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Research Article

Energetics of Surface-Active Terrestrial Salamanders in Experimentally Harvested Forest

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ABSTRACT Environmental temperatures affect nearly all aspects of ectotherm physiology, including terrestrial salamanders. Therefore, habitat disturbances that alter temperature regimes may interact with physiological processes to affect energy budgets of salamanders or constrain surface activity and possibly lead to changes in population-level parameters. We hypothesized that warmer surface temperatures following harvesting of canopy trees could cause surface-active salamanders to expend more energy for metabolism, potentially leaving a smaller proportion of the energy budget available for reproduction or storage. From 2006 to 2008, we quantified temperature regimes of salamander refugia in a field experiment replicated at 4 sites that included plots subjected to a timber harvest and plots not manipulated during this time period. At each site, we quantified temperature regimes in regenerating forest stands which, approximately 10 years earlier, experienced a range of harvest intensity from shelterwood to silvicultural clearcut. Further, we compared energetic parameters including 1) calories required to maintain homeostasis across an active season, 2) abundance of available potential energy (i.e., invertebrate prey), and 3) a measure of growth and storage (i.e., body condition index) among silvicultural treatments for surface-active salamanders. For surface-active eastern red-backed salamanders (*Plethodon cinereus*), mean calories required for maintenance were approximately 33% greater in recently harvested forest compared to unharvested controls, but body condition was inconsistent among treatments, and invertebrate abundances were similar among treatments but differed by study site. In contrast, we did not detect a treatment effect in any energetic metric 8–14 growing seasons after harvesting. Given that surface-active salamanders in recently harvested forest may be forced to restrain behaviors associated with foraging and mating or trade-off growth or reproduction for increased basic maintenance costs, energetics may be an important but overlooked short-term contributor to observed changes in abundances, reproductive demography, or surface activities after timber harvesting. Managing for both the rapid recovery of understory vegetation and retention of large stumps and logs may help mitigate warming of microclimate for salamanders and should be considered further. © 2011 The Wildlife Society.

KEY WORDS body condition, disturbance, energetics, forest harvesting, invertebrates, *Plethodon cinereus*, red-backed salamander, salamander, silviculture.

Terrestrial salamanders have experienced long-term declines in abundance (Petranka et al. 1993, Ash 1997, Dupuis and Bunnell 1999, Reichenbach and Sattler 2007, Homyack and Haas 2009) and negative changes related to reproductive demography (Dupuis and Bunnell 1999, Ash et al. 2003, Homyack and Haas 2009) associated with timber harvesting in eastern North America. Greater than 60 years may be necessary for populations to recover to pre-disturbance sizes following harvesting in Appalachian forest (Petranka et al. 1993, Homyack and Haas 2009). Researchers suggest that populations decline after timber harvesting because habitat conditions deteriorate and 1) salamanders disperse from unsuitable conditions to nearby habitat (evacuation hypothesis), 2) salamanders retreat belowground and persist until surface habitats recover (retreat hypothesis), or 3) salamanders die from a lack of prey or desiccation (mortality hypothesis; Ash and Bruce 1994; deMaynadier and Hunter 1995; Semlitsch et al. 2008, 2009). These hypotheses focus on dying or dispersing (either vertically or horizontally) individuals. However, little research has examined how changes to habitat may alter physiological or ecological processes that might cause the reported negative effects to fecundity or altered reproductive demography of salamanders remaining after harvesting, including proximate causes for vertical or lateral dispersal (deMaynadier and Hunter 1998, Ash et al. 2003, Welsh et al. 2008, Homyack and Haas 2009, Semlitsch et al. 2009).

Timber harvesting may reduce habitat suitability for terrestrial salamanders that persist in disturbed habitats because of changes to the microclimate, near-ground forest structure,

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and potential prey. After removal of canopy trees, soil and surface temperatures increase and soil surface moisture decreases as more sunlight and wind reaches the forest floor (Liechty et al. 1992, Chen et al. 1999, Harpole and Haas 1999, Zheng et al. 2000, Brooks and Kyker-Snowman 2008). In addition, microhabitat features important to foraging, thermoregulation, and reproduction, including abundant leaf litter and large, decayed coarse woody debris, often are lacking or are re-distributed soon after harvesting (deMaynadier and Hunter 1995, Harpole and Haas 1999, Reichenbach and Sattler 2007, Homyack 2009). As cutaneous respirators, plethodontid salamanders require cool and moist conditions for oxygen exchange and brooding eggs. At higher temperatures, their digestive efficiency decreases but energetic demands increase (Merchant 1970, Bobka et al. 1981, Homyack et al. 2010*a*). Therefore, the physiological limits of salamanders may be challenged by changes to microclimate and forest structure coupled with potential decreases to abundance of or quality of invertebrate prey caused by removal of forest products (Mitchell et al. 1996, Harpole and Haas 1999, Willet 2001, Kluber et al. 2009).

A plausible but mostly unexamined explanation linking altered demography and slow recovery of salamander populations to post-harvesting changes in habitat is modification of energy budgets. Put simply, an organism allocates energy to 4 components of an energy budget: maintenance, growth, reproduction, and storage. Differential allocation of energy among those components by an organism has fitness consequences that can be expressed in population demographics (Congdon et al. 1982, Spotila and Standora 1985, Sears 2005). Changes to microclimate, habitat, and prey that occur with timber harvesting could influence energy budgets of salamanders in a variety of ways. For example, increases in environmental temperatures affect nearly all physiological processes of salamanders, as they are ectothermic poikilotherms (Gatten et al. 1992, Rome et al. 1992). Maintenance costs increase with temperature and can account for >85% of an overall energy budget for ectotherms (Merchant 1970, Burton and Likens 1975, Congdon et al. 1982, Spotila and Standora 1985, Gatten et al. 1992). Basic maintenance costs can be estimated by the standard metabolic rate (SMR). Therefore, higher metabolic rates of salamanders resulting from warmer temperatures in harvested forest could cause individuals to 1) maintain the amount of total energy expended, but allocate less energy to growth, reproduction, or storage because basic maintenance costs increased (Congdon et al. 1982, Sears 2005, DuRant et al. 2007, Moore and Hopkins 2009) or 2) increase total energy expenditure, but maintain proportional allocations among competing functions. The latter option requires that salamanders acquire and assimilate more energy from their environment, which might increase predation risks and will depend on per capita resource availability. Over time, chronic changes to energy budgets could alter population dynamics through slower growth, reduced reproduction, or lower individual survival (Sears 2005).

Energetic metrics can provide powerful insights into why an animal selects and uses a particular habitat or why a particular habitat may be of higher quality (Buskirk and Millspaugh 2006, Homyack 2010). Our goal was to evaluate the energetic response of surface-active terrestrial salamanders to several types of timber harvesting as a potential contributor to observed patterns in abundance and demographics. First, we quantified the thermal profile of salamander refugia and modeled total basic maintenance costs for salamanders among silvicultural treatments. Second, we determined whether invertebrate prey (i.e., available energy) varied across treatments. Third, we compared an index of energy storage and growth for salamanders across treatments. We evaluated our predictions that salamanders in harvested forest had increased maintenance costs, decreased abundance of prey resources, and decreased allocation of energy to growth or storage.

