Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Quantifying multi-scale habitat use of woody biomass by southern toads

S.R. Fritts [a,*], S.M. Grodsky [a,1], D.W. Hazel [b,1], J.A. Homyack [c], S.B. Castleberry [d], C.E. Moorman [a,1]

[a] North Carolina State University, Department of Forestry and Environmental Resources, Fisheries, Wildlife, and Conservation Biology Program, Box 7646, Raleigh, NC 27695-7646, USA
[b] North Carolina State University, Department of Forestry and Environmental Resources, Box 7646, Raleigh, NC 27695-7646, USA
[c] Weyerhaeuser Company, 1785 Weyerhaeuser Road, Vanceboro, NC 28586-7606, USA
[d] University of Georgia, Warnell School of Forestry and Natural Resources, Athens, GA 30602-2152, USA

ABSTRACT

Woody biomass extraction for use as a feedstock for renewable energy may remove woody debris that provides suitable micro-climates for amphibians. We examined habitat use of the southern toad (*Anaxyrus terrestris*) as an indicator of relationships between amphibians and woody biomass in pine plantations of the southeastern United States using a controlled enclosure experiment and a field-based radio-telemetry study. In the enclosure experiment, we recorded toad selection among four 16-m^2 treatments that varied in area of ground surface covered by coarse woody debris (CWD) and spatial allocation of CWD. Treatments were: (1) ≈100% of the ground area covered by CWD in one large pile (volume of CWD = 1.10 m^3, 100CWD); (2) ≈50% of the ground area covered with CWD in one large pile (volume of CWD = 0.60 m^3, 50PILE); (3) ≈50% of the ground area covered with CWD dispersed throughout the treatment (volume of CWD = 0.25 m^3, 50DISP); and (4) no CWD (0CWD). In the radio-telemetry study, we identified southern toad daytime refuge locations and compared habitat characteristics to paired random locations. From May to August 2013, toads (*n* = 47) did not use enclosure treatments randomly during nocturnal hours (*P* < 0.01), and ranking of treatments from most to least selected was 0CWD, 100CWD, 50DISP, 50PILE. When no rain events occurred, toads spent a greater proportion of time during nocturnal hours in 100CWD as temperature increased (*P* = 0.03). Toads used 100CWD 75% of the time for diurnal refuge. Radio-marked toads (*n* = 37) avoided grass (*P* < 0.01) and bare ground (*P* < 0.01) as diurnal refuge sites. Although radio-marked toads used CWD, other cover sources also were used as refuge sites and toads did not select CWD cover (*P* = 0.11) over other diurnal refuge types. Our results suggest woody biomass in recently harvested pine plantations is not an essential habitat characteristic during nocturnal hours and therefore may not be important for foraging. Yet, woody biomass may provide diurnal refuge for southern toads, and likely other amphibians, when desiccation risk is high (i.e., temperatures are high and rain does not occur). Additionally, southern toads may use woody biomass for diurnal refuge when other cover sources are not available, but can exhibit behavioral plasticity when cover sources such as vegetation are accessible.

© 2015 Elsevier B.V. All rights reserved.

1. Introduction

Habitat degradation is a major cause of amphibian declines (Delis et al., 1996; Davidson et al., 2002; Stuart et al., 2004; Becker et al., 2007; Harper et al., 2008). The National Wildlife Federation and the Southern Environmental Law Center suggested woody biomass extraction for use as a renewable energy feedstock could contribute to degradation of habitat for many wildlife species (Evans et al., 2013). Although woody biomass has been harvested for energy production for decades (Stuart et al., 1981; Watson et al., 1986; Puttock, 1987), operational harvests in southeastern United States pine plantations can decrease downed woody debris by ≈81% compared to sites with only a roundwood harvest (Fritts et al., 2014). Despite the benefits of replacing non-renewable energy with woody biomass, reductions of downed woody debris following woody biomass harvests could alter ecosystem services and impact wildlife populations (Perschel et al., 2012; Evans et al., 2013).

