Field-Testing a Standard Metabolic Rate Estimation Technique for Eastern Red-Backed Salamanders

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ABSTRACT—Plethodontid salamanders are often monitored as indicator species for mature forest ecosystem health. In addition to relative abundance, differences in standard metabolic rate (SMR) between harvest treatments have been used to explain physiological stress in response to timber harvest. Nearly ubiquitous in forested stands throughout the northeastern United States, the Eastern Red-Backed Salamander (Plethodon cinereus) is often the focal species of such studies. In 2010, a predictive multiple regression equation was developed to calculate SMR of P. cinereus to 95% accuracy using salamander body mass and temperature. This method of SMR estimation has been implemented in field studies as a measure of salamander health. In these studies, temperature regime is the only variable measured, and SMR is calculated by standardizing on a 1-g salamander. In this study, we measured both body mass and temperature of each salamander encountered in harvested and unharvested stands and compared the published SMR calculation technique with SMR calculated using observed temperature and body mass data. We found larger variability in temperature in harvested stands using both methods but did not identify a similar trend in the SMR of observed salamanders. Differences in salamander body mass and snout–vent length between harvested and unharvested stands in Fall 2013 suggest that researchers should use caution when making claims about SMR when data on salamander body mass has not been measured.

Lungless salamanders, from the family Plethodontidae, are the most-abundant forest salamanders, often making up high percentages of the total vertebrate biomass in forest ecosystems (Burton and Likens, 1975; Jaeger, 1979). Plethodontids play a key role in energy and nutrient cycling by providing an essential trophic link between the numerous, but often energetically inaccessible, invertebrate fauna and the plethodontids’ vertebrate predators (Pough, 1983). Along with their integral role in forest ecosystems, the sensitivity of plethodontid salamanders to management practices has led some researchers to nominate them as ideal indicator species for mature forest ecosystem health; thus their abundance and diversity is often monitored as a surrogate for overall habitat quality within a complex forest ecosystem (Herbeck and Larsen, 1999; Welsh and Droge, 2001; Welsh and Hodgson, 2013).

Dependence on temperature and microclimate stability can make plethodontids vulnerable to timber harvest. In fact, multiple studies have shown negative effects of forest harvest practices on salamanders (as reviewed in DeMaynadier and Hunter, 1995). On the other hand, mature forests (>60 yr) allow for the development and stability of essential microhabitat characteristics and have been shown to support the highest diversity and abundance of terrestrial salamanders (Pough et al., 1987; Ford et al., 2002). Although forest harvesting impacts several components of salamander habitat (Grialou et al., 2000; Morneault et al., 2004), the presence, or absence, of dense canopy closure seems to be one of the most-important habitat characteristics for salamanders. Canopy removal results in excess microclimate variability (Zheng et al., 2000), which can affect plethodontid physiology (McKenny et al., 2006; Homyack et al., 2011). Therefore, some studies suggest that thinning, selection systems, and other silvicultural practices that maintain high residual canopy cover have limited or no negative effects on salamanders (Messere and Ducey, 1998; Brooks, 1999; Grialou et al., 2000; McKenny et al., 2006).

Many plethodontids are entirely terrestrial; they are dependent on specific microhabitat characteristics (i.e., leaf litter depth, canopy cover, aspect, slope, and coarse woody debris) for thermo- and osmoregulation and cutaneous respiration (Spotila, 1972; Pough et al., 1987; Petranka et al., 1994; Grover, 1998). Plethodontid foraging is limited to periods of higher humidity and higher forest floor moisture levels (Jaeger, 1978; Feder, 1983). Leaf litter depth, as one characteristic associated with forest floor microclimate, has been considered to be the best indicator of aboveground salamander activity (Pough et al., 1987; DeGraff and Yamasaki, 1992). Additionally, if leaf litter remains moist, salamanders (mostly nocturnal feeders) can continue to forage into the day (Jaeger, 1980).

Because they are ectothermic poikilotherms, plethodontid body temperature varies with the temperature of their surrounding environment (Feder, 1983), resulting in different physiological consequences associated with different temperature regimes (Careau et al., 2014). One way that Eastern Red-Backed Salamanders (Plethodon cinereus) adjust to changes in environmental conditions is to preferentially select habitat at a specific mild temperature (~16.2°C) (Spotila, 1972). In addition, plethodontids rely on cutaneous respiration for oxygen consumption; therefore, moisture and temperature greatly affect the efficiency of this process and thus influence standard metabolic rate (SMR) (Careau et al., 2014).

