitat relationships (deMaynadier and Hunter 1995, Petranka 1998, Russell et al. 2004a). Whether these salamanders represent residents, recent colonizers, or individuals dispersing to more suitable forest habitats is unknown (Marsh et al. 2004). Presence of salamanders may not accurately reflect habitat suitability if populations exhibit atypical age-class distributions, sex ratios, or physiological condition (Ash et al. 2003, Knapp et al. 2003). For example, Ash et al. (2003) reported that populations of southern graycheek salamanders (*Plethodon metcalfi*) found within clearcuts were almost exclusively adults, thereby suggesting that adult reproduction or survival of immature salamanders were altered. Larger adults may persist longer in poor-quality habitats because they are less prone to desiccation (Spotila 1972) and better able to defend remaining cover objects and burrows (Mathis 1990, Jaeger and Forester 1993). Because woodland salamanders are tied to the density and type of cover objects, presence of salamanders within meadows and silvopastures may reflect the presence of artificial cover (Hyde and Simons 2001, Marsh and Goicochea 2003) rather than the suitability of these habitats.

OBJECTIVES

My first objective was to determine if red-backed salamander presence and abundance responded to traditional pasture and silvopasture treatments within the Appalachian Mountains of southern West Virginia. To accomplish this objective, I surveyed extant salamanders and measured the associated habitat variables in plots representing a gradient of forest conversion and grazing intensity, including reference woodlands, woodland edges, silvopastures, and traditional ungrazed and grazed pastures. I then modeled salamander presence and abundance as a function of these habitat variables. I expected salamander responses to forest conversion to reflect the degree to which these treatments experienced alterations of required microclimates and microhabitats (deMaynadier and Hunter 1995, Russell et al. 2004a). For example, I expected salamander presence and abundance to decline in response to decreased cover of overhead canopy and removal of CWD associated with pasture and silvopasture management.

My second objective was to determine if silvopasture and pasture treatments influence salamander sex ratios, age-class structure, and physiological condition. To accomplish this objective, I compared sex ratios, age-class structure and physiological condition of salamander populations within edge, silvopasture, and meadow treatments to those within woodland reference stands. Differences in sex ratios, age-class structure, or physiological condition may indicate that these treatment types negatively influenced salamander populations. I expected salamanders of similar age to exhibit lower physiological condition in disturbed habitats than in woodland reference sites. I also expected silvopasture and pasture habitats to be populated primarily by adult salamanders because immature individuals have larger surface area to volume ratios, and thereby have a reduced ability to remain hydrated in areas with reduced canopy cover (Fraser 1976, Blymyer and McGinnes 1977, Jaeger 1980, Pough et al. 1987, Ash et al. 2003, Marsh and Goicochea 2003).

My third objective was to determine if red-backed salamanders in pasture and silvopasture treatments were residents, recent colonizers, or dispersing individuals (Marsh et al. 2004). To accomplish this objective, I used mark-recapture methods to estimate the ratio of immigration and emigration within and among treatment plots. When surveying silvopasture and pasture habitats, I expected to capture salamanders almost exclusively under coverboards because natural surface cover was lacking. I also expected to capture fewer salamanders under coverboards within reference woodlands, where natural cover likely was not a limiting factor, than in silvopasture or meadow sites.

Lastly, my final objective was to determine if the presence and abundance of red-backed salamanders in pasture and silvopasture treatments was a result of artificial cover object sampling. To accomplish this objective, I compared capture rates of salamanders from artificial cover objects with those from surveys of natural microhabitats and surface activity across the gradient of forest disturbance. Because traditional pastures and silvopastures are thought to represent unsuitable habitats for woodland salamanders, I expected a high degree of turnover in these habitats when compared to reference woodlands with salamanders in silvopastures and pastures being predominately dispersers attempting to find more suitable habitats.

METHODS

Study Area

My study area was the USDA Agricultural Research Service's Appalachian Farming System Research Center (AFSRC) near Beckley, in Raleigh County, West Virginia (Fig.1). The AFSRC occurs within the Allegheny Mountain and Plateau physiographic province, a landscape of relatively flat or rolling plateaus incised by deep narrow valleys (Fenneman 1938). Elevations range from 740 to 1200 m and the climate is generally cool and moist with average annual precipitation exceeding 198 cm, much of which can occur as snow from November through March (NOAA 2002). Forest cover of the region primarily was a mixed mesophytic-Allegheny hardwood (Strausbaugh and Core 1977) dominated by beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and black cherry (*Prunus serotina*). White oak (*Quercus alba)*, black oak (*Quercus velutina)*, chestnut oak (*Quercus montana)* blackgum (*Nyssa sylvatica)* and pitch pine (*Pinus rigida)* occur on xeric aspects, whereas hemlock (*Tsuga Canadensis)* and rhododendron (*Rhododendron maximum)* dominate mesic drains and creeks. The region was a complex matrix of forests, natural meadows and other grasslands, with numerous small farms comprised of both open pastures and small woodlots. The primary non-forest land use in the study area was pasture for livestock grazing.

I conducted my study at 3 AFSRC experimental farm sites. Reba (51 ha; 884-m elevation) and School (22 ha; 884-m elevation) Farms were used extensively for research and demonstrations by AFSRC since 1995 and included woodlands and traditional pasture. Reba Farm included silvopasture plots that were rotationally grazed. Beef cattle, sheep, and goats were grazed on both farms. The third site, Peters Farm (21 ha; 841-m elevation), was acquired by AFSRC in 1996 and was the least intensively managed of the 3 sites with no livestock grazing. By 2004, 13 treatment plots representing an increasing gradient of forest conversion and grazing intensity: reference woodlands, woodland edges, silvopastures, ungrazed hay meadows, and grazed pastures were established for research purposes (Table 2, Figs. 2-4).

Overstory trees on woodland and silvopasture plots primarily consisted of northern red oak, red maple, and blackgum. Silvopastures were created between 1997 and 2002 by reducing the basal area to 6.7 m^2/ha. Ground cover of woodland plots consisted of herbaceous species, CWD, and abundant emergent rock, but essentially all CWD and rocks were removed from silvopasture and pasture plots. Herbaceous species within pasture and silvopasture plots included cinquefoil (*Potentilla recta*), orchardgrass (*Dactylis glomerata*), ryegrass (*Lolium perenne*), tall fescue (*Festuca arundinacea*), and white clover (*Trifolium repens*).

Species

The red-backed salamander is a small (65-125 mm adult total length) terrestrial plethodontid found in forested habitats from North Carolina north to Quebec and west to Minnesota (Petranka 1998). They often are abundant within this range, commonly reaching average densities exceeding 2 individuals/m^2 (Burton and Likens 1975, Mathis

1991). In West Virginia, red-backed salamanders inhabit moist coniferous, deciduous, or mixed forest habitats up to 1,460-m elevation, and commonly are found under rocks, bark, logs, leaves, or other forest floor debris (Green and Pauley 1987). Several studies indicate that a large percentage of red-backed salamanders are underground at any time, and that individuals regularly move vertically between the soil and soil surface (Petranka 1998). Thus, only a small proportion of a population (e.g., 2-32%) is thought to be active on the ground surface at any moment (Taub 1961, Smith and Petranka 2000, Hyde and Simons 2001, Bailey et al. 2004). Soil moisture and temperature appear to be the primary influences on the vertical distribution of individuals in the soil (Taub 1961, Heatwole 1962).

Surface-active salamanders remain under cover during the day but emerge at night to prey on invertebrates and mate when weather conditions permit (Petranka 1998). Individuals forage directly on the forest floor or climb on vegetation (Burton and Likens 1975), but may restrict feeding to underneath cover objects during dry periods to avoid desiccation (Grover 1998). Red-backed salamanders in West Virginia breed in fall and spring, and females lay and brood eggs from May to July in crevices of rotting logs or bark, and under woody debris, rocks, and moss (Green and Pauley 1987). Clutch size ranges between 6 and 20 eggs, which are laid annually or biennially (Petranka 1998).

Both sexes are territorial (Petranka 1998), and territorial defense often is centered around a cover object, which is defended against other salamanders (Jaeger et al. 1982, Mathis 1991). Larger red-backed salamanders occupy higher-quality territories (Mathis 1990), and both size and density of natural cover are positively correlated with mean body size (Grover 1998, Marsh and Goicochea 2003). Average home ranges of red-backed salamanders have been estimated to be about 5 m^2 but can range <1-25 m^2 depending on habitat quality (Kleeberger and Werner 1982, Mathis 1991). Daily movements typically are small (e.g., 0.43 m) but individuals often move more than 1 m after periods of rain (Kleeberger and Werner 1982). Although red-backed salamanders generally are thought to be poor dispersers (Gibbs 1998, Marvin 1998), individuals have returned to their territories after displacement of up to 90 m (Kleeberger and Werner 1982, Marsh et al. 2004).

Salamander Sampling

Coverboards.—Plethodontid salamanders rapidly colonize artificial cover objects, particularly wood boards, consequently coverboards are widely used for salamander monitoring and studies of salamander behavior, ecology, and responses to disturbance (Grant et al. 1992, Monti et al. 2000, Hyde and Simons 2001, DeGraaf and Yamasaki 2002, Marsh and Goicochea 2003). Although detection probabilities of surface-active salamanders under coverboards can vary spatially and temporally (Bailey et al. 2004), captures of red-backed and other salamanders under coverboards and natural cover objects have been correlated with independent indices of abundance (DeGraaf and Yamasaki 1992) and absolute population size (Smith and Petranka 2000).

Personnel at the AFSCR established an array of 20 coverboards in each of the 13 study plots (Figs. 2-4). Because salamanders may avoid newly-installed coverboards (Grant et al. 1992, Monti et al. 2000), arrays were established at least 1 month prior to data collection. Coverboard arrays on Reba farm were established in 2002 and 2003, on School farm in 2003, and on Peters farm in 2004. Arrays within edge plots consisted of 2 rows of boards parallel to the woodland edge. One row was placed approximately 10 m inside and the other row an equal distance outside the woodland boundary. Each row consisted of 10 boards spaced approximately 15 m apart. For the remaining 10 plots, a 4 × 5 grid of boards was established in each plot, with boards spaced approximately 15 m apart when space, topography, and vegetation permitted. Coverboards were constructed from 3 white oak boards, with 2 boards on the bottom and 1 board placed on top for total dimensions of 30 cm × 46 cm × 5 cm. All surface debris was removed from under the boards so that each board lay flush against the topsoil. Each board was numbered for identification.