Sustainability of woody biomass harvests is of particular importance in the southeastern United States, which is considered a "wood basket" and currently is the largest exporter of wood pellets

* Corresponding author. Tel.: +1 678 836 7223; fax: +1 919 515 5110.
E-mail addresses: fritts.sarah@gmail.com (S.R. Fritts), smgrodsk@ncsu.edu (S.M. Grodsky), dennis_hazel@ncsu.edu (D.W. Hazel), Jessica.Homyack@weyerhaeuser.com (J.A. Homyack), scastle@warnell.uga.edu (S.B. Castleberry), chris_moorman@ ncsu.edu (C.E. Moorman).
[1] Fax: +1 919 515 5110.

in the world (Hanson et al., 2010; Evans et al., 2013; Goh et al., 2013). Growth of forest-based bioenergy production facilities is most rapid in the southeastern United States and use of woody biomass for power, heat, and liquid biofuels has been increasing in recent years (Mendell and Lang, 2012, REN21, 2013). However, this region is a global center of amphibian diversity (IUCN, 2013), and amphibians use downed woody debris for thermoregulation, protection from desiccation, reproduction, and as a feeding substrate (Jaeger, 1980; Hassinger, 1989; Whiles and Grubaugh, 1996; Butts and McComb, 2000). Previous studies in the southeastern United States have documented varying amphibian responses to experimental manipulations of downed woody debris (Owens et al., 2008; Davis et al., 2010; Homyack et al., 2013; Fritts, 2014), but conclusions often were based on relative abundance and species richness estimates from large-scale sampling studies. Although large-scale studies are useful, they often rely solely on count data and fail to identify individual-based behaviors that could better inform the mechanisms underlying population response (Schmidt, 2003; Muths et al., 2006). Individual movement behavior studies are particularly useful because results can be scaled up from the individual to the population level and can help predict amphibian habitat requirements (Lima and Zollner, 1996; Gibbs, 1998; Haddad, 1999; Graeter et al., 2008). Therefore, combining large-scale sampling to estimate abundance and species richness with fine-scale studies that identify underlying mechanisms responsible for population changes following a habitat disturbance can aid in developing sound management protocols.

Amphibians may indicate the ecological sustainability of woody biomass harvests because their physiology makes them particularly susceptible to forest disturbances and manipulations that alter forest-floor temperature and moisture regimes. As poikilothermic ectotherms, temperature affects nearly all physiological processes of amphibians (Gatten et al., 1992; Rome et al., 1992), including behavior and growth. Therefore, habitat selection can have direct physiological and functional consequences (Huey, 1991). Metabolism in ectotherms increases with environmental temperature and can account for more of the overall energy budget than the other components (i.e., growth, reproduction, and storage) combined (Pough, 1980; Spotila and Standora, 1985; Gatten et al., 1992). When surface temperatures are high, amphibians may decrease above-ground activities to avoid increased metabolic costs which could decrease energy available for growth or reproduction and consequently lead to population declines (Congdon et al., 1982). Further, amphibians risk desiccation because their skin does not prevent evaporative water loss (Jørgensen, 1997).

Thermoregulation coupled with the risk of desiccation may make downed woody debris particularly important to amphibians. Hence, amphibians often use downed woody debris, which provides micro-habitats in a range of temperature and moisture regimes, with the temperature under and inside woody refugia often lower than ambient (Graham, 1925; Whiles and Grubaugh, 1996; Butts and McComb, 2000; Kluber et al., 2009). Other than protection from desiccation and thermoregulation, amphibians use downed woody debris for reproduction and as a feeding substrate (Hassinger, 1989; Whiles and Grubaugh, 1996). Therefore, amphibian populations may be sensitive to reductions of downed woody debris associated with harvesting woody biomass.

We employed two methods to assess selection of downed woody debris by southern toads (*Anaxyrus terrestris*) in southeastern United States Coastal Plain loblolly pine (*Pinus taeda*) plantations following clearcut and woody biomass harvests: (1) a manipulative enclosure experiment that compared nocturnal habitat selection and diurnal refuge site selection among treatments with varying areas of ground covered by coarse woody debris (CWD; defined here as downed woody debris $\geq$ 7.62 cm in diameter for a length of at least 0.91 m; Woodall and Monleon, 2008) in

different spatial allocations of CWD (i.e., piled or dispersed); and, (2) a radio-telemetry study that investigated diurnal microhabitat selection in relation to availability of downed woody debris. We used the southern toad as an indicator of amphibian response to woody biomass harvests because southern toads are less susceptible to forest canopy removal than other amphibians and, therefore, are among the most abundant species in regenerating clearcuts (Homyack et al., 2013; Fritts, 2014). Southern toads are capable of storing and reabsorbing large quantities of water in their bladders and tolerate higher temperatures and desiccation risks than other amphibians (Thorson and Svihla, 1943; Hillyard, 1999). Hence, southern toads have been used as a conservative metric for examining potential impacts of silviculture on amphibians (Todd and Rothermel, 2006). We also examined relationships between environmental variables (i.e., rainfall and temperature) and selection of downed woody debris to assess how climatic conditions may affect the importance of woody biomass to amphibians. We predicted that toads would select downed woody debris for nocturnal activity and for diurnal refuges in both the enclosure and radio telemetry experiments, particularly during hot and dry weather conditions. Further, we hypothesized that piled CWD would provide cooler microclimates than CWD dispersed evenly across the same amount of ground area and predicted that toads would select piled CWD over dispersed CWD.