STUDY AREA

Our study area included 4 sites in Virginia and West Virginia and was part of a larger investigation of the long-term effects of oak regeneration methods on biodiversity, the Southern Appalachian Silviculture and Biodiversity (SASAB) project (Homyack 2009). We established study sites (blocks) within the Ridge and Valley and the Cumberland Plateau physiographic provinces in the Jefferson National Forest, Virginia (BB1, BB2), and the Mead-Westvaco Corporation's Wildlife and Ecosystem Research Forest (purchased by Penn-Virginia Corporation in 2007), West Virginia (WV1, WV2; Belote et al. 2008). Oaks (*Quercus* spp.) dominated the overstory forest canopy and sites included smaller components of red maple (*Acer rubrum*), yellow-poplar (*Liriodendron tulipifera*), American beech (*Fagus grandifolia*), and sourwood (*Oxydendron arboretum*; Wender 2000). Elevation of sites ranged from 710 m to 1,006 m, aspect ranged from 129° to 270°, pre-treatment basal area ranged from 25.5 m^2/ha to 35.2 m^2/ha, and site index for white oak (*Q. alba*) ranged from 22 m to 24 m at 50 years (Homyack 2009). Soils were typical of the Appalachian region; they were sandstone or shale derived, rocky and well-drained, and generally ranged from 0.4 m to 1.0 m depth to bedrock (Wender 2000).

Silvicultural treatments were applied randomly to 2-ha plots (experimental units, or EUs) and included a 1) a control where no silvicultural disturbance occurred, 2) shelterwood harvest where an initial partial harvest reduced overstory basal area by 41% and 12–14 m^2/ha of dominant or co-dominant stems were retained, 3) leave-tree harvest where a partial harvest created a 2-aged stand by reducing overstory basal area by 72% and retaining 4–7 m^2/ha of trees with 5–25 cm dbh and dispersed trees evenly within EUs, and 4) silvicultural clearcut where all stems >5 cm diameter at breast height (dbh) were harvested. Unmerchantable stems were felled and left on site. Treatments were applied to EUs from 1994 to 1998. At 4 years post-harvesting, soil temperatures at 2.5 cm and 10 cm depth were 4.4° C and 1.9° C higher, respectively, in silvicultural clearcuts than unharvested controls at the BB sites, confirming that tree canopy removal results in warmer soils (Knapp 1999).

A second overstory removal harvest (hereafter ORH) occurred in shelterwood EUs at BB1 and BB2 in winter 2007–2008 after 12–13 years of forest regeneration had occurred. During this entry, commercial loggers removed remaining overstory trees with chainsaws and skidders to release advanced regeneration of saplings, with approximately 6 m^2/ha basal area retained. These recently harvested plots were sampled in 2008 and represented immediate effects of forest harvesting. We intended for the ORH to occur at all sites, but changes in land ownership prevented treatment application at WV1 and WV2. This study design allowed us to examine a temporal gradient by quantifying energetics of salamanders in EUs directly following a harvest (the ORH in 2008) and 8–14 years following a disturbance (all other EUs, 2006–2008). Additional details about study sites and silvicultural treatments are provided by Knapp et al. (2003), Belote et al. (2008), Homyack (2009), and Homyack and Haas (2009).

METHODS

Temperature Regimes of Salamander Refugia

We investigated salamander energetics 8–14 years after timber harvesting, after recovery of some vegetation, microclimate, and salamander abundances occurred (Homyack and Haas 2009). Additionally, we investigated salamander energetics for the growing season immediately following a stand re-entry in a shelterwood system. For our model species, we investigated energetics of eastern red-backed salamanders (*Plethodon cinereus*), a small lungless species that can be abundant in eastern deciduous forest (Burton and Likens 1975) and was the most commonly captured species in our study area (Homyack and Haas 2009).

Terrestrial plethodontid salamanders are only active on the surface during a narrow range of cool and moist conditions (Jaeger 1980*a*). However, terrestrial salamanders spend considerable time under refugia, such as logs or rocks to maintain thermal and water balances (Jaeger 1980*b*, Keen 1984), to access to the leaf litter during foraging attempts (Jaeger et al. 1995*a*), to access potential mates during courtship (Jaeger et al. 1995*b*), or to brood eggs. Because refugia are linked to salamander life history requirements and artificial refugia (i.e., coverboards) were regularly used by terrestrial salamanders in our study area (Harpole and Haas 1999, Knapp 1999, Williams 2003, Kelly 2005), coverboards were an appropriate substrate for modeling energetic costs of salamanders among silvicultural treatments.

We monitored artificial salamander refugia with 5 coverboards per EU ($n = 20$ boards/site) that we installed March–April 2006 and left in place for the duration of the study. Following the ORH, coverboards disturbed by timber harvesting equipment were returned to their approximate original location. We installed 20-cm × 60-cm × 5-cm rough-cut yellow-poplar boards near transects that we used for night-time area-constrained salamander searches at plot corners and the center transect of the sampling grid (Knapp et al. 2003; Fig. 1). We selected coverboard dimensions based on previous success in detecting salamanders by earlier researchers on our study sites (Knapp 1999). We displaced leaf litter and installed boards where microtopography was minimal and the surface of the board was in contact with the O-soil-horizon. We placed coverboards

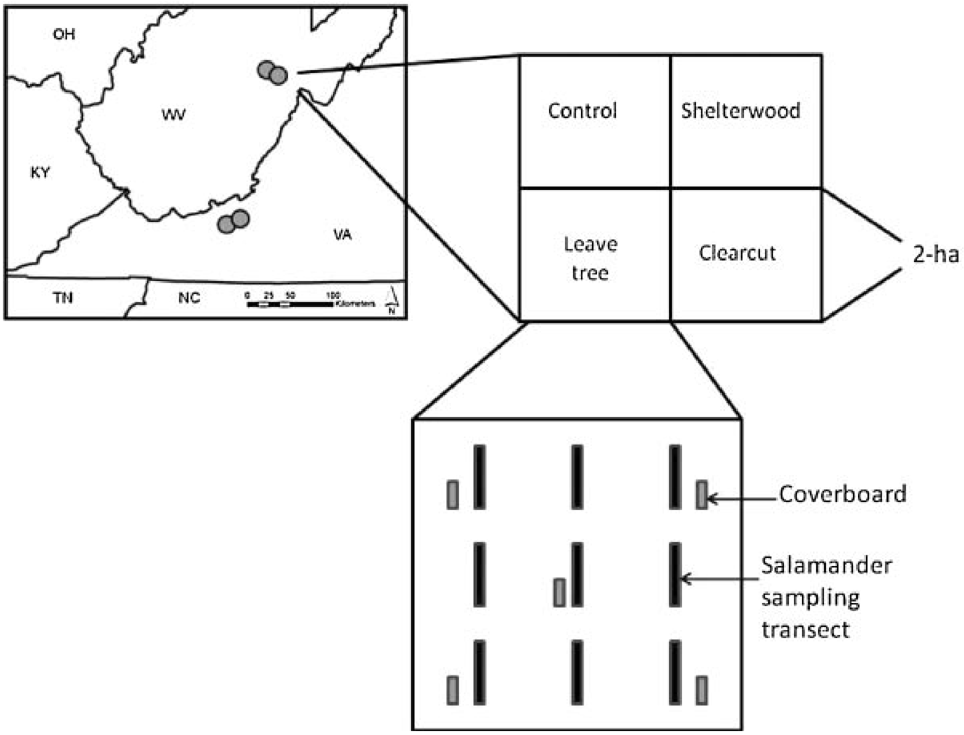

Figure 1. Study site locations and sampling design for quantifying the effects of silvicultural treatments on bioenergetics of surface-active terrestrial salamanders. We quantified temperature regimes under 5 coverboards/plot during spring-fall 2006–2008 at 4 study sites in Virginia and West Virginia, USA. Figure not to scale.