Given the importance of temperature and body mass for plethodontids, Homyack et al. (2010) developed a predictive multiple regression equation to calculate SMR of the Eastern Red-Backed Salamander (P. cinereus) using solely these two variables:

\[ \text{Log}_e (\text{SMR}) = 0.102(\text{temperature}) + 0.681[\text{Log}_e (\text{mass})] - 4.849 \]

This equation is useful for quantifying potential ecological consequences of surface-active salamanders at different temperature regimes (Homyack et al., 2011). Because P. cinereus is sedentary for a large majority of the time, SMR makes up a large portion of its daily energy budget (Spotila, 1972). As a result, the ability to discern differences in SMR between harvest treatments could provide a useful gauge of harvest-induced physiological stress. Although Homyack et al. (2011) used this equation to estimate the potential impacts of varying surface temperatures...
caused by different timber harvest regimes on SMR, to our knowledge no one has used this equation to calculate SMR of salamanders in situ. We compared the Homyack et al. (2010) method, which uses remotely sampled temperature regimes to calculate SMR based on a 1-g salamander, with an alternate method that uses observed capture temperature and body mass measurements from salamanders encountered in a field setting. Confirmation of the current technique would allow for researchers to continue using thermal profile data of different harvest regimes to calculate SMR of *P. cinereus* as a proxy of forest health.

**Materials and Methods**

This study took place at the Southeast Purdue Agricultural Center (SEPAC), Jennings County, Indiana, United States (Fig. 1). The study site consisted of a 46-ha mature oak-hickory (*Quercus-Carya*) stand subdivided into 10 separate treatment plots (mean 3.2 ha, range 2.35–4.61 ha). Timber on seven of the treatment plots was harvested in Fall 2012 as part of a multidisciplinary project through Purdue University in which harvest residues were removed to mimic a biomass harvest for cellulosic bioenergy. The three remaining treatment plots were left as unharvested stands.

**Salamander Sampling and Data Collection.**—In each treatment plot, we used 25, 30 × 30 × 5-cm untreated poplar boards as artificial cover objects (ACOs), arranged in a 5 × 5-m array. In Fall 2011, artificial cover object arrays (location recorded using the global positioning system [GPS]) were placed in the center of each treatment plot to minimize future edge effects after the harvest (DeMaynadier and Hunter, 1998). All 250 ACOs were removed prior to the timber harvest in September 2012 and replaced in their original locations following the harvest. Artificial cover objects remained in direct contact with the soil and were checked once every 2 wk (Marsh and Goicoecha, 2003) throughout the active season in the spring (March–June) and fall (September–November) during three sampling seasons: Spring 2013, Fall 2013, and Spring 2014. Because the purpose of this study was to compare SMR calculation methods based on temperature regime with SMR calculations from surface active salamanders in a field setting, we truncated each collection season to include only sampling days with at least 10 salamander captures. This ensured that we made comparisons only during periods when we could assume that salamanders were surface active.

We recorded body mass (±0.01 g) and snout–vent length (SVL) of each salamander encountered under the ACOs using a digital field scale (AT-100, American Weigh Scales, Inc., Norcross, Georgia, USA) and a ruler. Salamanders were classified into three stage classes according to their SVL: young of the year (<25 mm), juvenile (25–32 mm), and adult (>32 mm) (Moore 2009). We recorded salamander temperature manually with a noncontact infrared laser thermometer (±2°C; Raytek MT4, Fluke Inc., Everett, Washington, USA) immediately following detection underneath ACOs (Scheffers et al., 2009; Connette and Semlitsch, 2013). If the temperature of the salamander could not be recorded at first detection (e.g., the salamander tried to escape), we recorded the temperature of the soil where the salamander was sitting prior to capture.

We used three randomly placed Thermochron iButton dataloggers (±0.5°C; model DS1921G-F5, Maxim Integrated Products, Sunnyvale, California, USA) per ACO array to record temperature data every 3 h (eight measurements per day). These dataloggers were placed centrally underneath ACOs to measure refugia temperature at the interface of ACO and the soil (Homyack et al., 2011). We waterproofed dataloggers with red plasti-dip (Plasti-Dip International, Blaine, Minnesota, USA) prior to use in the field. Datalogger sampling points remained consistent throughout the study to allow between-season comparisons.