2. Methods

2.1. Study area

We examined habitat selection of southern toads in a regenerating loblolly pine stand in the southeastern Coastal Plain Physiographic Region in Beaufort County, North Carolina. The project was part of a large-scale study to evaluate wildlife response to woody biomass harvesting. The radio-telemetry study was conducted on a 75.4-ha site that contained six woody biomass treatments each with varying volumes of retained downed woody debris (Fritts et al., 2014). The enclosure was located in the same regenerating stand, but outside of the aforementioned treatment boundaries. The stand was clearcut for roundwood and woody biomass and had treatment implementation winter 2010–2011. The site received two post-harvest herbicide applications with Chopper© (BASF Corporation, Research Triangle Park, North Carolina): a broadcast application year one post-harvest and a banded application year two post-harvest (i.e., after re-planting). Following clearcut and woody biomass harvests but before our study, the site was V-sheared to prepare a planting surface. The site was bedded and replanted fall 2011-winter 2012 (i.e., year two post-harvest and before sampling) at a density of ≈1100 trees/ha. Parallel drainage ditches occurred throughout the sites to improve pine growth and survival.

2.2. Data collection

2.2.1. Enclosure trials

We compared southern toad habitat selection among treatments with varying ground area coverage and spatial distributions of CWD using an enclosure experiment during May–August 2013. In 2012 (after bedding and planting), we constructed an 8-m × 8-m (i.e., 64 m^2) enclosure $\geq$ 50 m from the nearest ditch or road. We randomly assigned four 16-m^2 treatments to the four quadrants of the enclosure: (1) ≈100% of the ground surface area covered by CWD in one large pile (volume of CWD = 1.10 m^3, 100CWD); (2) ≈50% of the ground area covered with CWD in one large pile (volume of CWD = 0.60 m^3, 50PILE); (3) ≈50% of the ground area covered with CWD dispersed throughout the

treatment (volume of CWD = 0.25 m^3, 50DISP); and (4) no CWD (0CWD). We chose these treatments because existing Biomass Harvesting Guidelines typically recommend retaining up to 50% of marketable woody biomass on the forest floor either dispersed or in piles (MFRC 2007, PA DCNR 2008). We designed the treatments to focus on the ground area of each unit covered by piled CWD; hence, the linearity of the volumes was a biproduct of treatment creation. We also were interested in whether distribution of CWD affects microclimate or selection of CWD by toads and subsequently added the 50DISP treatment. In 50PILE and 100CWD, a second layer of debris was added to the ground layer to create CWD piles with no sunlight penetration; thus, the 50PILE treatment had more than twice the volume of the 50DISP treatment with the same area of ground covered by CWD and the 100CWD had more than four times the volume of the 50DISP treatment with twice the ground area coverage. All CWD was ⩾20 cm from the treatment boundaries to avoid potential interference with antenna wires; therefore, an area with no CWD existed on the edges of all treatments including 100CWD. The outside barrier of the enclosure consisted of 1-m-tall silt fencing buried ⩾20 cm into the ground to avoid subterranean movement of toads. Each treatment contained approximately equal areas covered by bedded soil and seedling pine trees. We created treatments by clearing all vegetation, leaf litter, and woody biomass from inside the enclosure and placing large pine logs into the enclosed treatments. Woody biomass harvests typically glean CWD as opposed to smaller diameter downed woody debris; therefore, we exclusively used CWD in our enclosure experiment. We constructed the enclosure in 2012, one year prior to toad sampling, to allow CWD to weather so that the microhabitat under the wood would become well-established. Before sampling, CWD was progressing from decay stage two into decay stage three (Maser et al., 1979). We removed vegetation from the enclosure as needed to minimize effects from factors other than CWD.

We conducted habitat selection trials using an antenna system that detected Passive Integrated Transponder (PIT) tags (Oregon RFID, Portland, Oregon, USA). We created antennas using 10 American wire gauge thermoplastic high heat-resistant nylon coated wire and surrounded each treatment on two sides within the enclosure with one loop of wire to create one antenna per treatment (Fig. 1). Where wires intersected the silt fence, we pulled wires through the barrier so that toads traveling near the periphery would not continuously activate the antennas and drain the power source. We connected each antenna to a standard remote tuning board (Oregon RFID, Portland, Oregon, USA) and connected tuning boards to a multi-antenna HDX data logger (Oregon RFID, Portland, Oregon, USA) using Twinax cables (Oregon RFID, Portland, Oregon, USA). The system was powered with a 12-volt marine battery.