approximately 2 m from a salamander sampling transect but >28 m from the edge of EUs. We used coverboards rather than natural cover objects to standardize the surface area touching the forest floor, moisture content of wood, and decay class, which can vary among natural woody debris (Fraver et al. 2002).

Terrestrial salamanders act as nearly perfect poikilotherms with body temperatures closely following the substrate temperatures that they contact (Feder 1983). Thus, we quantified temperatures at the interface of the refugia and soil surface with small data loggers (Ibutton DS1921G; Dallas Semiconductor, Sunnyvale, CA) placed under the center of coverboards ($n = 80$) to estimate the body temperature of salamanders. We programmed data loggers to record temperatures simultaneously across all EUs every 90 min from 10 May to 15 September 2006 and every 120 min 1 May to 18 October 2007 and 5 May to 9 October 2008. Based on our $\geq$15 years of sampling salamanders, these periods encompass the surface-active period during which salamanders are most likely to experience high temperatures and include important periods for foraging and breeding. In 2006, we placed a datalogger on top of the leaf litter near the center of each EU at BB1 to record ambient air temperature. We averaged temperatures across subsamples within an EU to develop an average seasonal temperature profile for each treatment plot at the 4 study sites during each year. For sites with the ORH (BB1, BB2), we quantified temperature profiles in shelterwood EUs for 2 years prior to (2006, 2007) and 1 year after (2008) the second harvest. We compared the proportion of total temperatures quantified at an EU within the preferred range of temperatures (16.0–21.0° C) for eastern red-backed salamanders (Spotila 1972, Feder and Pough 1975). For each year, we ranked proportions and conducted a 2-way analysis of variance (ANOVA) on the ranked data with silvicultural treatment and site as factors.

Quantifying Energetic Costs to Salamanders

To determine whether the amount of energy required for basic maintenance differed for a salamander among silvicultural treatments, we translated seasonal temperature profiles into energy output with the functional equation described by Homyack et al. (2010*a*) for metabolism of eastern red-backed salamanders. Although estimating field metabolic rates of salamanders would have been preferable, standard methods such as doubly labeled water cannot be used for species like salamanders with high body water turnover (Butler et al. 2004).

We converted temperatures in the seasonal microclimate profiles to an estimate of total ml O_2 consumed per gram with a mathematical model describing the influence of temperature and body size on the standard metabolic rate (SMR) of red-backed salamanders [$\log_e(\text{SMR}) = 0.102\ (\text{temperature}) + 0.681(\log_e(\text{bodymass}) - 4.849)$] (Homyack et al. 2010*a*).

We standardized each temperature sampled from refugia for a 1-g salamander and converted it to a measure of basic maintenance costs, creating curves of energy expenditure through time for an average adult salamander. Next, we calculated the area under the curve for each treatment × site combination to quantify the basic maintenance costs to a red-backed salamander for an active season to understand how seemingly insignificant but chronic increases in temperatures could sum to considerable increases in energy requirements over longer time periods. We converted the volume of O_2 required for SMR in an active season to calories per gram by multiplying by 4.86 (Schmidt-Nielsen 1990), which produced a biologically meaningful estimate that could be incorporated into future energetic models (Dorcas et al. 2004). Because our caloric estimate is based on measures of SMR, it included energy to maintain homeostasis, but excluded energy used for digestion, movements, or other behaviors. However, maintenance costs generally account for most of an ectotherm's energy budget (Burton and Likens 1975, Congdon et al. 1982), so we assumed it represented a large proportion of plethodontid salamanders' total energy requirements.

To examine effects of the $\geq$8-year-old harvests or the recent ORH, we determined whether estimated caloric expenditures of salamanders differed among silvicultural treatments with a 2-way ANOVA (control, shelterwood, leave tree, silvicultural clearcut, ORH) blocked by site (BB1, BB2, WV1, WV2). We conducted year-specific ANOVAs because we included the ORH in 2008 and because our sampling periods differed slightly among years. When we detected significant differences, we compared means with Bonferroni adjusted P values. Prior to analysis, we evaluated data with normal probability plots and modified Levene's tests and log-transformed data that failed to conform to the assumptions of ANOVA (Neter et al. 1996).

Effects of Forest Disturbance on Invertebrate Prey

Terrestrial salamanders are euryphagic predators that consume a wide array of detrital invertebrates (Jaeger 1972, Fraser 1976, Maglia 1996, Homyack et al. 2010*b*). Invertebrates sampled from leaf litter were representative of prey consumed by eastern red-backed salamanders in a companion study examining use and availability of invertebrates (Homyack et al. 2010*b*). Thus, we quantified relative abundances of invertebrates from leaf litter adjacent to coverboards 3 times per sampling season (2 times for coverboards in WV1 and WV2 during 2006) as a measure of potential available energy. During litter sampling events we collected a small (<20 g) litter sample adjacent to each coverboard, transported samples to the laboratory in individual, sealed plastic bags, weighed them, and placed litter in Berlese funnels for 48 hr. We collected litter samples from all treatments within a site within 3 hr, so that samples were subjected to similar climatic conditions. We stored invertebrates in 70% ethyl alcohol and sorted them to group (i.e., mites, springtails, spiders, larvae [dipterans, lepidopterans, and coleopterans], ants, adult dipterans, centipedes, proturans, roaches, pseudoscorpions, millipedes, snails, bees, other hymenopterans, moths, crickets, beetles, or unknown). We converted counts of invertebrates to abundance per gram of wet weight of leaf litter and averaged this measure of relative abundance within a sampling season. We analyzed abundances of invertebrates rather than biomass because converting numbers to mass from overly generalized regressions is known to be highly biased for many invertebrate taxa (Hodar 1996).

We compared differences in invertebrate abundances among treatments with multivariate analysis of variance (MANOVA), testing for effects of treatment (control, shelterwood, leave tree, silvicultural clearcut, and recent ORH) and site (BB1, BB2, WV1, WV2) on relative abundance of invertebrate groups. We included only those groups whose abundances made up >2% of total numbers. We conducted MANOVAs separately by year because we sampled the ORH only at 2 of 4 sites in 2008. When a MANOVA was significant, we examined individual variables to determine which invertebrate taxa differed (Johnson 1998). Secondly, we determined whether the summed total abundance of invertebrates differed among treatments or sites with year-specific 2-way ANOVAs. We examined normality and homogeneity of variance for invertebrate abundances with normal probability plots and modified Levene's tests, and we log transformed any variables that failed to conform to parametric assumptions.