AFSCR staff or I checked coverboards weekly during 17 May-10 August 2004, and 1-2 times monthly between September and December. In 2005, coverboards were checked once in March and April, weekly during 30 May–2 August, and monthly from September through November. I used weekly surveys, when possible, because more frequent checking of cover objects may reduce salamander use (Marsh and Goicochea 2003, Williams and Berkson 2004). Searches were performed during the day, and I attempted to check all boards over the course of 2 days to avoid time-since-rainfall effects. I measured soil temperature under each board with an IR 101 InfraScan Infrared Thermometer (La Crosse Technology, La Crescent, Minnesota, USA) during each sample period. I also measured soil moisture to a depth of 12 cm under each cover board with a HydroSense Portable Probe (Campbell Scientific, Inc., Logan, Utah, USA). I recorded the following information for each captured salamander: species, snout-vent length (SVL) and tail length (nearest 0.1 mm), mass (nearest 0.01 g), juvenile or adult age class (juveniles ≤34 mm SVL; Petranka 1998), and presence of previous marks. I also noted whether tail autotomy had occurred, and measured the length of the regenerated portion of the tail on salamanders that experienced tail loss (Grover 1998). I determined sex and presence and number of eggs by holding salamanders up to a fiber-optic light (Gillett and Peterson 2001). Males were identified by the presence of pigmented testes and inspection of external morphological characteristics (e.g., inter-nares difference, head shape, swollen mental and nasiolabial glands; Petranka 1998, Quinn and Graves 1999). I marked salamanders for individual recognition by toe-clipping (Donnelly et al. 1994) or injecting a small amount of fluorescent elastomer (Northwest Marine Technology, Inc., Shaw Island, Washington, USA) at up to 4 body locations (base of each limb; Davis and Ovaska 2001). After measurements and marking, salamanders were released next to the coverboard (Monti et al. 2000, Marsh and Goicochea 2003). Salamanders were only marked and measured during the summer field seasons. During spring and fall sampling because of time constraints, salamanders were not measured, sexed, or marked during these periods.

Area-constrained searches.—Salamander use of coverboards may depend on the density and type of natural cover available (Hyde and Simons 2001). For example, if natural cover is limited, adding coverboards may attract salamanders to areas that otherwise are unsuitable (Monti et al. 2000). Thus, animals found under artificial cover objects may not accurately reflect populations under natural cover (Marsh and Goicochea 2003) or population responses to disturbances that reduce or eliminate cover (Hyde and Simons 2001). Additionally, differences in the type and quality of cover objects and associated habitat characteristics underneath these objects (e.g., soil moisture, arthropod prey abundance) may influence the surface activity of red-backed salamanders (Grover 1998, Hyde and Simons 2001). Low-quality or limited density of cover objects may force salamanders to forage more often in the open, thereby increasing the risk of desiccation or predation (Jaeger 1980, Hill et al. 1982, Grover 1998).

To provide an independent assessment of red-backed salamander populations, habitat characteristics, and surface activity within each treatment plot, I used 2 area-constrained sampling methods: daytime searches for salamanders under natural cover objects along transects (Monti et al. 2000, Hyde and Simons 2001) and opportunistic night-time surface counts (Hyde and Simons 2001, Knapp et al. 2003, Williams and Berkson 2004) within circular plots surrounding coverboards. Each transect and circular plot was sampled once during May-August of both 2004 and 2005, and all treatments within a farm site were sampled on the same day or night to minimize weather- or season-related influences on salamander activity. I established 3 approximately 60 m × 3 m natural cover transects between and parallel to coverboard rows in each treatment plot. For edge plots I established 1 long transect between and parallel to the coverboards. I searched each transect for salamanders by turning and replacing all natural cover (e.g., logs, sticks, and rocks). Because the success of daytime cover object searches has been shown to be negatively correlated with mean daily temperature (Williams and Berkson 1994), I only conducted searches on relatively cool days. Day transect surveys were conducted during 10 June – 13 July 2004 and 6-14 July 2005. I recorded the type of cover object where each salamander was found and placed a numbered flag at the location.

I used a headlamp to conduct night-time surveys for surface-active salamanders within a 3-m radius plot centered on each coverboard. I began night-time surveys approximately 20 min after sunset and continued until all plots at a farm were sampled. I hand-captured salamanders on the surface or climbing vegetation and flagged their locations but did not disturb potential cover objects or leaf litter. Surface foraging activity of red-backed salamanders is regulated by humidity and soil moisture levels (Feder 1983, Grover 1998). Accordingly, I only conducted surface counts on cool, humid nights within 24 h of precipitation (Williams and Berkson 1994). Night surface surveys were conducted during the weeks of 11 July 2004 and 19 June 2005. Soil moisture and surface temperature were measured under each cover object or salamander surface location (night-time surveys). I marked and recorded data for all salamanders as previously described and released them at the point of observation.

Habitat Sampling

Vegetation and climate.— Because red-backed salamanders are territorial and will defend cover objects from conspecifics, I used coverboards and flagged locations of salamanders found under natural cover as sampling foci for habitat variables. During the summers of 2004 and 2005, I measured biotic and abiotic variables that were potentially important habitat correlates of red-backed salamander occurrence and abundance (e.g., deMaynadier and Hunter 1995, Petranka 1998, DeGraaf and Yamasaki 2002, Russell et al. 2004a). Habitat features were measured within the 3-m radius plots centered on each board or natural cover object. I recorded the species and diameter at breast height (dbh) of all trees larger than 10 cm DBH within each plot. I estimated percent canopy closure above each board with a spherical densitometer. Densiometer readings were taken from each cardinal direction and then averaged for the plot.

Within each plot, I visually estimated percent cover of CWD (≥10 cm diameter), fine woody debris (FWD; <10 cm diameter), woody shrubs (≤1.5 m high), herbaceous plants, planted livestock forage, emergent rock, bare soil, and leaf litter. I also measured total length and mid-point height of all CWD to calculate actual areal cover. I used a ruler to measure leaf litter depth adjacent to each board and at 4 random locations within each plot.

I acquired weather data, including temperature, rainfall, and humidity (recorded every 30 min) from permanent weather stations at the farms. Weather data were not available at Peters Farm for 2004.

Soil.—Because of their permeable skin, salamander distribution can be influenced by soil acidity (Mushinsky and Brodie 1975, Sugalski and Claussen 1997), and many plethodontid salamanders have been associated with less acidic soil with higher pH (Vernberg 1955, Mushinsky and Brodie 1975, Wyman 1988). I collected soil samples within 1 m of each coverboard for pH analyses. The humus layer was cleared away and soil samples were collected down to 10 cm below the surface. Samples were placed in paper bags and air dried to a constant weight and then coarsely ground through a 2 mm sieve. I placed samples in sealed plastic bags and kept them in cool storage until analysis. Samples were then sent to the University of Wisconsin's Soil and Forage lab in Marshfield, Wisconsin for pH measurement, which was determined by a 1:1 paste of air dried soil and deionized water (USDA, NRCS 1996) using a digital ionanalizer pH meter and combination electrode.

The moist, permeable skin of red-backed salamanders makes them vulnerable to desiccation and limits activity on the forest floor to periods when humidity and soil moisture are high (Spotila 1972). Therefore, salamanders are often restricted to moist, cool underground burrows (Taub 1961, Fraser 1976). The red-backed salamander lacks the strength to dig its own burrows and instead uses burrows constructed by other organisms. At my site, the ability of moles, shrews, ants, and earthworms to create burrows is influenced by soil strength or soil penetrability. Soil penetrability is a measure of the ease with which an object can be pushed or driven into the soil (Vas et al. 2001). I used an electronic soil cone penetrometer to assess soil penetrability (Kpa) around each coverboard (Vas et al. 2001). Four readings (2 each at depths of 5 cm and 10 cm) were taken within 1 m of each coverboard. Penetration resistance is influenced by soil factors such as water content and bulk density. I averaged the 4 values to determine mean soil penetrability immediately surrounding each coverboard. All penetrometer readings were collected within 24 h of a rain event to minimize variation in water content.

Data Analyses

To detect potential weather differences between Reba and School farm during 1 May – 5 December 2004, I used t-tests to compare mean daily temperature, precipitation, and minimum and maximum relative humidity. A permanent weather station was not installed on Peters Farm until 2005. I used a 1-way analysis of variance (ANOVA) to compare weather data among all 3 farms during 1 March–4 September 2005.

Habitat Relationships.— I used an information-theoretic modeling approach (Burnham and Anderson 2002, Russell et al. 2004b, 2005) to examine habitat relationships of red-backed salamanders across the gradient of forest disturbance and livestock grazing. Because few salamanders were captured during area-constrained and night searches, only coverboard captures were used to model habitat relationships. Prior to model specification, I eliminated redundant variables (Spearman's $r^2 \geq 0.70$) and retained 22 variables for inclusion in models (Tables 3, 4). I examined scatterplots and residual plots to ensure that variables met assumptions of analyses (i.e., linearity, normality, colinearity). I used the square-root transformation on abundance to approximate normality. Abundance was defined as the total number of red-backed salamanders observed under a coverboard per year. Since coverboards with 0 observations were accounted for in the presence/absence modeling, I only included boards where at least 1 salamander was observed when modeling abundance. Because some salamanders were not individually marked, some individuals were likely counted multiple times during a year. Thus, these counts more accurately reflected an index of abundance and not population estimates. Treatments were coded on a gradient of their perceived level of habitat disturbance: woodland reference, edge, silvopasture, ungrazed meadow, and grazed meadow (least disturbed to most disturbed).

I specified a set of plausible *a priori* candidate models explaining salamander presence and abundance using my prior knowledge and a review of relevant literature. I specified 13 models: a global model containing all variables and subset models representing potential influences of abiotic and biotic habitat attributes on red-backed salamanders (Table 5). I analyzed the model set separately for salamander presence using logistic regression and abundance using linear regression. Prior to model selection, I examined fit of global models by examination of residuals, measures of fit, classification tables, and histograms of expected probabilities (Burnham and Anderson 2002). Because, abundance of salamanders under coverboards was significantly higher in 2005 than in 2004 ($t = -2.58$, $P = 0.01$), I modeled habitat relationships separately for each year.

Because the number of coverboards sampled (n = 260) was small relative to the number of parameters (K) in most models (i.e., $n/K < 40$), I used Akaike's Information Criterion corrected for small sample size (AIC$_c$) for model selection (Hurvich and Tsai 1989, Burnham and Anderson 2002) for maximum likelihood (logistic regression):

$$AIC_c = -2\log(L(\hat{\theta})) + 2K\left(\frac{n}{n-K-1}\right)$$

and least-squares (linear regression):

$$AIC_c = n\log\left(\hat{\sigma}^2\right) + 2K\left(\frac{n}{n-K-1}\right)$$

where the penalty term, $2K$, is multiplied by the correction factor $n/(n-K-1)$. I ranked all candidate models according to their AIC$_c$ values, and the best model (i.e., most parsimonious) was the model with the smallest AIC$_c$ value (Burnham and Anderson 2002). I ranked other models relative to the best model using Δ AIC$_c$, which was the difference between the lowest AIC$_c$ value (AIC$_{cmin}$) and AIC$_c$ values from the other models. I drew primary inference from models within 2 units of AIC$_{cmin}$, although models within 4 units may have limited empirical support (Burnham and Anderson 2002). I also calculated Akaike weights (w_i) to determine the weight of evidence in favor of each model (Burnham and Anderson 2002).