We averaged iButton refugia temperature data within each ACO array for each of the eight time points and calculated daily maximum and minimum temperatures for each array. We used these refugia temperature dataloggers at the interface of the soil and ACOs to estimate seasonal SMR trends based on a 1-g surface-active salamander using the predictive multiple regression equation developed by Homyack et al. (2010). In addition to using iButton refugia thermal profile, we also calculated SMR using observed salamander temperature and body mass for comparison. Salamanders with malformations (e.g., missing limbs, autotomized tails, etc.) were excluded from these analyses.

**Data Analysis.**—We used R (R Development Core Team, 2013) and package ‘car’ (Fox and Weisberg, 2011) to perform temperature and SMR analyses. We set alpha equal to 0.05 and established significance at $P < 0.05$ and marginal significance as $0.1 > P > 0.05$ for all statistical tests. We compared daily maximum refugia temperature between harvested and unharvested stands (Welch’s *t*-test) as an indicator of the most-extreme temperature that could be encountered by a surface-active salamander throughout each season. Because temperature extremes are different between the fall and spring field seasons, we also tested differences in the mean and variance of daily extremes are different between the fall and spring field seasons, we also tested differences in the mean and variance of daily

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Fig. 1. Location of the Southeast Purdue Agricultural Center in Jennings County of southern Indiana, United States.
Table 1. Comparison by season of iButton maximum refugia temperature (Max refugia temp; °C), salamander capture temperature (Cap temp; °C), natural log of standard metabolic rate (lnSMR), natural log of salamander mass (lnmass), and snout-vent length (SVL; mm) between harvested and unharvested stands (data are reported as means ± SD). Significance of t- and F-tests (***P < 0.001, **P < 0.01, *P < 0.05, –P > 0.05) comparing means and variance between harvested and unharvested stands are reported in columns 3 and 4, respectively. Statistical analyses were performed on the complete dataset including all encountered salamanders.

<table>
<thead>
<tr>
<th></th>
<th>Harvested</th>
<th>Unharvested</th>
<th>Difference in mean</th>
<th>Difference in variance</th>
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<tr>
<td>Spring 2013</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max refugia temp</td>
<td>15.37 ± 5.72</td>
<td>12.64 ± 4.39</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Cap temp</td>
<td>8.36 ± 4.41</td>
<td>7.31 ± 3.36</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>lnSMR</td>
<td>-4.20 ± 0.58</td>
<td>-4.32 ± 0.53</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>lnmass</td>
<td>-0.34 ± 0.58</td>
<td>-0.32 ± 0.59</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>SVL</td>
<td>37.0 ± 5.85</td>
<td>35.84 ± 6.94</td>
<td>–</td>
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<tr>
<td>Fall 2013</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Max refugia temp</td>
<td>12.94 ± 4.50</td>
<td>13.12 ± 3.68</td>
<td>–</td>
<td>*</td>
</tr>
<tr>
<td>Cap temp</td>
<td>10.99 ± 4.50</td>
<td>10.69 ± 3.54</td>
<td>–</td>
<td>**</td>
</tr>
<tr>
<td>lnSMR</td>
<td>-4.22 ± 0.58</td>
<td>-4.32 ± 0.53</td>
<td>–</td>
<td>*</td>
</tr>
<tr>
<td>lnmass</td>
<td>-0.47 ± 0.53</td>
<td>-0.38 ± 0.48</td>
<td>–</td>
<td>*</td>
</tr>
<tr>
<td>SVL</td>
<td>35.08 ± 7.15</td>
<td>37.07 ± 6.18</td>
<td>*</td>
<td>**</td>
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<tr>
<td>Spring 2014</td>
<td></td>
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</tr>
<tr>
<td>Max refugia temp</td>
<td>14.18 ± 5.31</td>
<td>12.36 ± 4.62</td>
<td>***</td>
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<tr>
<td>Cap temp</td>
<td>8.31 ± 4.00</td>
<td>8.29 ± 4.32</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>lnSMR</td>
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<td>–</td>
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</tr>
<tr>
<td>lnmass</td>
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<td>–</td>
<td></td>
</tr>
<tr>
<td>SVL</td>
<td>35.79 ± 6.71</td>
<td>36.73 ± 5.87</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

RESULTS

We encountered a total of 670 Plethodon cinereus over three sampling seasons (Spring 2013, Fall 2013, Spring 2014). After removing malformed and injured individuals, the sample size consisted of 566 salamander encounters made up of 443 unique individuals.