Effects of Forest Disturbance on Body Condition of Salamanders

We examined body condition of eastern red-backed salamanders as an index to individual energetic state (deMaynadier and Hunter 1995). We captured and measured salamanders on a 3 × 3 grid of salamander sampling transects at EUs each year of this study (2006–2008). On warm (>7° C) rainy nights April–November, 2–3 observers conducted area-constrained searches for surface-active salamanders on one randomly selected transect (2 m × 15 m in size) per EU. We marked the location of each capture with individually numbered pin flags and transported salamanders to the lab where we weighed them to the nearest 0.01 g. We also measured snout-vent length (SVL) to the posterior edge of the vent and tail length (TL) from the posterior edge of the vent to the tip of the tail with dial calipers. We summed the 2 lengths to obtain estimates of total length (TOTL) (Welsh et al. 2008). We included tails in our measure of body condition because they are a lipid storage site for salamanders, which can be important for reproduction and metabolic maintenance (Fitzpatrick 1976, Maiorana 1977). Salamanders were fully hydrated when weighed, as they were housed in plastic bags with wet leaves for 6–12 hr prior to measurements. We excluded gravid female salamanders as determined by candling (Gillette and Peterson 2001). We returned salamanders to their point of capture within 24 hr. Additional details regarding methods to capture and measure salamanders are provided by Homyack and Haas (2009).

We used least squares regression of log-transformed mass on log-transformed TOTL as an index to the amount of energy reserves when accounting for body size (Schulte-Hostedde et al. 2005, Welsh et al. 2008). Using this technique, we considered salamanders with a positive residual to be in "good" body condition and individuals with a negative residual to be in "poor" body condition (Welsh et al. 2008). Due to small sample sizes, we pooled data across 2006–2008, but examined them for treatment effects separately by site to reflect potential differences in resource availability across our broad study area. For BB1 and BB2, we considered the ORH a fifth treatment. We conducted a one-way ANOVA on ranked residuals corrected for ties to determine if mean body condition of salamanders differed among treatments (Welsh et al. 2008). We conducted analyses with SAS 9.2 (SAS Institute, Inc., Cary, NC). All animal capture and handling procedures were approved by the Institutional Animal Care and Use Committee at Virginia Tech (IACUC no. 06-049-FIW) and we obtained appropriate state permits.

RESULTS

Effects of Forest Disturbance on Energy Budgets

Across 3 years of sampling, we logged 477,920 temperatures under coverboards. Temperatures at the soil refugia interface rarely (3 of 477,920 temperatures) exceeded the mean critical thermal maximum for red-backed salamanders of 34.6° C (Spotila 1972). In general, temperatures were greatest in the ORH, and they reached their highest values during July–August (Appendices A and B, Fig. 2a,b). Mean maximum and minimum temperatures during 2008 were 2.5° C warmer in the ORH than control EUs at BB1 and BB2. The proportion of temperatures at the preferred range (16–21° C) for red-backed salamanders (Spotila 1972, Feder and Pough 1975) differed among sites in all years ($P < 0.05$) with BB1 and BB2 having, on average, 19–24% more temperatures within the preferred range compared to WV1 and WV2, which were cooler. We detected a treatment effect in 2008 ($F_{4,\,12} = 4.45$, $P = 0.035$) when preferred temperatures occurred 12–18% less often in the ORH compared to the control EUs ($P = 0.049$). Ambient air temperatures were highly and positively correlated ($R \geq 0.828$, $P < 0.001$) with temperatures under adjacent coverboards across all silvicultural treatments at BB1.

Using our field-measured temperatures, we estimated that basic maintenance requirements ranged from 644 to 1,070 calories per active season for a 1.0-g red-backed salamander. We detected a treatment effect on the energy required for basic maintenance (Figs. 3 and 4) in 2008 ($F_{4,\,12} = 43.70$, $P < 0.001$), with the ORH having greater caloric requirements than all other treatments. Approximately 347 more calories were required by salamanders in ORH compared to control EUs, but the other silvicultural treatments did not differ from one another ($P > 0.78$, Fig. 3). In contrast, we did not detect a treatment effect on total number of calories prior to implementation of the ORH when we compared silvicultural treatments in 2006 ($F_{3,\,12} = 2.05$, $P = 0.178$) and 2007 ($F_{3,\,12} = 0.51$, $P = 0.683$).

We detected a significant site effect on the total number of calories expended for basic maintenance costs in all years (2006, $F_{3,\,12} = 93.84$, $P < 0.001$; 2007, $F_{3,\,12} = 15.32$, $P < 0.007$; 2008, $F_{3,\,12} = 94.11$, $P < 0.001$), with more calories required by salamanders in the Virginia sites compared to the West Virginia sites. Approximately 127, 123, and 204 more calories were required by a 1.0-g red-backed salamander at the Virginia sites compared to the West Virginia sites in 2006, 2007, and 2008, respectively.