Physiological condition, sex ratio, and age class.— Physiological condition is an important determinant of individual fitness (Green 2001). Animals in good condition are assumed to have more energy reserves than those in poor condition. Salamanders of relatively high mass for their length are assumed to be in better physical condition than those of relatively low mass for their length (Grover 1998). Indices of physiological condition attempt to determine the mass of the individual associated with energy reserves after correcting for body size (Green 2001, Schulte-Hostedde et al. 2005). A common method to measure physiological condition involves regression of body mass on a linear index of body size and using the residuals from this regression as an index of physiological condition (Jakob et al. 1996, Green 2001, Schulte-Hostedde et al. 2005). An individual with a positive residual is considered to be in better condition than an individual with a negative residual (Jakob et al. 1996, Green 2001).

I limited analyses of physiological condition to salamanders with marks, known age and sex. Of 568 individually-marked salamanders captured from the 13 treatment plots, 52 were eliminated from analyses because of missing data. Mean length, mass, and physiological condition were used for salamanders captured more than once within a treatment type. If a salamander was captured in more than one treatment type (n = 15), measurements from each treatment type were used. Thus, 531 salamander observations were used for these analyses (Table 6). Because of the limited number of individually-marked salamanders from grazed meadow treatments (n = 4), I combined these data with those from ungrazed meadows. Since weight increases with age, the process error around the weight-length relationships is multiplicative, not additive. Therefore I log transformed the model to estimate the parameters using linear regression with additive errors. I defined physiological condition of a salamander as the residual of the regression of log mass on log SVL. Because body condition changes with age, log(mass) – log(SVL) residuals can be confounded with age (Ormerod and Tyler 1990, Green 2001). Therefore, I calculated residual indices separately for adult and immature salamander age classes.

Red-backed salamanders commonly experience tail loss, and tail autonomy could influence body mass that is not accounted for by SVL, thereby biasing condition indices. However, the frequency of tail autonomy was similar among treatments ($\chi^2 = 2.118$, df = 3, $P = 0.463$). Consequently, differences in condition indices among treatments were not likely influenced by tail autonomy.

I used a 2-way ANOVA to examine how physiological condition of salamanders varied by sex among treatments. Determining sex of immature salamanders is unreliable without dissection, so I did not specify sex for salamanders shorter than 34 mm SVL. I examined interactions between treatment and sex-class to assess whether adult males, adult females, and immature salamanders responded differently to treatment types in their physiological condition.

I used a 1-way ANOVA to determine if sex ratios and age-class structure of salamander populations varied among woodland reference ($n = 3$), edge ($n = 3$), silvopasture ($n = 3$), and meadow ($n = 3$) treatments. Because treatments were applied to plots rather than individual salamanders, the plot mean square was used as the error term when evaluating the statistical significance of treatment effects. When an ANOVA yielded a significant *F*-statistic, I used Tukey's honestly significant difference (HSD) to test significant differences among treatment means (Systat 2002, SPSS 2005). Means are presented ± 1 Standard Error (SE) and the significance level for all tests was $\alpha = 0.05$.

Residents, dispersers, and use of artificial cover.—Insufficient mark-recapture data and small sample sizes from area-constrained and night searches precluded statistical analyses of either salamander movements among treatments or potential influence of artificial cover objects. Thus, I present only qualitative results for these datasets.

RESULTS

I captured 2,749 red-backed salamanders from the 3 farms during coverboard, area-constrained, and night surface searches in 2004 and 2005. Of these, 2,675 salamanders (97.3%) were captured under coverboards. During the study, 568 salamanders were captured, measured, and marked. Incidental captures of other salamander species included southern two-lined salamanders (*Eurycea cirrigera*; *n* = 37), northern dusky salamanders (*Desmognathus fuscus*; *n* = 10), red spotted newts (*Notophthalmus v. viridescens*; *n* =10), ravine salamanders (*Plethodon richmondi*; *n* = 7), northern slimy salamanders (*Plethodon glutinosus; n* = 5), northern red salamanders (*Pseudotriton r. ruber*; *n* = 2), and green salamanders (*Aneides aeneus*; *n* = 1).

In 2004, Reba farm received significantly more precipitation than School farm (t = 2.644; df = 436; *P* = 004). Mean air temperature and minimum and maximum relative humidity were not significantly different between the two farms (t = -0.649, df = 436, *P* = 0.258; t = 0.169, df = 436, *P* = 0.433; and t = 1.165, df = 436, *P* = 0.122, respectively). In 2005, mean air temperature, precipitation, and minimum relative humidity were similar among farms (F = 0.138, *P* = 0.871; F = 1.321, *P* = 0.268; F = 2.492, *P* = 0.084). However, Peters farm had significantly higher maximum relative humidity (F = 14.189, *P* ≤ 0.001) than both Reba and School farms.

Habitat Relationships

Presence.— I observed 1,268 red-backed salamanders under 195 of 260 coverboards (75.0%) in 2004 and 1,481 salamanders under 203 of 260 boards (78.1%) in 2005. Woodland edge and woodland reference plots contained the largest percentage of occupied coverboards in 2004 and 2005, respectively (Fig. 5). Ungrazed meadows had the lowest percentage of occupied coverboards in both years (Fig. 5).

In 2004, "herbaceous disturbance" as the best model of 13 logistic regression models explaining salamander presence (Table 7). Salamander presence was positively associated with greater cover of herbaceous vegetation and negatively associated with treatment disturbance (Table 8). The second-best model, with a single variable for "treatment", received limited empirical support ($\Delta AIC_c < 4$; Table 7) and indicated that salamander presence decreased in increasingly disturbed treatments (Table 8). Weight of evidence ($w_{\text{best model}}/w_{\text{second best model}}$) for the "herbaceous disturbance" model was 4.3 times greater than for the "treatment" model, thereby indicating relatively little uncertainty in selection of the best candidate model (Burnham and Anderson 2002). However, evidence for a treatment effect on salamander presence was strong in that the sum of Akaike weights for the 2 supported models containing this variable was 0.85 (Table 7). The remaining 11 models explaining salamander presence in 2004 received no empirical support ($\Delta\ AIC_c > 4$, $w_i \leq 0.07$; Table 7).

In 2005, the best-approximating model explaining salamander presence was the "multi-level" model (Table 9) that included variables for treatment, herbaceous vegetation, soil moisture, canopy cover, and rock cover. Salamander presence was positively associated with increasing cover of herbaceous vegetation and overhead canopy (Table 8). This model also indicated that salamander presence was less likely in more disturbed habitat types, particularly grazed meadow habitats (Table 8). Weight of evidence for the "multi-level" model was 99 times greater than that of the "treatment" model, thereby indicating almost no uncertainty in selection of the best candidate model.

The remaining 12 models explaining salamander presence in 2005 received no empirical support (Δ AIC_c >9, $w_i \leq 0.01$; Table 9).

Abundance.— In 2004, the best-approximating model explaining abundance of red-backed salamanders was the single variable “herbaceous vegetation” (Table 10). Salamander abundance increased with greater cover of herbaceous vegetation (Table 11). The second-best model, “multi-level,” also received strong empirical support (Δ AIC_c = 1.12; Tables 10-11). A third model, “ground cover,” received only limited empirical support (Δ AIC_c = 3.99; Tables 10, 11). This model indicated that salamander abundance was positively associated with increased cover of leaf litter (Table 11). Weight of evidence for the herbaceous vegetation model was only about 1.7 times greater than the multi-level model, thereby indicating some uncertainty in selection of the best candidate model. However, evidence for the effect of herbaceous vegetation on salamander abundance was strong in that the sum of Akaike weights for the 3 supported models containing this variable was 0.97 (Table 10). The remaining 10 models explaining salamander abundance received no empirical support (Δ AIC_c >8, $w_i \leq 0.01$; Table 10).

In 2005, the best-approximating model explaining salamander abundance was the “ground cover” model (Table 12). Salamander abundance was positively associated with increasing amounts of herbaceous vegetation and leaf litter (Table 11). The second-best model, “multi-level,” also received strong empirical support (Δ AIC_c = 0.26; Table 12). This model indicated that salamander abundance was positively influenced by increased herbaceous cover and soil moisture, and negatively associated with rock cover, canopy cover, and treatment disturbance (Table 11). The third-best model, “herbaceous vegetation,” also received strong empirical support (Δ AIC_c = 0.79; Table 12). Weight of evidence was similar for all 3 models, and the ground cover model was only about 1.2 times greater than the multi-level model, thereby indicating considerable uncertainty in selection of the best candidate model (Burnham and Anderson 2002). Collectively, these models provide evidence for a positive effect of herbaceous vegetation and a negative effect of treatments on salamander abundance, as the sum of Akaike weights was 0.97 (Table 12). The remaining 10 model sets explaining salamander abundance in 2005 received no empirical support (Δ AIC$_c$ >5, $w_i \leq 0.02$; Table 12).

Physiological condition, sex ratio, and age class

Mean physiological condition of red-backed salamanders did not differ significantly among treatments (Table 13). Mean physiological condition did not differ significantly between sexes, and the physiological condition between sexes did not differ significantly among treatments (Table 13).

Sex ratios of red-backed salamander populations did not differ significantly among treatments (Table 14). In contrast, age-class structure of red-backed salamanders differed significantly among treatments. Adult salamanders were almost twice as abundant as immature salamanders in all 5 treatment types. However, although age-class was skewed regardless of treatment, the proportion of adults to immature salamanders differed significantly among treatments (Table 14) with the proportion of adult salamanders being significantly higher in meadow treatments than other treatment types.

Residents, dispersers, and use of artificial cover

Silvopasture, ungrazed meadow, and grazed meadow habitats contained nearly half of all salamander observations in 2004 and 2005. In 2004, 621 salamanders (49.0 % of total observations) were observed in these treatment plots (Table 15, Fig. 6). In 2005, 696 salamanders (47.0 % of total observations) were from silvopasture, and grazed and ungrazed meadows (Table 15, Fig. 6). I only observed salamanders in meadow habitats during fall 2004 (September –December) and during spring (March-May) and fall (September-November) 2005 (Table 15).

Of 568 marked salamanders, 193 were recaptured at least once, for a total recapture rate of 34 % (Table 16). Eighty-one salamanders were recaptured at a different coverboard from where they were originally marked, of which 24 moved among different treatment types. Fifteen of these salamanders were recorded moving from a less disturbed habitat (e.g., woodlands) to a more disturbed habitat (e.g., ungrazed meadows). Nine salamanders were recorded moving from a more disturbed habitat to a less disturbed habitat. Of the 24 salamanders dispersing among habitat types, 6 returned to the original habitat of capture. Only 1 salamander that moved among treatments was a juvenile (SVL at final capture = 32.90 mm). Mean change in body mass of salamanders that moved from less disturbed to more disturbed treatments ($\bar{x}$ 0.068 g ± 0.105 g) did not differ significantly from that of salamanders that moved from more disturbed to less disturbed habitats ($\bar{x}$ 0.072 g ± 0.112 g; t = 0.021, df = 22, P = 0.492).