Refugia Temperature.—Mean maximum refugia temperature was higher in harvested than unharvested stands in Spring 2013 (t_{428.8} = 6.30, P < 0.001) and Spring 2014 (t_{289.0} = 3.65, P < 0.001) but it was not different in Fall 2013 (t_{307.1} = -0.43, P = 0.332; Table 1). The mean maximum refugia temperature was larger in harvested stands in all three seasons: Spring 2013 (F_{1,588} = 15.15, P < 0.001), Fall 2013 (F_{1,448} = 6.35, P = 0.01), and Spring 2014 (F_{1,448} = 4.35, P = 0.038). The mean maximum SMR test statistics and P-values were identical to those of the refugia temperature analysis between harvested and unharvested stands because of the use of a standardized body mass conversion factor.

Mean daily refugia temperature range was significantly higher in harvested stands in all three seasons: Spring 2013 (t_{459.4} = 11.15, P < 0.001), Fall 2013 (t_{413.0} = 10.72, P < 0.001), and Spring 2014 (t_{520.4} = 9.04, P < 0.001). Levene’s test for homogeneity of variance also confirmed that variation of daily temperature range in harvested stands was significantly larger in all three seasons: Spring 2013 (F_{1,588} = 20.86, P < 0.001), Fall 2013 (F_{1,448} = 35.64, P < 0.001), and Spring 2014 (F_{1,448} = 29.20, P < 0.001).

Salamander Capture Temperature.—Mean salamander capture temperatures were not different between harvested and unharvested stands in Spring 2013 (t_{103.2} = 1.61, P = 0.056), Fall 2013 (t_{217.7} = 0.56, P = 0.29), or Spring 2014 (t_{109.2} = 0.40, P = 0.52). The variance of capture temperatures, however, did vary between harvested and unharvested stands in the Spring 2013 (F_{1,156} = 15.56, P < 0.001) and Fall 2013 (F_{1,222} = 7.50, P = 0.007) sampling seasons.

Standard metabolic rate calculated from observed salamander body mass and capture temperatures did not differ between harvested and unharvested treatments in any season. Using the complete dataset, the variance of SMR was larger in harvested stands in Fall 2013 (F_{1,222} = 4.63, P = 0.032); however, after

Because our study design involved resampling ACOs several times over the course of a single season, we encountered some individuals more than once. Although this paper does not present results on abundance analyses, all encountered salamanders were marked with visible implant elastomers (Northwest Marine Technology, Inc., Shaw Island, Washington, USA) as part of another mark-release-recapture study. To avoid violating the assumption of independence, we randomly removed all but one encounter of each individual per season and created an adjusted dataset consisting solely of unique encounters. We performed a side-by-side comparison of analyses using both the complete dataset and the adjusted dataset. Results from adjusted dataset analyses varied depending on which encounters of individual salamanders were randomly retained. We performed the analyses several times, however, and with the exception of one F-test, all results and trends remained consistent regardless of whether we used the complete dataset or the adjusted dataset. For the sake of clarity and consistency, we report results from the complete dataset and make explicit the one discrepancy.
removing individuals randomly to avoid violating the assumption of independence, this trend, although still evident in the adjusted dataset, was only marginally significant (mean \(P\)-value of 0.069, significant \(P < 0.05\) on 490 of 1,000 randomized iterations).