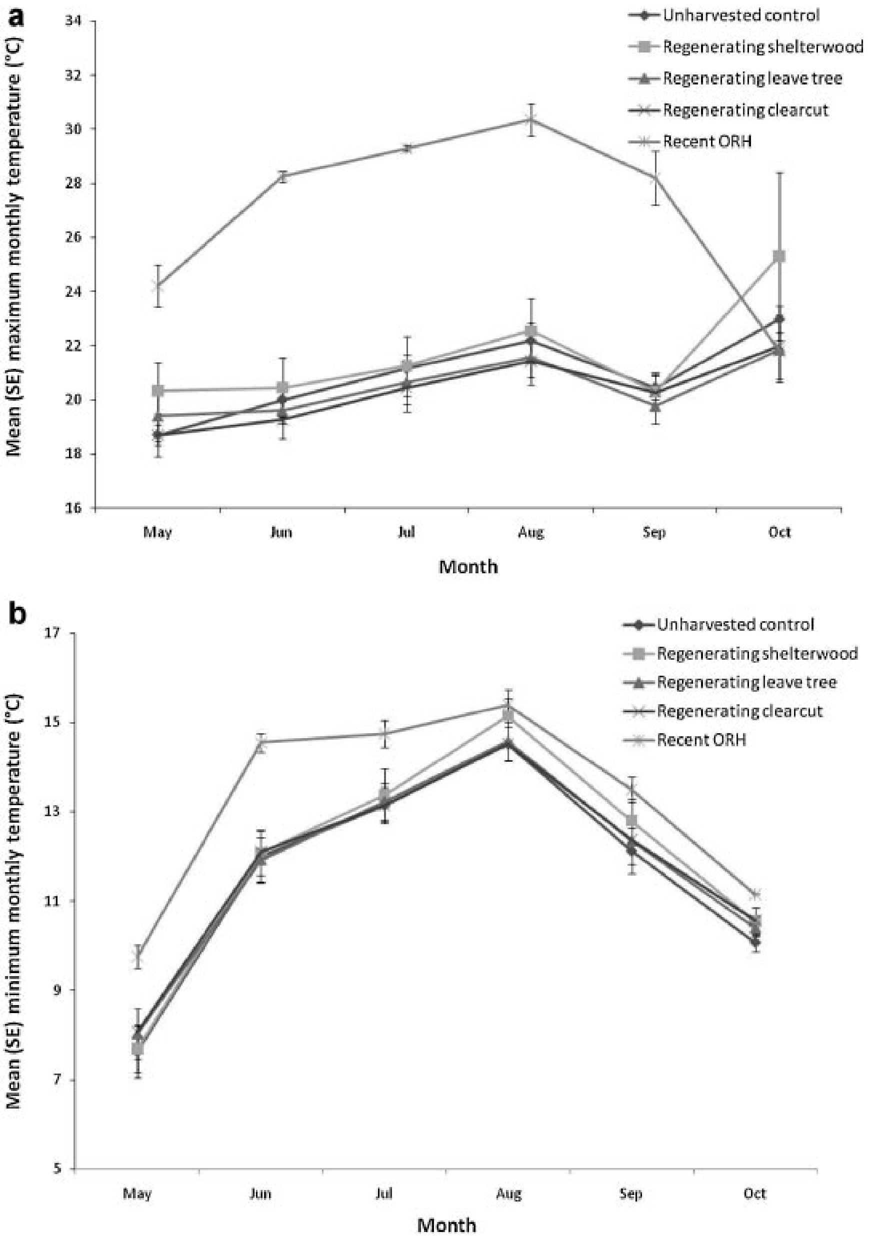

Figure 2. Mean maximum (SE) (a) and mean minimum (SE) (b) monthly temperatures quantified under coverboards averaged across 4 study sites in Virginia ($n = 2$) and West Virginia ($n = 2$) in 2008. Prior to the 2008 season, the shelterwood plots ($n = 2$) were subjected to an overstory removal harvest (ORH).

Effects of Silvicultural Treatments on Invertebrate Prey

We sorted and identified 13,967 invertebrates collected from leaf litter to taxonomic groups. Of those, 61.5% were mites, 28.8% were Collembola, 3.8% were lepidopteran, dipteran, or coleopteran larvae, 2.6% were ants, and 2.1% were spiders. Adult dipterans, centipedes, proturans, roaches, pseudoscorpians, millipedes, snails, bees, other hymenopterans, moths, crickets, beetles, and unknown invertebrates each accounted for $\leq$1% of the total.

The omnibus test of multivariate comparisons of relative abundance (invertebrates/g leaf litter) was significant for 2006 due to a site effect (Wilks' $\lambda = 0.002$, $F_{18,\,12} = 4.92$, $P = 0.004$), but not for the separate 2007 MANOVA (Wilks' $\lambda = 0.076$, $F_{18,\,12} = 0.98$, $P = 0.532$) or the separate 2008 MANOVA (Wilks' $\lambda = 0.015$, $F_{18,\,9} = 1.72$, $P = 0.204$). Despite the significant MANOVA for 2006, we did not detect an effect of silvicultural treatment on multivariate comparisons of invertebrates (i.e., MANOVA) in 2006 ($P > 0.05$) or on total numbers of invertebrates (i.e., from the ANOVA) in any year (2006, $F_{3,\,12} = 2.60$, $P = 0.117$; 2007, $F_{3,\,12} = 0.30$, $P = 0.822$; 2008, $F_{4,\,11} = 1.53$, $P = 0.283$). Thus, no measure of invertebrate abundance differed among treatments, including after the ORH in any year. Instead, we detected a site effect for the 2006 MANOVA on the number of Collembola ($F_{3,\,12} = 8.23$, $P = 0.006$) and larvae ($F_{3,\,12} = 3.48$, $P = 0.046$), but no effects of site in 2007 or 2008. Site BB1 had a greater abundance of Collembola than the BB2, WV1, or WV2 sites, and BB2 had a greater abundance of larvae than either WV1 or WV2. We did not detect a site effect on the summed total number of invertebrates in 2006 or 2007 from the ANOVA. However, in 2008 the ANOVA

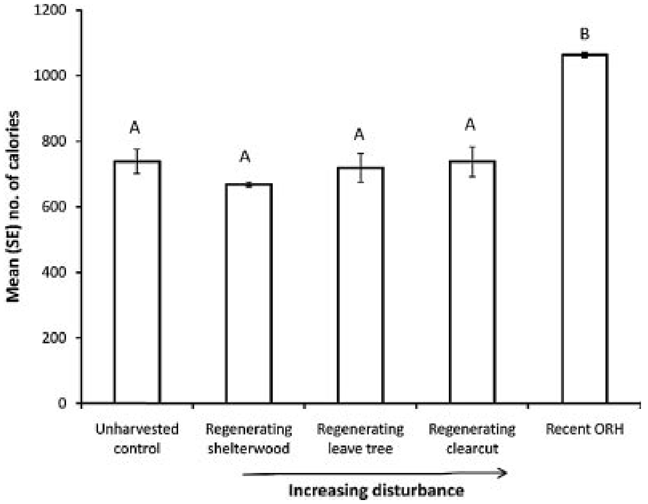

Figure 3. Mean (SE) number of calories required for the standard metabolic rate of a 1.0-g eastern red-backed salamander across a season (May–Oct) in 5 silvicultural treatments as estimated from temperature regimes. Prior to the 2008 season, the shelterwood plots ($n = 2$) were subjected to an overstory removal harvest (ORH). Different letters indicate statistical differences among treatments (Analysis of Variance, $P < 0.05$).

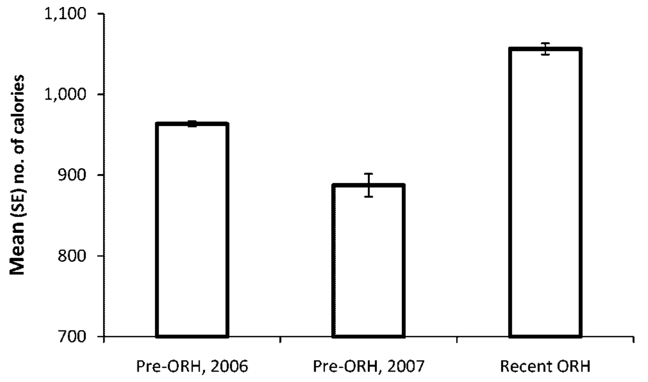

Figure 4. Mean (SE) number of calories required for the standard metabolic rate of a 1.0-g eastern red-backed salamander across a season (May–Oct) 2 years prior and 1 year after an overstory removal harvest (ORH) at 2 experimentally harvested sites, Virginia.

was significant ($F_{3,\,12} = 9.74$, $P = 0.005$), with the WV1 and WV2 having fewer total invertebrates than BB1 or BB2 ($P < 0.05$).