I only observed red-backed salamanders in woodland reference and woodland edge plots during daytime area-constrained searches and night surface surveys in 2004 and 2005. During daytime surface searches, I captured, marked, and measured 39 salamanders in 2004 and 34 salamanders in 2005, most of which were juveniles (Table 17). Red-backed salamanders were found under a variety of cover objects, including CWD, FWD, and emergent rock. Salamanders were captured most often under rocks in both 2004 (48% of captures) and 2005 (47% of captures), and less often under FWD

(33% in 2004 and 18% in 2005) and CWD (18 % in 2004 and 35% in 2005). No salamanders were captured during daytime surveys while raking through leaf litter. Most CWD in woodland reference and edge plots consisted of newly-fallen limbs with little decay. No logs were torn open during daytime searches to prevent habitat disturbance and because few logs had decayed enough to allow sampling. Only 1 juvenile salamander was captured on leaf litter during night surface surveys in 2004 and no salamanders were captured during night searches in 2005.

DISCUSSION

Habitat Relationships

My primary result was the specification and evaluation of multivariate models that explained responses of red-backed salamanders to a gradient of forest disturbance and conversion. According to the models that received empirical support for explaining both presence and abundance, red-backed salamanders appeared to be negatively associated with more disturbed habitats over woodland reference plots. Management practices that create canopy gaps and subsequently modify temperature and moisture regimes of the forest floor influence microclimates and therefore the microhabitats available for terrestrial salamanders (Heatwole 1962, Herbeck and Larsen 1999). Most studies examining the response of salamanders to different silvicultural practices have found that salamander abundance typically is lower in clearcuts when compared to older or more closed-canopy stands (Pough et al. 1987, deMaynadier and Hunter 1995, Herbeck and Larsen 1999, Grialou et. al. 2000). For example, Herbeck (1998) found 5 times more salamanders in old-growth stands when compared to second growth stands and 20 times more salamanders in second growth than in regeneration cuts. Similarly, I found that salamander presence and abundance was lower in open-canopy treatments than in woodland reference plots. Salamander abundance also was negatively associated with increasingly disturbed treatment types. Specifically, grazed meadows had the lowest coverboard occupancy rates and lowest relative abundance during both years of the study.

Because salamanders respond to changes in their environment, resulting in the occupancy of specific microhabitats (Heatwole 1962), I assumed that open and partial canopy habitats would be unsuitable for terrestrial salamanders. The unexpected abundance of salamanders in silvopasture and meadow treatments indicates that the retention of dense vegetation and low grazing pressure can allow salamanders to occupy these areas. While intensive livestock grazing has been attributed to declines of California tiger salamander (*Ambystoma californiense*) populations through soil compaction and loss of vegetative cover (Harvey et al. 2000), light grazing does appear to be compatible with the persistence of this species (Marty 2005). Red-backed salamander presence and abundance increased as herbaceous vegetation increased, therefore the lack of constant disturbance and presence of a thick vegetative layer (0.30 – 1.2 m tall) may possibly compensate for the lack of canopy cover, leaf litter, and natural cover objects normally found in a woodland site. For example, the ungrazed meadow at Peters farm had the highest relative abundance of red-backed salamanders per coverboard and the highest percentage of natural herbaceous vegetation, no livestock, and was never mowed for hay during the course of my study. The lack of agriculturally-related disturbance to this site since purchased by AFSRC in 1996 has allowed this meadow habitat to begin natural succession. Livestock forage had been primarily replaced with native herbaceous vegetation and small woody saplings were beginning to grow on site by the completion of my study.

Similar to my results, previous research has demonstrated the positive influence of herbaceous vegetation on presence and abundance of terrestrial salamanders, particularly in degraded habitats. For example, amphibian abundance in upland forests of the Chicago region was positively associated with increased cover of herbaceous vegetation in an area where the majority of forests were altered by grazing, logging, fire exclusion, and excessive deer herbivory (Nuzzo and Mierzwa 2000). Similarly, red-backed salamander abundance within clearcut treatments was positively associated with percent herbaceous and shrub cover (Duguay and Wood 2002).

My results demonstrate the influence of ground cover and lack of habitat disturbance on presence and abundance of red-backed salamanders. However, although silvopasture and meadow habitats appear to negatively influence red-backed salamander presence and abundance, the retention of dense natural herbaceous vegetation may at least partially mitigate the loss of canopy cover, CWD, and leaf litter. Conversion of forest stands to silvopastures and hay meadows has been assumed to represent more drastic and permanent impacts on salamander populations than traditional forest management practices, but I observed hundreds of salamanders in agriculturally altered habitats, which indicates that red-backed salamanders may be more resilient to disturbance than previously thought (Marsh et al. 2004). Whether, with cover, the number of salamanders retained or present in silvopasture and meadow sites is biologically meaningful remains to be determined. If populations within silvopastures are determined to be viable then silvopasture systems may achieve multiple use goals for agriculture, forestry, and wildlife.

Physiological condition, sex ratio, and age class

Meadows and silvopastures, especially those regularly disturbed by the presence of livestock, should represent harsh habitats for poorly dispersing woodland species like red-backed salamanders. Increased surface temperatures and decreased soil moisture could lead to increased rates of desiccation, increased time in fossorial refuges, fewer opportunities to forage, and thus decreased physiological condition. Some studies investigating impacts of forest management practices on salamander body size also indicate that thinning of the forest canopy may not be as detrimental to the physiological condition of salamanders as previously thought (Dupuis and Bunnell 1999, Rothermel and Luring 2005). For example, body length of western red-backed salamanders (*Plethodon vehiculum*) was unrelated to forest cover in coastal British Columbia (Dupuis and Bunnell 1999). Similarly, 90% of juvenile mole salamanders (*Ambystoma talpoideum*) without access to burrows, survived in thinned stands without apparent negative impacts on body condition (Rothermel and Luring 2005).

In contrast, size of western red-backed salamanders in southwestern Washington was smaller in clearcuts than in uncut forests (Grialou et al. 2000). Significant difference in SVL between adult male and female southern graycheek salamanders were observed in the southern Blue Ridge Mountains, with mature females being significantly larger than adult males on clearcut treatments (Ash et al. 2003). Mass and size-corrected mass (mass/SVL) of gravid red-backed salamanders were also found to be higher on harvested than on uncut plots in the southern Appalachian Mountains of Virginia and West Virginia (Knapp et al. 2003).

Sex ratios of surface-active red-backed salamanders, based on studies conducted in Michigan, New York, and Virginia appear to be approximately 1:1 (Hood 1934, Test 1955, Mathis 1991). My results indicate that sex ratios of red-backed salamanders in silvopastures and meadows were similar to those in woodland habitats. Similarly, Williams (2003) found no significant differences in adult sex ratios of 6 salamander species before and after clearcutting in a central Appalachian industrial forest.

In addition to skewed sex ratios, changes to age-class structure resulting from habitat disturbance could influence the viability of salamander populations. Populations with altered sex or age distributions often are characterized as “sinks” because of reduced reproductive success (Pulliam 1988). All treatment types had approximately twice as many adults as juveniles under coverboards. However, the proportion of adult salamanders was significantly higher in meadow treatments when compared to the other treatments. This may be a result of sampling bias and the territorial behavior of red-backed salamanders (Mathis 1990, Marsh and Goicochea 2003). Territorial defense often is centered on a cover object, which is defended against both conspecific and heterospecific intruders, with larger individuals generally having a territorial advantage, especially when cover objects are limited (Jaeger et al. 1982, Mathis 1990, Smith and Pough 1994). Likewise, populations of southern graycheek salamanders in clearcut stands in the Blue Ridge Mountains were composed almost entirely of adults (Ash et al. 2003). Proportions of juvenile slimy salamanders in uncut forested plots were also significantly higher than in cut plots (Knapp et al. 2003).

Contrary to my results, previous studies have reported higher proportions of small adult and immature salamanders than larger adults in open fields and clearcuts compared to forested plots (Mathis 1990, deMaynadier and Hunter 1998, Marsh et al. 2004). These studies indicate that open-canopy sites may serve as sink habitats for non-breeding "floaters" that are excluded from mature forest territories by larger, competitively dominant salamanders and forced to search for territories in less suitable habitats (Moore et al. 2001).

The near-absence of juveniles within meadow treatments may indicate that on-site reproduction was poor or that immature salamanders could not survive within open canopy habitats. The presence of artificial cover objects (i.e., coverboards) or underground refugia in silvopasture and meadows may mitigate negative effects of habitat disturbance on salamanders. Alternatively, salamanders observed in silvopastures and meadows may represent recent dispersers from adjacent woodland habitats. The inconsistency among studies suggests that our understanding of forest disturbance effects on amphibian physiological condition, sex ratio, and age structure remains unclear.

Residents, dispersers, and use of artificial cover

Similar to the impacts of clearcutting, agricultural landscapes should limit colonization by desiccation prone, poorly dispersing woodland salamanders. Currently, little is known about the extent to which matrix habitats reduce amphibian dispersal. Some species appear to be adverse to crossing roads (deMaynadier and Hunter 2000, Marsh and Beckman 2004), open habitats (Rothermel and Semlitsch 2002, Marsh et al. 2004), or forests (deMaynadier and Hunter 1998, DeGraaf and Yamasaki 2002) even if they may be physiologically capable of doing so. Other amphibians may enter matrix habitats but suffer high mortality while dispersing through (Hels and Buchwald 2001). Red-backed salamanders have been previously observed colonizing coverboards in open field plots in the spring and fall, which had been unexpected, given that dispersal to new habitats had not been documented previously as an important feature in terrestrial salamander life histories (Marsh et al. 2004). Marsh et al. (2004) concluded that salamander dispersal was limited more by distance than by the absence of forest cover.

The lack of salamander observations in meadow treatments during the summer may indicate that individuals observed in the spring and fall were dispersers from surrounding habitats. The timing of these captures coincides with red-backed salamander courtship and breeding behavior (Petranka 1998). Additionally, Jaeger (1980) found that high-density red-backed salamander populations in Appalachian woodland habitats tended to be near carrying capacity, putting a premium on dispersal to new breeding territories.

Woodland salamanders typically have relatively short dispersal patterns, with home ranges <1 m^2 (Kleeberger and Werner 1982, Mathis 1991). Some terrestrial salamanders exhibit seasonal fluctuations in dispersal patterns (Petranka 1998), which coincides with my observations of peak activity in open habitats during the spring and fall breeding seasons. Species of plethodontid salamanders have been reported to move 25-60 m in a 12-hr period during the breeding season (Madison and Shoop 1970). During one sample period in October 2004, I collected 146 salamanders from the 2 ungrazed meadow treatments. I brought these salamanders to the AFSRC lab for processing and returned them to their respective boards the following morning. I discovered that many of the boards had already been re-colonized by new salamanders,

<12 hr since I originally checked them. These findings add further support to my hypothesis that salamanders were dispersing rapidly into the open habitat matrix.

It is possible that salamanders were not observed in meadow treatments throughout the summer via any of the surveying techniques because they were in subterranean retreats, yet it is unlikely that salamanders would be able to survive for such an extended period of time without experiencing declined physiological condition (Stebbins 1954, Heatwole 1962, Jaeger 1980, Feder 1983, Morneault et al.2004). Lunglessness coupled with ectothermy results in lower rates of metabolism for plethodontids when compared to other vertebrates (Merchant 1970). Several studies indicate that up to 68 % of a population may be in underground burrows at any time, (Taub 1961, Smith and Petranka 2000, Hyde and Simons 2001, Bailey et al. 2004) limiting the ability to detect salamanders during sampling efforts. This behavior may be especially likely in areas with high densities of ant colonies, which provide an abundant food source and access to subterranean retreats (Cadwell and Jones 1973, Pauley 1978).