The variance of salamander capture temperature was significantly different in Spring 2013 and Fall 2013, but the variance of SMR showed this trend only in Fall 2013 (although not in the adjusted dataset). Therefore, we examined salamander body mass and SVL to see if changes in seasonal salamander size assemblages could potentially influence SMR calculations. Body mass was not significantly different between harvested and unharvested stands in Spring 2013 (\(t_{128.9} = -0.15, P = 0.44\)) or Fall 2013 (\(t_{205.1} = -1.23, P = 0.109\)). The variance of body mass also was not significantly different between harvested and unharvested stands in Spring 2013 (\(F_{1,156} = 0.10, P = 0.75\)). There was a difference, however, in the variance of salamander body mass between harvested and unharvested stands in Fall 2013 (\(F_{1,222} = 5.66, P = 0.02\); Fig. 2). Snout–vent length also was significantly lower (\(t_{210.0} = -2.21, P = 0.01\)), with a significantly larger variance in harvested stands in Fall 2013 (\(F_{1,156} = 1.56, P = 0.21\)); whereas mean and variance of SVL were not different in harvested and unharvested stands in Spring 2013 (\(t_{143.2} = 1.13, P = 0.13; F_{1,156} = 1.56, P = 0.21\)).

Season was a significant predictor of salamander SMR (\(F_{4,561} = 12.10, P \leq 0.001\)), but harvest type and aspect had no effect on SMR (\(F_{4,561} = 0.0412, P = 0.84; F_{4,561} = 2.70, P = 0.101\), respectively). Similarly, season was a significant predictor of salamander capture temperature (\(F_{4,561} = 34.29, P \leq 0.001\)), but harvest type and aspect had no effect (\(F_{4,561} = 1.52, P = 0.219; F_{4,561} = 0.58, P = 0.446\) respectively).

**DISCUSSION**

Researchers have suggested that plethodontids are good candidate bioindicator species for mature forest ecosystems (Welsh and Droege, 2001), a possibility that makes the study of methods that assess their health beneficial for conservation science. Upon investigation of the field implementation of SMR calculation using an equation developed by Homyack et al. (2010), this method has the potential to serve as a noninvasive monitoring technique—but not as currently applied. In previous studies, this equation has been used to estimate SMR of surface-active salamanders based on different temperature regimes resulting from different timber harvest treatments (Homyack et al., 2011). These temperature regimes were collected during the summer months, however, representing the most-severe temperatures encountered by a surface-active \(P.\) cinereus. In our study, few if any salamanders were encountered under ACOs during the hot summer months (Fig. 3). Temperature differences between harvest treatments are most distinct at this time, but if salamanders are subterranean, extrapolation of surface-active SMR is not ecologically relevant. To maintain adequate sample size, and to ensure that we were calculating SMR of surface-active salamanders, we truncated seasons to include only sampling days when at least 10 \(P.\) cinereus were encountered.

The discrepancy in time of year may account for some of the differences between SMR estimates from iButton temperature dataloggers and estimates from salamander capture temperature and body mass measurements; however, similar trends in variability were noticeable using both methods. Our results support the demonstrated importance of body mass as one of the most-influential factors in SMR calculation (Whitford and Hutchison, 1967; Gifford et al., 2013), and we suggest...
researchers use caution when making claims based on differences in calculated mean SMR when data on salamander body mass have not been taken.

Temperature dataloggers exhibited a noticeable difference in temperature regime between harvested and unharvested stands in all three seasons. Subsequently, when we calculated SMR based on the predictive regression equation, the results showed identical differences in SMR for harvested and unharvested stands in all three seasons; however, we did not see this same trend in observed SMR based on salamander capture temperature and body mass measurements. Observed SMR was not significantly different between harvested and unharvested stands in any season.

The iButton dataloggers indicated consistently larger variance of maximum refugia temperature in harvested stands than in unharvested stands in all three seasons. We expected this, because harvested forest stands are known to have a larger variability in climate (Zheng, 2000). Variance of salamander capture temperature also was larger in harvested stands in both Spring 2013 and Fall 2013; however, this difference was not as extreme as suggested by the iButton data, and it was also not seen in Spring 2014. Temperature dataloggers were placed underneath three randomly selected ACOs per array to record the thermal profile of each array. Perhaps this small subsample of the available ACOs did not provide an adequate thermal profile of the array and, therefore, the discrepancy between refugia and capture temperature data may be because of salamander selection of more-hospitable microclimate under cooler ACOs. Also, by Spring 2014, the study site had more herbaceous and woody ground cover, which provide moisture and shade in recently harvested stands (<5 y; Morneault et al., 2004) and potentially mitigate effects of harvest on temperature regime.