Effects of Forest Disturbance on Abundance and Body Condition of Salamanders

We analyzed body condition of 534 red-backed salamanders (excluding 30 gravid females; Table 1). Similar to results from long-term analyses of salamander relative abundances among silvicultural treatments (Homyack and Haas 2009), control EUs accounted for most red-backed salamander captures; 58% of captures were in control EUs, 9% were in shelterwood EUs, 13% were in leave tree EUs, 16% were in clearcut EUs, and 2% were in ORH EUs. Based on analysis of residuals, body conditions of salamanders differed among treatments at BB2 ($F_{4,\,104} = 2.67, P = 0.036$). Post-hoc comparisons indicated that red-backed salamanders from the ORH EU had a greater body condition index than salamanders from the shelterwood EU the previous years (i.e., body condition of red-backed salamanders was greater after the second stand entry; $P = 0.029$) and a greater body condition than salamanders in the control plot ($P = 0.049$; Fig. 5). In contrast, we did not detect a treatment effect on body condition of red-backed salamanders at BB1 ($F_{4,\,300} = 2.24$, $P = 0.065$), WV1 ($F_{3,\,67} = 1.06$, $P = 0.374$), or WV2 ($F_{3,\,45} = 0.22$, $P = 0.885$).

DISCUSSION

A repeated-entry to harvest overstory trees in an Appalachian hardwood forest changed the thermal environment by increasing temperatures near the forest floor, but effects were likely short-term because microclimate was not warmer 8–14 years after initial harvest. Consequently, our models suggest that eastern red-backed salamanders that do not die or disperse off-site after forest harvesting would require more calories for basic maintenance costs and face greater energetic challenges or alternatively would reduce surface activity with probable negative consequences to foraging and reproductive behaviors. Although relative abundance of salamanders were lower in ORH EUs, invertebrate prey did not decline in these newly harvested plots, and body condition of salamanders appeared inconsistently affected by the ORH. In contrast, when understory herbaceous and woody vegetation had 8–14 growing seasons to recover from harvesting, temperature regimes, energetic requirements, body condition of salamanders, and invertebrate prey abundances were similar among unharvested and harvested forest treatments. Thus, it appears that considerable recovery occurred across silvicultural treatments when under- and mid-story vegetation had grown and apparently mitigated temperature changes, even after complete overstory removal.

Warming of surface or soil temperatures is a hypothesized mechanism of post-harvesting declines in salamander abundances (Petranka et al. 1993, Harper and Guynn 1999, Brooks and Kyker-Snowman 2008). However, researchers have related direct mortality of salamanders to microclimatic

Table 1. Number of eastern red-backed salamanders captured for analyses of body condition at 4 sites in Virginia and West Virginia, 2006–2008. Regenerating shelterwood, leave tree, and silvicultural clearcut treatments were implemented 8–14 years prior to sampling; recent overstory removal harvest treatments were 1 year old.

Site	Unharvested control	Regenerating shelterwood	Leave tree	Silvicultural clearcut	Recent overstory removal harvest
BB1	194	23	34	46	8
BB2	50	16	14	25	4
WV1	45	3	12	11	
WV2	23	8	12	6	

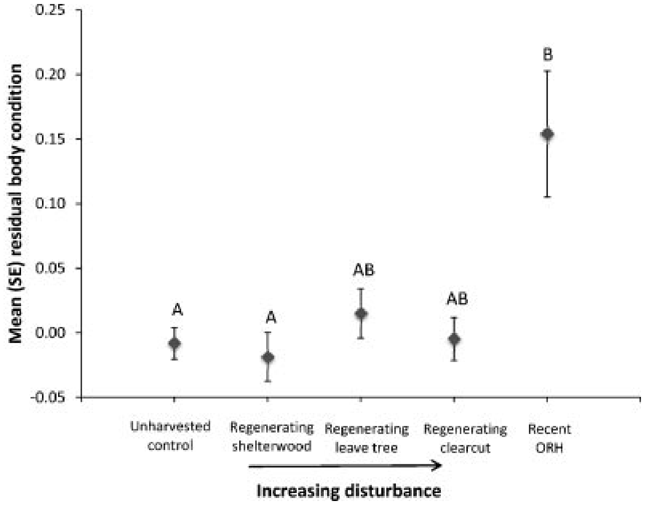

Figure 5. Mean (SE) residuals from a regression of log body mass on log body length as a measure of body condition for eastern red-backed salamanders across a silvicultural disturbance gradient, 2006–2008 at a Virginia study site (BB2). Salamanders with positive residuals have better body condition than those with negative residuals. Different letters indicate statistical differences among treatments (Analysis of Variance, $P < 0.05$).

changes only on limited occasions (Chazal and Niewiarowski 1998, Rothermel and Luhring 2005), and prior studies generally have not focused on the potential for more subtle effects on individuals from increasing temperatures. Assuming other components of the energy budget remained equal, the total amount of calories required for basic maintenance was approximately 33% greater for eastern red-backed salamanders 1 year after ORH than in unharvested forest during the same period. Most research has reported <3° C increases in near-ground temperatures following forest disturbances in eastern North America (Chazal and Niewiarowski 1998, Rothermel and Luhring 2005, Brooks and Kyker-Snowman 2008). Mole salamanders (*Ambystoma talpoideum*) experienced increased desiccation and lower survival in a recent clearcut harvest that was approximately 2.6° C warmer than a control (Rothermel and Luhring 2005). Similarly, our results illustrate how even a 2.5° C increase in temperature from a partial overstory removal could measurably increase metabolic costs or cause altered surface activity of plethodontid salamanders in central Appalachian forests, at least in the short-term. Differences in microclimate were ameliorated by 8–14 years in central Appalachian forest, but timeframes for recovery elsewhere will vary by ecosystem and climate. Complete overstory removal harvests without protection of understory vegetation, such as with some clearcuts, may have even more dramatic effects on near-ground temperatures and salamander energetics and should be a priority for future research.

Changes to maintenance costs can influence rates of growth or reproduction of ectotherms (Sears 2005, DuRant et al. 2007) and may be related to our observations of fewer eggs per gravid female and smaller proportion of juvenile salamanders in harvested treatments on these study sites (Homyack and Haas 2009). In addition to increasing maintenance costs of salamanders, warmer temperatures could decrease the amount of energy assimilated from their prey and further contribute to a negative energy budget (Merchant 1970, Bobka et al. 1981). Red-backed salamanders may be in an energy deficit at 20° C or higher (Merchant 1970), and may need to increase prey consumption to maintain a positive energy balance. In our study, 48% of temperatures >20° C (averaged across subsamples within EUs) were in the ORH during 2008, suggesting this was an energetically costly treatment, at least in the short-term.

Our results provide evidence that habitat disturbance can increase the energy required for basic maintenance costs of surface-active terrestrial salamanders. However, our estimates of maintenance costs assumed that salamanders remained at the interface of the soil and refugia for the entire active season and did not account for changes in moisture. Although examining the influence of moisture on salamander energetics was outside the scope of our project, plethodontids rely on moisture for cutaneous gas exchange (Feder 1983, Feder and Londos 1984). Drying of the soil surface occurs after timber harvest (Harpole and Haas 1999), likely resulting in reduced opportunities for foraging and reproduction and possibly causing mortality of individuals (Rothermel and Luhring 2005, Rittenhouse et al. 2008). Therefore, quantifying the effects of temperature independent of moisture is a simplification of the complex microclimate salamanders encounter in the wild, but our analyses illustrate the trade-offs surface-active salamanders face when allocating energy to competing physiological functions (Congdon et al. 1982).