During area constrained surveys, salamanders were observed only in woodland reference and woodland edge plots, indicating that silvopasture and meadow plots represented unsuitable habitats without the presence of artificial cover objects. The limited number of salamanders captured during area constrained searches prohibited statistical analyses and further research is needed to fully assess the role of artificial cover in the agriculturally altered habitats.

Because area-constrained searches were conducted only once, in mid-summer, rather than during optimal weather conditions in spring and fall, it is possible that some salamanders were in subterranean retreats and thus went undetected. The fossorial behavior of red-backed salamanders and the timing of searches may account for the low number of observations during night surface surveys. However, the absence of salamander detections in silvopastures and meadows during cover object surveys, combined with the lack of natural cover in these habitats, supports the conclusion that artificial coverboards most likely are responsible for the presence of salamanders within silvopastures and meadows. Additionally, salamanders were only observed in large numbers under coverboards in meadows and silvopastures in the spring and fall when air temperatures were lower and relative humidities higher than in the summer.

Thus, artificial cover objects within silvopastures and meadows may mitigate the negative impacts of agricultural conversion on red-backed salamanders. Further, it is possible that coverboards provide "stepping stones" that facilitate dispersal through these open habitats. Previous research indicates that retention of CWD during forest management may mitigate some detrimental effects of clearcutting, particularly for species strongly associated with ground cover (Aubry et al. 1988, Grover 1998). Therefore, it is possible that artificial cover objects may provide the same role in agriculturally disturbed habitats. Further research is needed to assess whether salamanders within silvopastures and meadows represent residents or dispersers (Marsh et al. 2004), and why red-backed salamanders appear to using what historically have been considered unsuitable habitats.

MANAGEMENT IMPLICATIONS

The sse of silvopasture and other agroforestry systems is increasing in the Appalachians (Buergler 2004), but my findings suggest that managers may need to more closely consider effects of these practices on woodland salamanders and other disturbance-sensitive species. Densities of terrestrial salamander populations track habitat features such as age, soil moisture, and amounts of CWD. Even selection harvest methods, which typically retain much of the overhead canopy and structural characteristics of the original stand, have been shown to temporarily affect plethodontid salamanders. Thus, open and disturbed habitats such as traditional pastures and silvopastures also should be unsuitable habitats for desiccant-prone woodland salamanders. Habitat modeling of presence and abundance indicated that pasture and silvopasture conversion negatively influenced red-backed salamander populations and confirmed previous research that woodland salamanders are sensitive to habitat disturbance (deMaynadier and Hunter 1995, Petranka 1998, Russell et al. 2004a).

The presence of red-backed salamanders in disturbed habitats and the apparent lack of disturbance effects on physiological condition or sex ratios that I found indicate that this species may be less sensitive to or recovers more quickly from habitat disturbance than previously thought. Although previous research has documented red-back salamanders dispersing across fields (Marsh et al. 2004) and into residential areas (Gibbs 1998), no studies have reported viable, resident populations of woodland salamanders in open, disturbed habitats. Although I was unable to determine if salamanders in silvopasture and meadow habitats represented residents or dispersers, my qualitative results suggest that they may be using these habitats during seasonal dispersal. If resident populations of red-backed salamanders can persist within grazed pastures, recommendations to protect plethodontids in eastern deciduous forests (e.g., prohibiting clearcutting; Petranka et al. 1993, 1994) may need to be revisited. Viable populations of red-backed salamanders in heavily-disturbed, open-canopy habitats may also indicate that they are not suitable indicators of biodiversity and forest ecosystem integrity (Jung et al. 2000, Welsh and Droege 2001). However, presence or abundance of salamanders within meadows and silvopastures may not reflect population viability or habitat suitability if populations are atypical with respect to age structure, sex-ratios, or physiological condition (Hairston 1983, Ash et al. 2003). Thus, managers must consider the possibility that although salamanders may persist in open, disturbed habitats these populations may not reflect those associated with more suitable forest stands.

Although red-backed salamanders were capable of dispersing across open fields, successful colonization of adjacent forest patches has been found to decrease as distance to forest increased (Marsh et al. 2004). If persistence of red-backed salamanders in pastures and silvopastures depends on presence of coverboards, these artificial microhabitats may not only partially mitigate effects of habitat disturbance for resident salamanders but also provide temporary refugia for dispersers. Red-backed salamanders tend to be highly territorial and larger individuals (i.e., older adults) have a territorial advantage (Mathis 1990). Thus, these refugia may be particularly important for newly mature salamanders as they disperse to find new breeding territories (Marsh et al. 2004). Research has indicated that forestry practices that leave woody debris on the forest floor may mitigate some negative effects of intensive timber harvesting (Aubry et al. 1988, Grover 1998). While management of actively used agricultural hay meadows for salamanders is unlikely, my results suggest that the placement of artificial cover objects in a restoration setting may be useful for linking isolated patches of woodlands and accelerate the recovery of salamanders in disturbed habitats.

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Table 1. Observations of red-backed salamanders from preliminary research of coverboard sampling at 2 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2002-2003.

Treatments	2002	2003
Reba Silvopasture	23	56
Reba Grazed Meadow	.	32
School Grazed Meadow	.	5
Reba Ungrazed Meadow	.	119
School Woodland Reference	.	67
Reba Woodland Reference	11	48
Reba Woodland Edge	5	92
School Woodland Edge	.	77

Table 2. Description of 13 treatment plots from 3 Appalachian Farming Service Research Center farm sites sampled for red-backed salamanders, in Raleigh County, West Virginia, USA, 2004-2005.

Farm	Treatments	Dominant vegetation
Peters	Woodland Reference	Northern red oak, maple, pine
	Woodland Edge	Northern red oak, maple
	Ungrazed Meadow	Mixed grasses, cinquefoil
Reba	Woodland Reference	Northern red oak, maple, blackgum
	Woodland Edge	Northern red oak, maple, blackgum
	Silvopasture A	Northern red oak, ryegrass, orchardgrass, white clover
	Silvopasture B	Northern red oak, ryegrass, orchardgrass, white clover
	Silvopasture C	Northern red oak, ryegrass, orchardgrass, white clover
	Ungrazed Meadow	Tall fescue
	Grazed Meadow	Orchardgrass, white clover
School	Woodland Reference	Northern red oak, maple, blackgum
	Woodland Edge	Northern red oak, maple, blackgum
	Grazed Meadow	Tall fescue, orchardgrass

Table 3. Biotic and abiotic habitat variables measured within 3-m radius circles centered over salamander locations, included in logistic and linear regression models explaining habitat relationships of red-backed salamanders from 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

Variable	Units	Abbreviation	Description
Livestock Presence	-	LIVE	Presence or absence of livestock species
Treatment	-	TREAT	Treatment type (woodland, edge, silvopasture, ungrazed meadow, grazed meadow)
Average Diameter at Breast Height	cm	DBH	Average diameter at breast height for trees
Percent Bare Soil	%	SOIL	The percent area of bare soil
Percent Canopy Cover	%	CC	The average percent canopy closure
Percent Coarse Woody Debris	%	CWD	The percent area of coarse woody debris
Percent Emergent Rock	%	ROCK	The percent area of emergent rock
Percent Fine Woody Debris	%	FWD	The percent area of fine woody debris
Percent Herbaceous Vegetation	%	HERB	The percent area of herbaceous vegetation
Percent Leaf Litter	%	LL	The percent area of leaf litter
Percent Woody Shrubs	%	WOODY	The percent area of woody shrubs
Soil Moisture	%	MOIST	The soil moisture at the time of sampling
Soil pH	-	pH	The soil pH for the top 10 cm of soil
Surface Temperature	°F	TEMP	The surface temperature at the time of sampling
Overstory	-	OVER	Tree type (Coniferous, Deciduous, Mixed, None)
Average Soil Compaction	kPa	COMPACT	The average compaction of the soil

Table 4. Measurements of mean biotic and abiotic attributes in woodland reference, woodland edge, silvopasture, ungrazed meadow, and grazed meadow treatments on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005. Abbreviations correspond to model variables in Table 3.

	Woodland Reference[a]		Woodland Edge[a]		Silvopasture[a]		Ungrazed Meadow[b]		Grazed Meadow[b]	
Variable	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE
DBH	22.27	1.91	21.30	2.46	17.27	3.10	0.00	0.00	0.00	0.00
CC	95.03	0.48	90.85	1.04	54.42	1.90	0.00	0.00	0.00	0.00
CWD	2.83	0.76	2.73	0.98	0.00	0.00	0.00	0.00	0.00	0.00
FWD	8.95	1.19	8.83	1.31	0.13	0.04	0.00	0.00	0.00	0.00
WOODY	11.33	1.88	22.82	3.08	0.13	0.06	0.13	0.09	0.00	0.00
HERB	9.90	1.49	31.75	3.20	1.15	0.41	39.23	6.30	0.00	0.00
ROCK	2.10	0.57	1.98	0.57	0.43	0.19	0.00	0.00	0.00	0.00
SOIL	4.58	1.17	4.80	1.26	1.43	0.41	0.08	0.06	0.58	0.14
LL	60.35	3.38	18.03	2.97	0.02	0.02	0.00	0.00	0.00	0.00
pH	4.27	0.04	4.47	0.07	5.70	0.06	5.51	0.10	5.87	0.08
COMPACT	1849.23	98.85	2188.65	112.06	1782.80	80.17	1053.88	59.87	1709.98	96.06
TEMP 2004	55.30	0.07	54.93	0.11	59.25	0.13	58.56	0.24	59.41	0.22
MOIST 2004	32.59	0.43	33.81	0.71	34.72	0.59	39.57	0.64	35.86	0.49
TEMP 2005	55.85	0.09	56.51	0.14	59.20	0.14	60.82	0.33	59.48	0.24
MOIST 2005	21.03	0.42	21.38	0.54	25.51	0.50	26.98	0.42	24.14	0.57

[a] n = 60.

[b] n = 40.

Table 5. Logistic and linear regression models explaining influence of biotic and abiotic habitat attributes on presence and abundance of red-backed salamanders at 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005. Abbreviations correspond to model variables in Table 3.

Model	Variables					
Global	ALL					
Abiotic	SOIL	ROCK	COMPACT	pH		
Canopy Cover	CC					
Disturbance	TREAT	LIVE	COMPACT			
Ground Cover	CWD	FWD	ROCK	LL	HERB	
Microclimate	MOIST	TEMP				
Overstory	DBH	CC	OVER			
Herbaceous Vegetation	HERB					
Soil	MOIST	pH	TEMP			
Treatment	TREAT					
Vegetation	OVER	CC	WOODY	LL	DBH	HERB
Herbaceous Disturbance	TREAT	HERB				
Multi-level	TREAT	HERB	MOIST	CC	ROCK	

.