Although the variance of salamander capture temperature was larger in harvested stands in both Spring 2013 and Fall 2013, observed SMR seemed to follow this trend only in Fall 2013. Upon further analysis, both body mass and SVL also had significantly larger variance in harvested stands in Fall 2013, and mean SVL was significantly lower in harvested stands during that year. Capture temperature also differed between harvested and unharvested stands in Spring 2013; however, body mass and SVL did not.

Body mass (in concert with temperature) is a crucial element for SMR calculation, and if salamander body mass has the potential to differ between harvest treatments, standardizing to a 1-g salamander might not be a valid method of SMR estimation. Because the average difference in body mass of recaptured P. cinereus fluctuated by 0.086 g (11% of average body mass) within a season, body mass is a transient measurement. Plethodontid body mass is subject to soil moisture levels (Heatwole, 1960) and can also change by as much as 0.1 g (13% of average body mass) in one meal (PJR, pers. obs.). Body mass fluctuation over the course of a season is common in many terrestrial ectotherms (Bennett and Nagy, 1997; Bonnet et al., 2001). Because of the intrinsic problems with body mass measurements of organisms that vary so much with one meal, it is impossible to ensure that all salamanders measured in a field environment are in a standardized post-absorptive or hydrated state; however, SVL is a reliable measurement of P. cinereus stage class (Moore, 2009). In addition to the differences in the variance of P. cinereus body mass, differences in mean SVL between harvested and unharvested stands call into question the validity of SMR calculation standardized on a 1-g salamander as an accurate proxy of ecosystem health. This is an important consideration in

![Fig. 3](image.png)  
**Fig. 3.** Total number of salamanders encountered (N = 567) under ACOs by month in 2013 (gray) and 2014 (black).

![Table 2](image.png)  
**Table 2.** Total number of individuals in each stage class (young of the year, juvenile, adult) by season (Spring 2013, Fall 2013, Spring 2014) and harvest treatment (harvested, unharvested).
determining the most-accurate method of SMR estimation in conservation studies.

There are several potential explanations for the discrepancy in salamander body mass and stage class (SVL) observed in Fall 2013; however, we do not consider our use of ACOs to have introduced a size bias. Artificial cover object searches have performed comparably to (if not better than) transect, quadrate, and natural cover object searches (Monti et al., 2000; Moore, 2009; Hesed, 2012). Salamanders sampled with ACOs do not differ in weight, SVL, or sex ratio from those captured under natural cover objects (Monti et al., 2000; Marsh and Goicoechea, 2003; Moore, 2009). In addition, P. cinereus are not drawn to ACOs from nearby natural cover objects (Monti et al., 2000).

While we do not consider our sampling method to have introduced a bias, the differences in microclimate between harvested and unharvested stands may have affected the socioecology, territoriality, and behavior of P. cinereus (Jaeger, 1979; Jaeger, 1995). Jaeger (1979) noted that social boundaries and territoriality are more extreme in the harsher climates and conditions that often are associated with the drier summer months. If temperature differences between spring and fall field seasons affect territoriality, this could explain the discrepancy in stage class between harvested and unharvested treatments. On the other hand, while larger P. cinereus compete for territories and exclude smaller individuals from high-quality cover objects in a typical forest habitat (Mathis, 1990), adverse environmental conditions present in harvested stands at our site may have caused the territoriality framework to break down (Mathis, pers. comm.). If this happened, one might expect to see a relaxation of territorial behavior and increased tolerance of smaller individuals. Regardless of the cause of the discrepancy in stage class between harvested and unharvested stands, our data suggest that researchers should take caution using methods that assume standard mass to calculate SMR of P. cinereus in timber stands that have been subject to different harvest treatments.

Our study highlights the importance of carefully weighing the pros and cons and potential biases associated with both methods of SMR estimation, especially in research with forest conservation implications. In the literature, SMR is defined as the metabolic rate of an organism in a rested, fasted, and awake state in a thermoneutral environment (IUPS Thermal Commission, 2003). Therefore, our measurement of surface-active individuals encountered under ACOs is not a direct measure of traditional SMR; rather, our estimates best represent that of resting metabolic rate. On the other hand, the method of Homyack et al. (2010) is not able to account for site-specific differences in salamander mass. Neither method can adequately account for the subtle differences in microclimate that may occur across the landscape. Determining which method is more reliable may be impossible, but the inherent biases in both should be carefully weighed and acknowledged along with the results in studies of this nature.

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LITERATURE CITED


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