Additionally, surface-active plethodontid salamanders only represent a portion of the super-population of salamanders that occur below-ground and at the soil–litter interface (Taub 1961; Bailey et al. 2004*a*,*b*; Mazerolle et al. 2007). Our estimates of calories required to support metabolism assumed that salamanders stayed under coverboards for an entire active season, but estimates of detectability from mark-recapture models (Bailey 2004) and field experiments (Taub 1961) indicate this was unlikely. The full range and duration of temperatures that salamanders are exposed to as they move to above- and below-ground habitats during an active season has yet to be quantified, but soil temperatures ≥10 cm depth are warmer after harvesting (Liechty et al. 1992, Harpole and Haas 1999, Knapp 1999), suggesting that even salamanders below-ground could experience effects to energy budgets from removal of canopy trees. Alternatively, salamanders could alter behavior and spend less time at the surface, but this too could have negative consequences by reducing access to invertebrate prey during rain events or reducing reproductive opportunities. Despite some limitations, these data suggest energetics may play a mechanistic role behind smaller salamander populations and reduced fecundity in recently harvested forest.

Although invertebrate abundances did not differ among treatments, forest harvesting reportedly can affect invertebrate abundance and diversity (Huhta 1976, Mitchell et al. 1996, Su and Woods 2001, Willet 2001, Bonham et al. 2002), with potential effects on salamander diets (Mitchell et al. 1996). In California redwood (*Sequoia sempervirens*) forest, abundance of both spiders and arthropods were negatively correlated with the frequency of logging (Willet 2001). Abundance and vertical distribution of invertebrates varied among shelterwood, selection, and clearcut harvested stands, with the greatest proportion of near-ground insects occurring in clearcuts in Maine (Su and Woods 2001). Quality of prey consumed by Peaks of Otter salamanders (*Plethodon hubrichti*) was lower in harvested forest because salamanders ate fewer soft-bodied prey items (Mitchell et al. 1996). A companion study on the diet of eastern red-backed salamanders near the Virginia sites indicated that eastern red-backed salamanders were euryphagic but preferred herbivores (primarily dipteran larvae) over predators or detritivores (e.g., collembolans, mites) and that our methods to sample invertebrates from leaf litter represented taxa consumed by salamanders (Homyack et al. 2010*b*). Our current research suggests that availability of invertebrate prey in leaf litter, including larvae, did not differ among silvicultural treatments (but did vary among study sites). However, because we did not quantify consumption of prey by salamanders (but see Homyack et al. 2010*b*), it is possible that ingestion rates of preferred or high-quality taxa varied with treatments or that detrital invertebrates were not representative of larger prey typically consumed during rainy nights (Jaeger 1978).

Lastly, we predicted that salamanders in control EUs would have larger energy stores than salamanders in harvested forest, as a result of either a lower cost of maintenance (Wieser 1991) or greater prey availability. In contrast, body condition of red-backed salamanders was greater in recently harvested forest at BB2 (Fig. 5), but not at BB1. A better body condition in the ORH EU could have occurred because of decreased competition in marginal habitats (Welsh et al. 2008), because of shifts in diet related to changed prey availability on herbaceous vegetation (Mitchell et al. 1996), because only salamanders with the best body condition were able to remain active on the surface and forage (Knapp et al. 2003), or because surviving salamanders forfeit reproduction to increase body size (Ash et al. 2003). Relative abundances of salamanders were reduced by approximately 50% the first (Homyack 2009) and second year (C. Haas, Virginia Tech, unpublished data) after the ORH, suggesting that competition for resources may have been minimized as populations declined after forest harvesting. However, we only captured a limited number of red-backed salamanders in the ORH EUs (BB1, $n = 8$; BB2, $n = 4$), so our body condition index should be viewed cautiously. Future sampling of the ORH EUs will provide additional evidence to support or refute the link between body condition of salamanders and forest harvesting.

In addition to examining treatment effects, we observed differences in invertebrate abundances and basic maintenance costs across study sites. The Virginia sites were warmer, leading to a greater seasonal energetic requirement for SMR and, invertebrates, including common prey items of red-backed salamanders (e.g., collembolans and dipteran larvae), were more abundant (Homyack et al. 2010*b*). Based on >14 years of monitoring salamanders, terrestrial salamanders are more abundant at the Virginia sites (J. Homyack, Virginia Tech, unpublished data), but the contribution of energetics to this observation is unclear. There are some differences in land use history of the 2 areas. Regional climatic or physiographic differences were thought to contribute to variation in responses and effect-sizes in other amphibian studies (Semlitsch et al. 2009) and highlight the necessity of multi-regional experiments for increasing our understanding of the mechanisms behind population dynamics.

Documenting changes to the use or availability of energy and alterations of growth rates or reproductive output could further link energetics to fitness of plethodontid salamanders after experimental forest disturbance. For example, sagebrush lizards (*Sceloporus graciosus*) from populations with lower resting metabolic rates had 12.5% more energy available for growth (Sears 2005). Monitoring growth rates or field metabolic rates of plethodontid salamanders through time and among silvicultural treatments, including even-aged management regimes, should be future research priorities. Studies of individual growth or reproductive rates may need to use in situ enclosures with caged animals (e.g., Chazal and Niewiarowski 1998, Rothermel and Luhring 2005) because adequate recapture rates are difficult to achieve for terrestrial salamanders (Bailey et al. 2004*b*, Kelly 2005). However, in situ enclosures can impede normal behavioral responses, such as horizontal movements, and thus do have limitations. Field experiments should continue to play a central role in understanding the complex interactions among anthropogenic alteration of habitat, physiological processes of individuals, demography, and population growth rates.

Our evidence suggests even small but chronic increases in temperature that occur in recently harvested forest can negatively influence energetics of individual salamanders, even those under refugia. As forest stands regenerated, however, differences in temperature regimes under refugia disappeared and energetics of salamanders was not affected by harvests 8–14 years after the disturbance. Understory woody stem densities in the ORH averaged 2,273 stems/ha, whereas those in the other harvested treatments were >14,200 stems/ha (Homyack 2009). Thus, in the temperate forests of the central Appalachian Mountains, regrowth of over- and understory vegetation may be as important for mediating near-ground microclimate in the first years after a disturbance (Heatwole 1962, Rittenhouse et al. 2008) as the presence of coarse woody debris (deMaynadier and Hunter 1995, Brooks 1999). Additionally, a well-developed under- and mid-story reportedly provide more successful foraging opportunities for salamanders than the forest floor (Jaeger 1978) and have been positively related to salamander abundances across regions and spatial scales (Pough et al. 1987, Brooks 1999, Homyack 2009).