Table 6. Sex and age frequencies of red-backed salamanders by treatment type on 3 Appalachian Farming Services Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

Treatments	Adult Female	Adult Male	Immature	Total
Woodland Reference	51 (29.0%)	53 (30.1%)	72 (40.9%)	176
Woodland Edge	53 (31.7%)	61 (36.5%)	53 (31.7%)	167
Silvopasture	30 (42.3%)	16 (22.5%)	25 (35.2%)	71
Meadow	48 (41.1 %)	52 (44.4%)	17 (14.5%)	117

Table 7. Logistic regression models explaining the influence of biotic and abiotic habitat attributes on presence of red-backed salamanders in 2004 on 3 Appalachian Farming Services Research Center experimental farms in Raleigh County, West Virginia, USA.

Model[a]	-2 log likelihood	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
Herbaceous Disturbance	246.672	6	259.004	0.000	0.692
Treatment	251.678	5	261.914	2.910	0.161
Multi-level	244.744	9	263.464	4.460	0.074
Vegetation	241.281	11	264.346	5.342	0.048
Disturbance	251.647	7	266.091	7.087	0.020
Canopy Cover	267.127	2	271.174	12.170	0.002
Overstory	259.355	6	271.687	12.683	0.001
Ground Cover	259.459	6	271.791	12.787	0.001
Abiotic	264.466	5	274.702	15.698	0.000
Soil	266.764	4	274.921	15.917	0.000
Global	230.499	22	278.769	19.765	0.000
Herbaceous Vegetation	275.709	2	279.756	20.752	0.000
Microclimate	277.243	3	283.337	24.333	0.000

[a] Variables in each model are indicated in Table 5.

[b] Number of estimable parameters in approximating model.

[d] Akaike's Information Criterion corrected for small sample size.

[e] Difference in value between AIC_c of the current model versus the best approximating model (AIC_{cmin}).

[f] Akaike weight. Probability that the current model (*i*) is the best approximating model among those considered.

Table 8. Parameter estimates (B) and standard errors (SE) from the most highly supported models explaining the influence of biotic and abiotic habitat attributes on presence of red-backed salamanders on 3 Appalachian Farming Services Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005. Coefficients of the categorical variable treatment were calculated relative woodland reference treatments.

Model	B	SE	R^{2a}
Herbaceous Disturbance[b]			0.239
Herbaceous Vegetation	0.020	0.010	
Woodland Edge	-0.197	0.611	
Silvopastures	-0.940	0.499	
Ungrazed Meadows	-1.377	0.576	
Grazed Meadows	-2.356	0.525	
Multi-level[c]			0.391
Herbaceous Vegetation	0.033	0.012	
Percent Rock	-0.296	0.083	
Canopy Cover	0.003	0.021	
Average Soil Moisture	-0.074	0.050	
Woodland Edge	-5.448	1.987	
Silvopastures	-4.951	2.205	
Ungrazed Meadows	-6.163	2.916	
Grazed Meadows	-6.721	2.872	

[a] Nagelkerke R Square

[b] Logistic regression model explaining presence of red-backed salamanders in 2004.

[c] Logistic regression model explaining presence of red-backed salamanders in 2005.

Table 9. Logistic regression models explaining the influence of biotic and abiotic habitat attributes on presence of red backed salamanders in 2005 on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA.

Model[a]	-2 log likelihood	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]
Multi-level	197.098	9	215.818	0.000	0.991
Global	177.051	22	225.321	9.503	0.009
Disturbance	218.516	7	232.960	17.142	0.000
Herbaceous Disturbance	220.897	6	233.229	17.411	0.000
Treatment	225.889	5	236.125	20.307	0.000
Ground Cover	229.132	6	241.464	25.646	0.000
Overstory	231.338	6	243.670	27.852	0.000
Vegetation	221.941	11	245.006	29.188	0.000
Canopy Cover	242.490	2	246.537	30.719	0.000
Abiotic	240.094	5	250.330	34.512	0.000
Soil	248.749	4	256.906	41.088	0.000
Microclimate	260.137	3	266.231	50.413	0.000
Herbaceous Vegetation	266.163	2	270.210	54.392	0.000

[a] Variables in each model are indicated in Table 5.

[b] Number of estimable parameters in approximating model.

[c] Akaike's Information Criterion corrected for small sample size.

[d] Difference in value between AIC_c of the current model versus the best approximating model (AIC_{cmin}).

[e] Akaike weight. Probability that the current model (*i*) is the best approximating model among those considered.

Table 10. Linear regression models explaining influence of biotic and abiotic habitat attributes on the abundance of red-backed salamanders under coverboards in 2004 on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA.

Model [a]	Residual Sum of Squares	K [b]	AIC_c [c]	ΔAIC_c [d]	w_i [e]
Herbaceous Vegetation	165.164	3	-26.256	0.000	0.573
Multi-level	153.763	10	-25.134	1.122	0.327
Ground Cover	161.409	7	-22.267	3.989	0.078
Herbaceous Disturbance	164.911	7	-18.082	8.174	0.010
Global	136.230	23	-17.482	8.774	0.007
Vegetation	156.529	12	-17.139	9.117	0.005
Disturbance	187.556	8	9.184	35.440	0.000
Soil	200.706	5	15.942	42.198	0.000
Microclimate	212.403	4	24.880	51.136	0.000
Canopy Cover	229.937	3	38.263	64.519	0.000
Overstory	229.549	7	46.407	72.663	0.000
Abiotic	232.802	6	46.999	73.255	0.000
Treatment	234.188	6	48.156	74.412	0.000

[a] Variables in each model are indicated in Table 5.

[b] Number of estimable parameters in approximating model.

[c] Akaike's Information Criterion corrected for small sample size.

[d] Difference in value between AIC_c of the current model versus the best approximating model (AIC_{cmin}).

[e] Akaike weight. Probability that the current model (*i*) is the best approximating model among those considered.

Table 11. Parameter estimates from the most highly supported models explaining the influence of biotic and abiotic habitat attributes on abundance of red-backed salamanders on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

Model	B	SE	R^2
Herbaceous Vegetation[a]			0.299
Herbaceous Vegetation	0.022	0.002	
Multi-level[a]			0.347
Herbaceous Vegetation	0.020	0.003	
Percent Rock	-0.035	0.020	
Canopy Cover	-0.009	0.004	
Treatments	-0.289	0.133	
Ground Cover[b]			0.191
Herbaceous Vegetation	0.019	0.003	
Coarse Woody Debris	-0.001	0.015	
Percent Rock	-0.056	0.030	
Fine Woody Debris	-0.006	0.010	
Percent Leaf Litter	0.007	0.003	
Herbaceous Vegetation[b]			0.154
Herbaceous Vegetation	0.017	0.003	
Multi-level[b]			0.216
Herbaceous Vegetation	0.016	0.003	
Percent Rock	-0.067	0.030	
Canopy Cover	-0.011	0.005	
Average Soil Moisture	0.031	0.021	
Treatment	-0.499	0.155	

[a] Linear regression models explaining abundance of red-backed salamanders in 2004.

[b] Linear regression models explaining abundance of red-backed salamanders in 2005.

Table 12. Linear regression models explaining influence of biotic and abiotic habitat attributes on the abundance of red-backed salamanders under coverboards in 2005 on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA.

Model [a]	Residual Sum of Squares	K [b]	AIC_c [c]	ΔAIC_c [d]	w_i [e]
Ground Cover	230.596	7	40.449	0.000	0.379
Multi-level	223.540	10	40.712	0.263	0.333
Herbaceous Vegetation	241.340	3	41.240	0.791	0.256
Herbaceous Disturbance	236.992	7	46.003	5.554	0.024
Vegetation	227.669	12	48.924	8.475	0.005
Soil	246.641	5	49.834	9.385	0.003
Global	210.848	23	59.868	19.419	0.000
Disturbance	258.943	8	66.153	25.704	0.000
Abiotic	266.724	6	67.849	27.400	0.000
Microclimate	279.710	4	73.273	32.824	0.000
Canopy Cover	285.100	3	75.066	34.617	0.000
Treatment	283.312	6	80.097	39.648	0.000
Overstory	281.896	7	81.226	40.777	0.000

[a] Variables in each model are indicated in Table 5.

[b] Number of estimable parameters in approximating model.

[c] Akaike's Information Criterion corrected for small sample size.

[d] Difference in value between AIC_c of the current model versus the best approximating model (AIC_{cmin}).

[e] Akaike weight. Probability that the current model (*i*) is the best approximating model among those considered.

Table 13. Results of 2-way ANOVA of physiological condition by treatment, and sex of red-backed salamanders on 3 Appalachian Farming Services Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

Source	df	MS	F	P
Treatment	3	0.003	1.696	0.196
Sex	2	0.000	0.154	0.858
Treatment x Sex	6	0.001	0.864	0.536
Error	23	0.001		

Table 14. Results of 1-way ANOVA of salamander sex and age by treatment type from coverboard searches on 3 Appalachian Farming Service Research Center experimental farms near Beckley, West Virginia, USA, 2004-2005.

	Source	df	MS	F	P
Sex	Between Treatments	3	0.02	1.144	0.389
	Within Treatments	8	0.018		
	Total	11			
Age	Between Treatments	3	0.053	12.534	0.002
	Within Treatments	8	0.004		
	Total	11			

Table 15. Total observations of red-backed salamanders by treatment type during 19 coverboard sampling efforts in 2004 and 14 coverboard sampling efforts in 2005 on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA.

2004

Treatments	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
Woodland Reference	.	.	13	43	26	8	34	72	54	8	258
Woodland Edge	.	.	6	24	24	7	80	161	68	19	389
Silvopasture	.	.	6	5	2	0	23	109	45	0	190
Grazed Meadow	.	.	0	0	0	0	1	15	10	0	26
Ungrazed Meadow	.	.	0	0	0	0	49	233	114	9	405
Total	.	.	25	72	52	15	187	590	291	36	1268

2005

Treatments	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
Woodland Reference	39	70	68	110	59	10	40	53	14	.	428
Woodland Edge	69	75	41	46	19	7	41	69	16	.	357
Silvopasture	33	65	1	6	2	1	3	146	16	.	273
Grazed Meadow	0	1	1	0	0	0	0	29	21	.	27
Ungrazed Meadow	37	59	2	0	0	0	4	265	29	.	396
Total	175	263	105	151	76	17	85	535	74	.	1481

Table 16. Number of marked and recaptured red-backed salamanders on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

Farm	Total marked	Total Recaptured	% Recapture Rate
Reba	189	43	22.75
School	118	38	32.20
Peters	261	112	42.91
Total	568	193	33.98

Table 17. Number of red-backed salamanders captured in woodland reference and woodland edge plots via day transect and night surface surveys on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

	2004				2005			
Treatments	Female	Male	Juvenile	Total	Female	Male	Juvenile	Total
Reba Woods	8	2	5	15	5	3	10	18
School Woods	2	0	4	6	1	1	4	6
Peters Woods	0	1	4	5	1	2	2	5
Reba Edge	2	0	2	4	0	1	3	4
School Edge	1	0	5	6	0	0	0	0
Peters Edge	0	0	3	3	0	0	1	1
Total	13	3	23	39	7	7	20	34

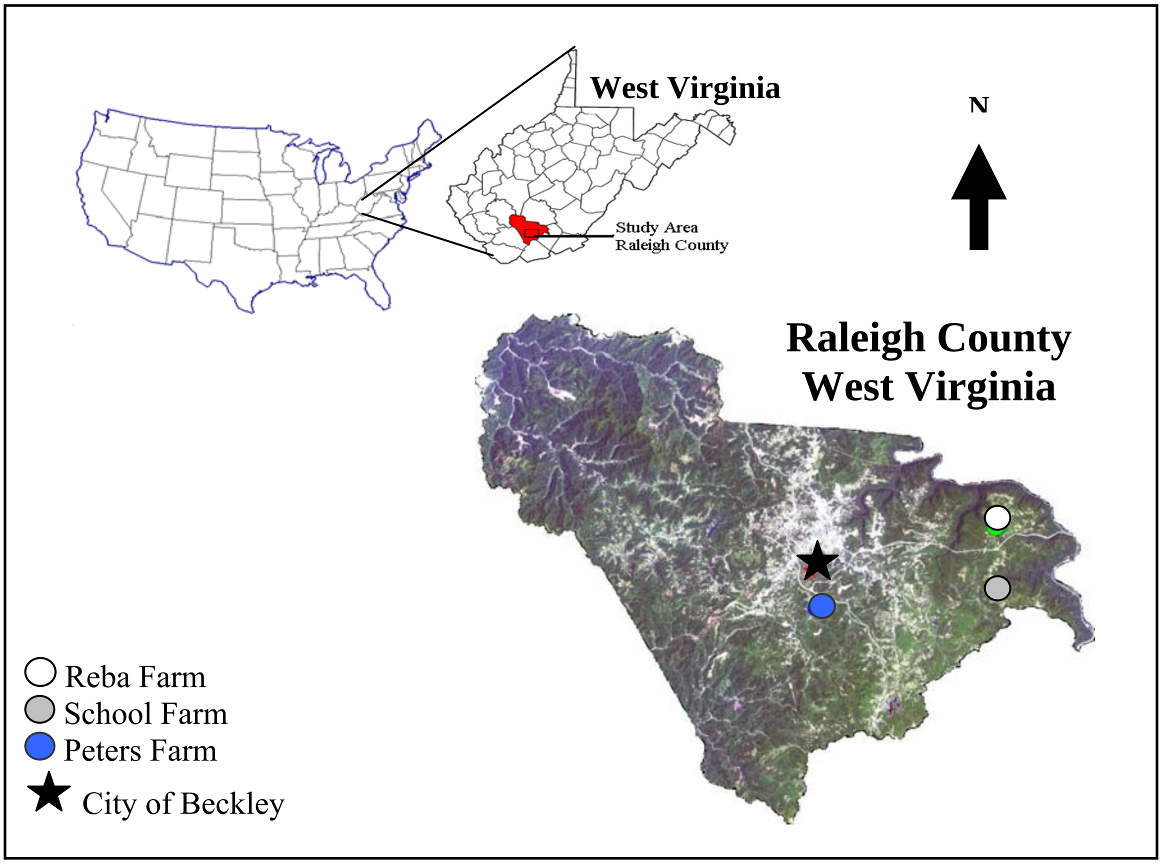

Figure 1. Approximate locations of the 3 Appalachian Farming Service Research Center experimental farm sites in Raleigh County, West Virginia, USA, 2004-2005.

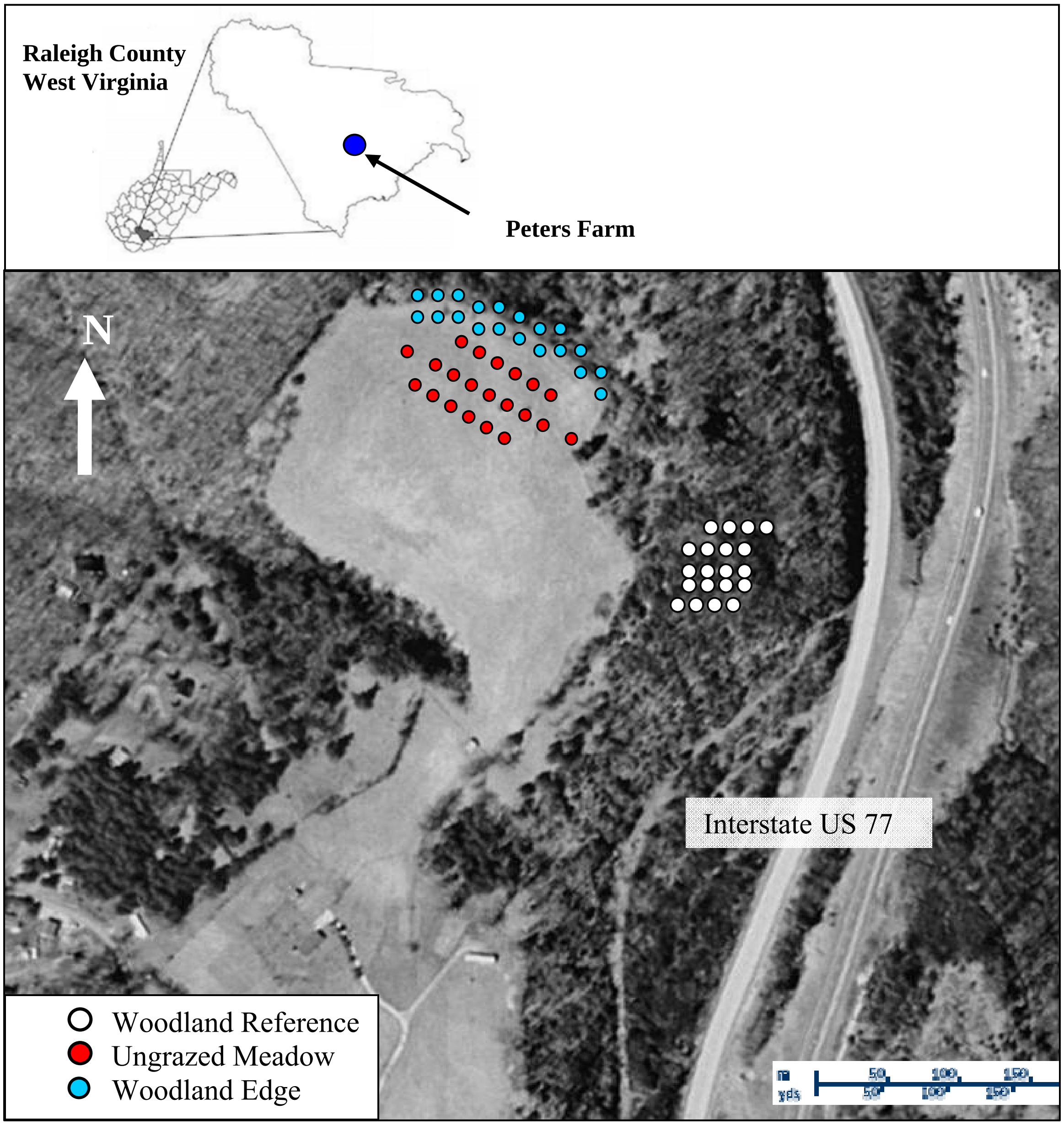

Figure 2. Coverboard placement at the Appalachian Farming Service Research Center Peters experimental farm, 4 km Southwest of Shady Spring, Raleigh County, West Virginia, USA, 2004-2005.

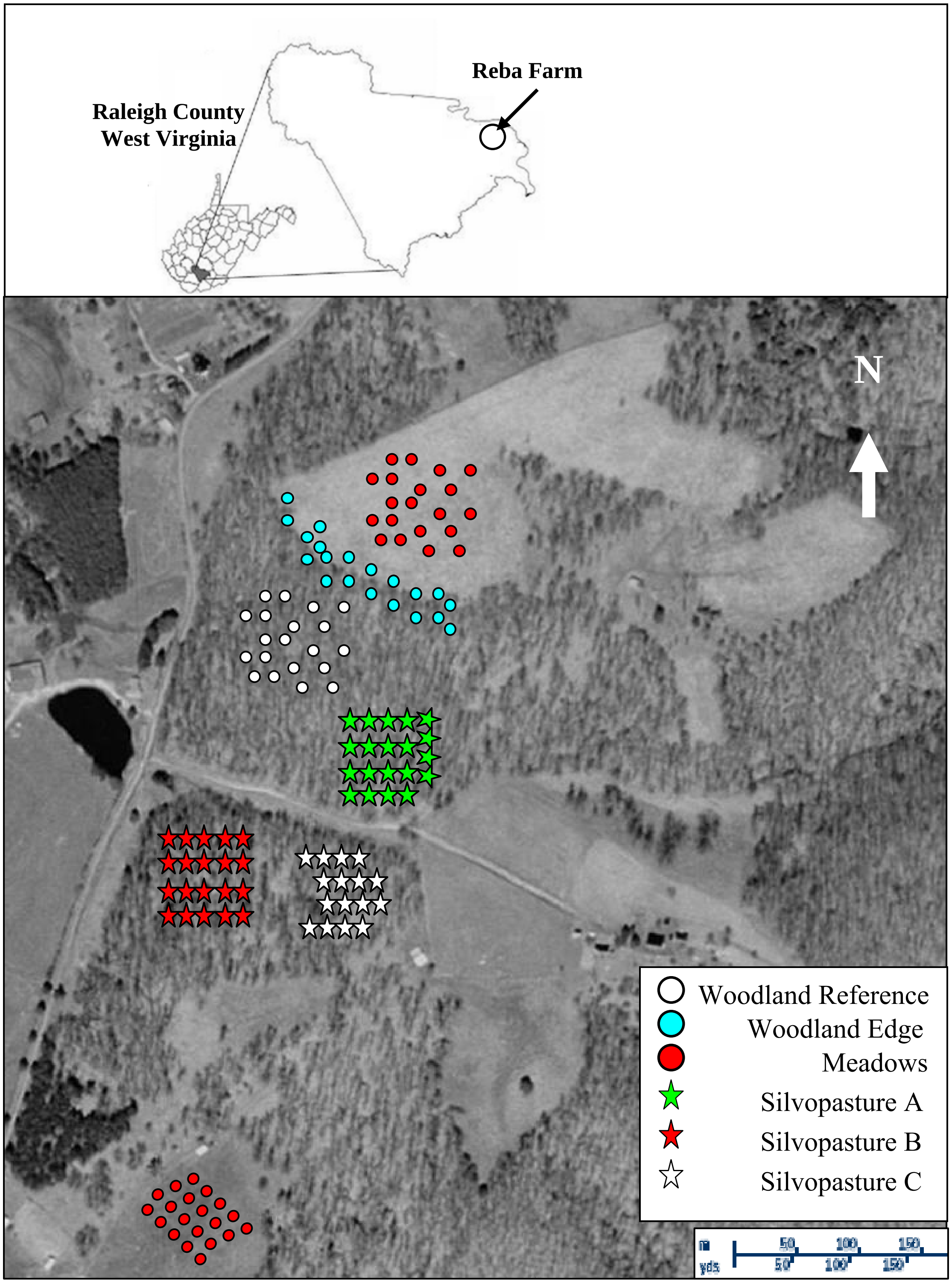

Figure 3. Coverboard placement at the Appalachian Farming Service Research Center Reba experimental farm, 4 km West of Meadow Creek, Raleigh County, West Virginia, USA, 2004-2005.