MANAGEMENT IMPLICATIONS

Retention of large, downed logs and stumps following harvesting is recommended for salamanders to provide refuge from temperature extremes and to meet their life history requirements (deMaynadier and Hunter 1995, Cole et al. 1997, Brooks 1999, Kluber et al. 2009). However, our research indicates that temperatures are warmer under wood cover objects in recently (<1 yr) harvested forest compared to unharvested areas, which may have significant effects on bioenergetics of terrestrial salamanders. Because these temperature-related effects appeared to disappear with understory regrowth, we recommend that forest stands be managed both for rapid recovery of understory vegetation and for retention of large stumps and logs throughout a rotation. The range of silvicultural treatments that provide these conditions will vary based on site quality, prior stand conditions, and how managers apply harvests. In Central Appalachian hardwood forests, some forms of partial harvests may provide suitable habitat structure to support more rapid recovery of plethodontid salamanders including large quantities of coarse woody debris and complex understory vegetation. However, given the negative effects of stand reentry on energy demands of salamanders, forest managers must also consider the effects of partial harvesting and repeated stand-entries on soil disturbance, oak regeneration, and financial returns when planning future timber harvests (Homyack and Haas 2009).

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Appendix A. Mean monthly maximum temperature (°C) under coverboards averaged across 2006–2008 sampling seasons at 4 study sites in Virginia ($n = 2$) and West Virginia ($n = 2$) and 5 silvicultural treatments. Regenerating shelterwood, leave tree, and silvicultural clearcut treatments were implemented 8–14 years prior to sampling; recent overstory removal harvest treatments were 1 year old.

		Silvicultural treatment								
		Unharvested control		Regenerating shelterwood		Leave tree		Silvicultural clearcut		Recent overstory removal harvest
Month	**Site**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**
May	BB1	19.7	0.7	21.3	1.7	19.0	0.7	20.3	1.6	23.1
	BB2	18.8	0.3	22.4	0.7	20.7	0.5	19.9	0.9	25.3
	WV1	18.3	0.3	17.5	0.7	16.9	0.5	17.3	0.9	
	WV2	18.0	0.0	20.1	0.8	21.0	0.7	17.3	1.8	
Jun	BB1	21.0	0.2	21.0	0.2	20.5	0.9	20.8	0.6	28.0
	BB2	20.7	0.7	23.4	1.3	20.6	0.3	19.8	0.2	28.5
	WV1	19.7	0.7	18.6	0.2	18.4	0.3	18.8	0.2	
	WV2	18.6	0.2	18.8	0.2	18.9	0.2	17.6	1.5	
Jul	BB1	22.3	0.6	23.3	0.1	21.9	0.9	22.5	0.5	29.4
	BB2	21.5	0.4	22.9	0.3	22.1	0.4	21.2	0.3	29.2
	WV1	20.7	0.6	19.4	0.6	19.2	0.4	19.5	0.5	
	WV2	20.1	0.7	19.4	0.4	19.4	0.5	18.6	1.9	
Aug	BB1	23.9	1.4	24.8	0	22.6	1.1	23.5	0.6	29.5
	BB2	22.5	0.7	24.4	0.2	23.0	0.4	22.0	0.6	31.2
	WV1	21.4	0.1	20.6	0.6	20.3	0.7	20.6	0.9	
	WV2	20.9	0.2	20.4	0.8	20.3	1.1	19.6	2.2	
Sep	BB1	21.5	1.4	21.6	1.7	20.3	0.3	21.8	1.1	29.6
	BB2	20.8	1.1	21.4	1.7	21.4	1.2	20.8	1.1	26.8
	WV1	20.0	1.7	19.0	1.0	18.6	1.2	18.7	1.2	
	WV2	19.5	1.6	19.2	1.2	18.8	1.0	19.8	1.3	
Oct	BB1	23.7	5.0	30.3		23.5	5.5	23.9	4.8	22.0
	BB2	23.9	5.3	30.9		24.1	5.1	23.9	5.3	21.6
	WV1	22.3	5.0	20.8	5.1	20.6	5.6	21.2	6.1	
	WV2	22.2	3.9	24.6	2.7	21.4	3.2	21.8	5.3	

Appendix B. Mean (SE) monthly minimum temperature (°C) under coverboards averaged across 2006–2008 at 4 study sites in Virginia ($n = 2$) and West Virginia ($n = 2$) and 5 silvicultural treatments. Regenerating shelterwood, leave tree, and silvicultural clearcut treatments were implemented 8–14 years prior to sampling; recent overstory removal harvest treatments were 1 year old.

		Silvicultural treatment								
		Unharvested control		Regenerating shelterwood		Leave tree		Silvicultural clearcut		Recent overstory removal harvest
Month	**Site**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**
May	BB1	9.1	0.6	8.2	0.3	9.2	0.4	9.3	0.5	9.4
	BB2	8.0	0.9	8.9	0.1	8.8	0.4	9.2	0.4	10.1
	WV1	6.7	0.3	7.1	0.6	7.1	0.3	7.1	0.3	
	WV2	6.7	0.3	6.6	0.4	7.0	0.3	6.7	0.5	
Jun	BB1	13.1	0.4	12.9	0.4	12.7	0.1	13.2	0.3	14.3
	BB2	13.1	0.3	13.0	0.8	13.0	0.3	13.2	0.3	14.8
	WV1	10.7	0.4	11.2	0.7	10.7	0.4	11.3	0.6	
	WV2	11.1	0.6	11.2	0.5	11.3	0.6	10.7	0.9	
Jul	BB1	13.7	0.3	14.1	0.4	13.6	0.4	14.2	0.2	14.4
	BB2	14.1	0.1	14.6	0.2	14.3	0.1	14.1	0.3	15.1
	WV1	12.3	0.3	12.5	0.2	12.3	0.2	12.4	0.2	
	WV2	12.5	0.1	12.3	0.3	12.7	0.3	11.9	0.9	
Aug	BB1	14.9	0.5	15.6	0.9	14.9	0.6	15.3	0.6	15.2
	BB2	15.4	1.1	16.6	0.9	15.6	1.0	15.2	0.8	15.6
	WV1	13.8	0.8	14.3	0.6	13.7	0.7	14.0	0.7	
	WV2	14.0	1.0	14.1	0.7	14.1	0.9	13.6	1.6	
Sep	BB1	13.0	0.8	13.3	1.1	13.3	0.7	13.1	1.6	13.1
	BB2	13.0	0.6	13.9	0.5	13.2	0.6	13.5	0.7	13.9
	WV1	11.3	0.6	11.9	0.9	11.4	1.0	11.5	0.9	
	WV2	11.2	0.6	12.1	0.3	11.5	0.6	11.4	0.8	
Oct	BB1	9.6	0.4	9.9		9.9	0.1	10.4	0.1	11.1
	BB2	10.3	0.1	10.3		10.5	0.2	10.6	1.3	11.2
	WV1	10.2	2.0	11.2	1.3	10.7	1.4	10.6	1.3	
	WV2	10.2	2.1	10.8	1.5	10.5	2.0	10.7	2.6	