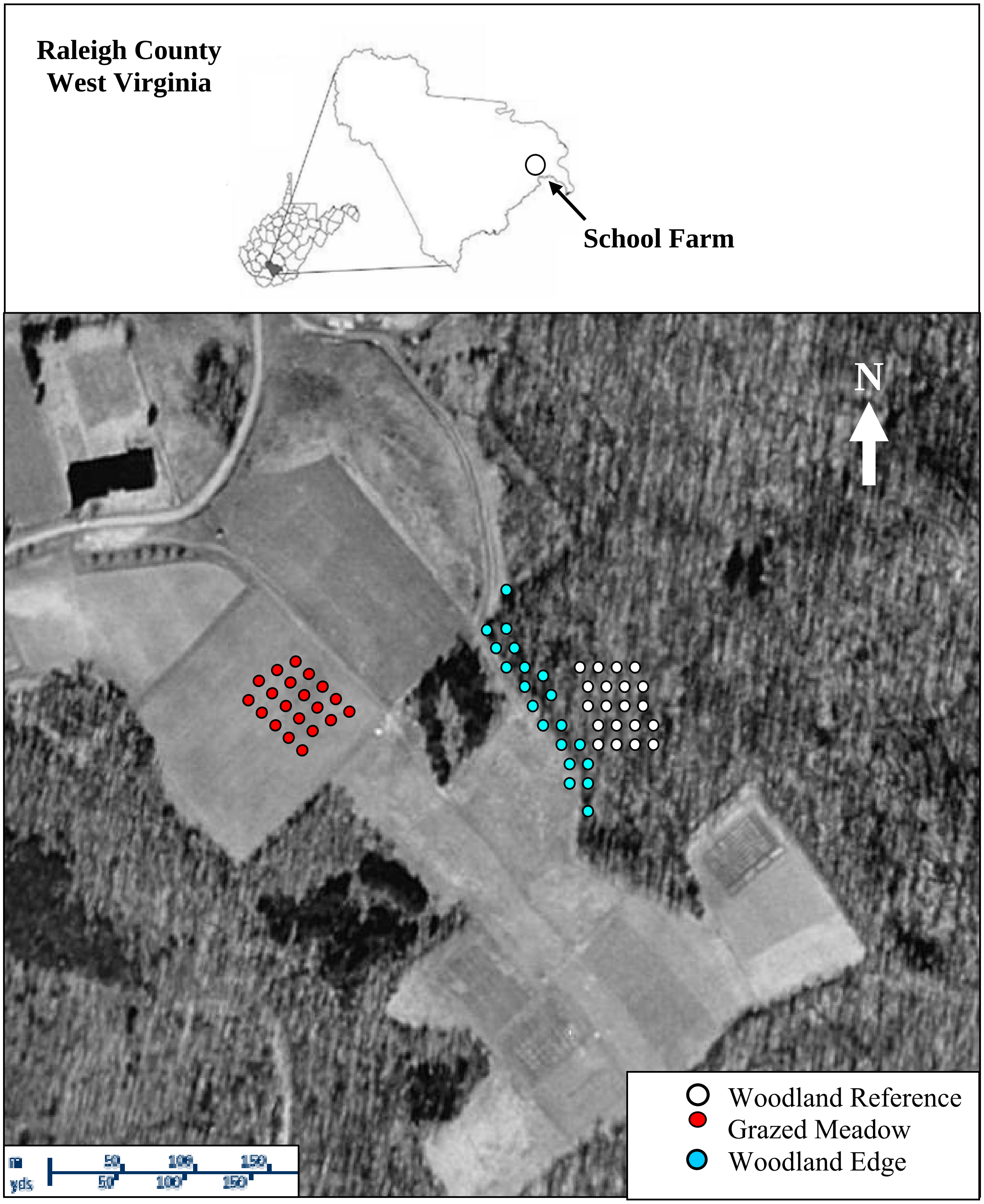

Figure 4. Coverboard placement at the Appalachian Farming Service Research Center School experimental farm, 12 km North East of Shady Spring, Raleigh County, West Virginia, USA, 2004-2005.

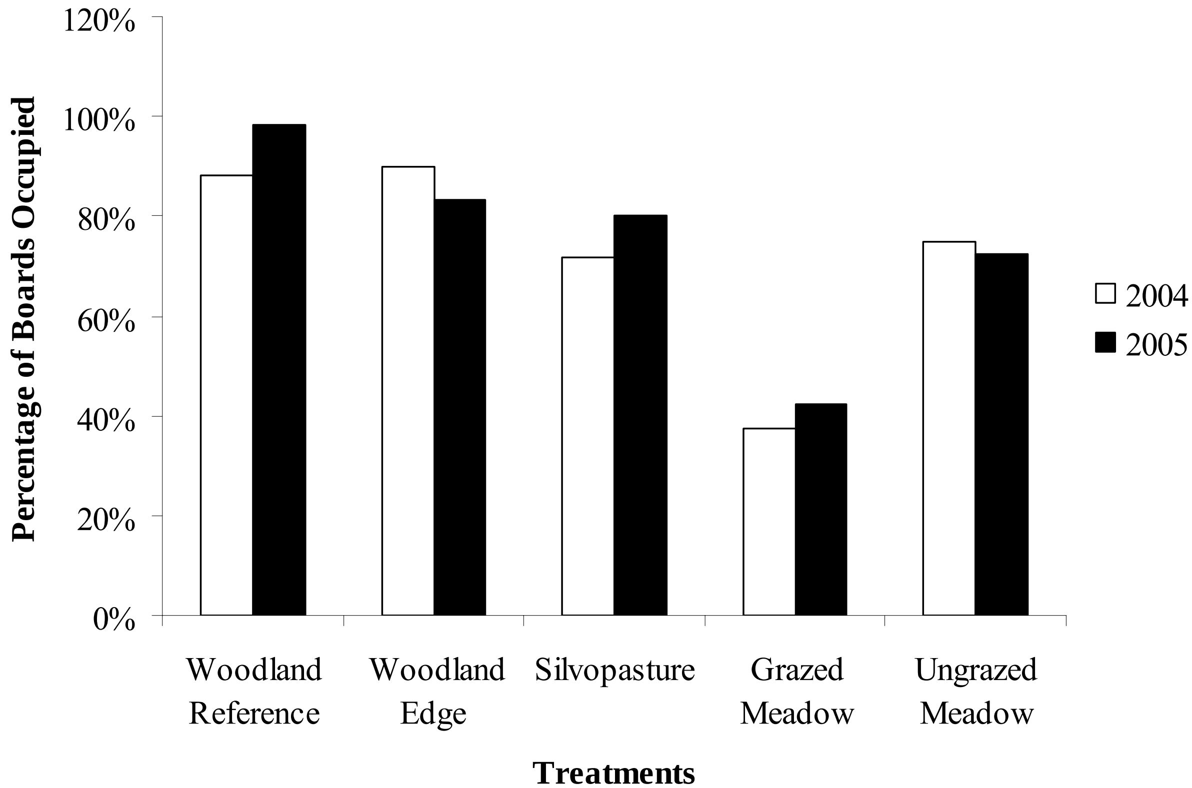

Figure 5. Percentage of coverboards in each treatment occupied by red-backed salamanders on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA, 2004-2005.

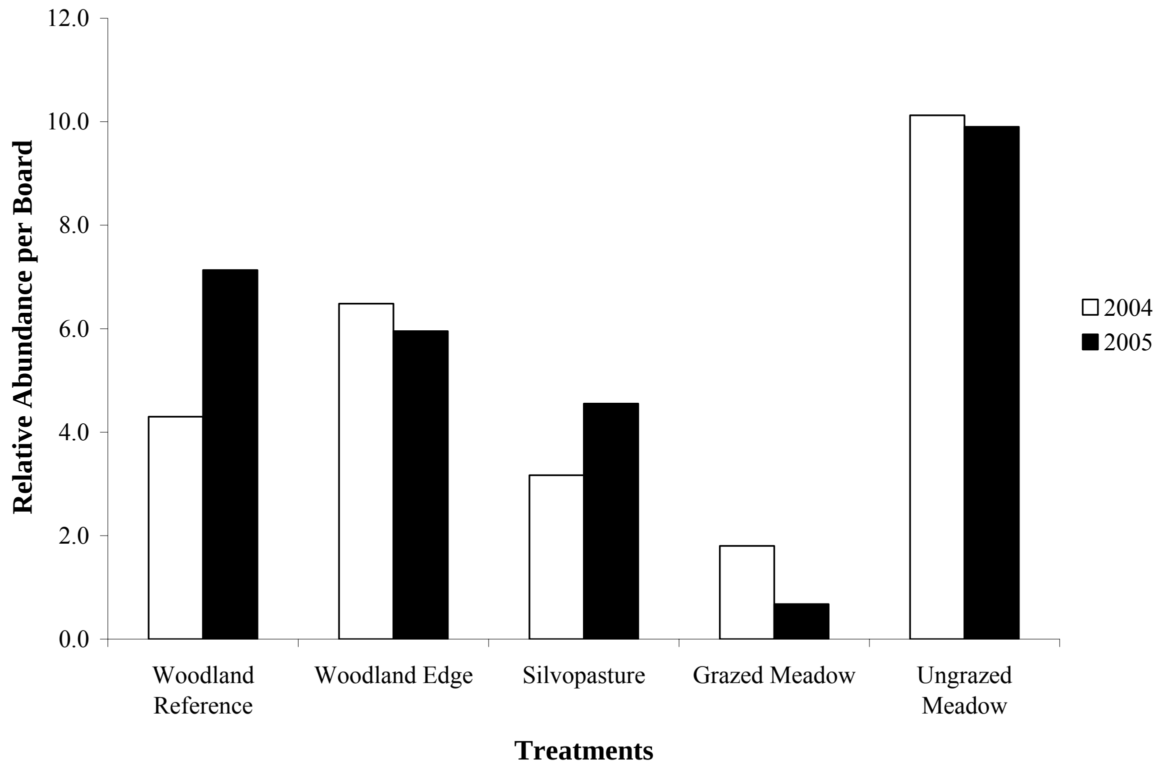

Figure 6. Relative abundance of red-backed salamanders per coverboard by treatment on 3 Appalachian Farming Service Research Center experimental farms in Raleigh County, West Virginia, USA. There were 3 plots for woodland reference, woodland edge, and silvopasture treatments (coverboards = 60) and 2 plots for grazed and ungrazed meadow treatments (coverboards = 40). Coverboards were sampled 19 times in 2004 and 14 times in 2005.