We captured adult male and female toads active on forest roads at night within an 8-km radius of the enclosure. We captured toads from all directions from the enclosure site. We placed individuals in a 1-m diameter × 50-cm deep plastic container with soil and distilled water for 24–72 h, to ensure toads started the experiment hydrated. We fed crickets (*Acheta domesticus*) to toads *ad libitum*. The plastic container remained outdoors but was shaded so that toads were exposed to natural temperatures and photoperiod. Before using toads in a trial, we glued a 12-mm PIT tag (Oregon RFID, Portland, Oregon, USA) onto the posterior dorsum using medical-grade cyanoacrylate gel adhesive. Cyanoacrylate adhesive has been used on anurans with no detectable adverse effects (Christy, 1996; Horan, 2007). We released ⩽5 toads, depending on our ability to capture study animals, at the center of the enclosure between 2030 and 2130 for 48-h trials. We restricted trials to 48 h to limit potential PIT tag loss from the toads shedding their skin. Our experimental density of ⩽5 toads within one 16-m^2 treatment was lower than natural, post-metamorphic densities of

southern toads along pond margins (Beck and Congdon, 1999). We placed antenna wires ≈10 cm within each treatment and ⩾10 cm from woody debris, and we tuned antennas so that PIT tags within ≈10 cm of an antenna would activate a transfer of data from the PIT tag to the data logger (i.e., a "hit"). Therefore, a hit was possible only when a toad was within the treatment and not between treatment boundaries. Antennas scanned for PIT tags in sequence (i.e., Treatment 1 (100CWD), Treatment 2 (50PILE), Treatment 3 (50DISP), and Treatment 4 (0CWD)) every 2.3 s. For each hit, the date, time, PIT tag number, and antenna number (i.e., treatment plot location of a toad) were stored on the data logger. We downloaded data from the data logger every other day. Following enclosure trials, we released recovered toads near their capture site, although exact capture locations were not recorded. All procedures were approved by the North Carolina State University Institutional Animal Care and Use Committee (11-022-O) and the North Carolina Wildlife Resources Commission (scientific collection permit number 11SC00534).

We quantified ground temperatures every 30 min using a pair of Thermocron I-buttons (Maxim, San Jose, California, USA) at three locations in each treatment plot: in the center; on the interior edge; and halfway between the center and interior edge (Fig. 1). We placed I-buttons either under CWD or in the open (i.e., not under CWD) and inside 10-cm-tall segments of PVC piping hammered 4 cm into the ground to prevent loss. In 100CWD and 50PILE, we positioned two I-buttons (i.e., one container) under the center of the downed woody debris pile, two under downed woody debris on the edge of the pile, and two in the open to collect ground temperatures. In 50DISP, we positioned two I-button containers, each with two I-buttons, under separate logs and the third container in the open. In 0CWD, all I-buttons were in the open because no CWD was present. We used the temperature data to determine the mean ground temperature during each 48-h toad trial. We estimated daily rainfall using a rain gauge (Rainwise, Trenton, Maine, USA) located ≈6 km from the enclosure.

2.2.2. Radio-telemetry

We captured toads using 18 'Y'-shaped drift fence arrays with 7.6-m arms within the study area (Fritts, 2014). Drift fences were constructed of silt-fence material with a 19-L plastic bucket buried flush with the ground at each end. We drilled three small holes in the bottom of each bucket for water drainage and every day wetted sponges in each pitfall trap. We housed toads as described above. We attached Holohil BD-2 transmitters (0.90 g, Holohil Systems, Ltd., Carp, Ontario, Canada) to female toads weighing ⩾20 g using a belt attachment. The belt and transmitter weighed ≈1.1 g. Belts and transmitters were <10% of the toad's body weight (Berteaux et al., 1994). We threaded flexible silicone tubing with a 1.5-mm inside diameter (Harvard Apparatus, Holliston, Massachusetts, USA) through a loop soldered onto each radio to make the belts. We threaded medium-weight, nylon monofilament fishing line through the silicone, placed the belt with the attached radio transmitter around the toad directly anterior to the hind legs with the transmitter resting dorsally, and tied a knot in the fishing line. All fishing line was covered by the silicone tubing to limit skin irritation.

We released toads at random locations within the clearcut ⩾50 m from the nearest road, ditch, or stand edge between 2030 and 2130. We located each toad daily between 0700 and 1800 with a handheld three-element Yagi antenna by homing (White and Garrott, 1990) until we visually located individuals or their burrow or cover source. We estimated groundcover at each toad location and at a paired location at a random direction 10 m from each toad location. The clearcut had relatively homogenous vegetation structure and 10 m from the toad location provided potential access to each type of available groundcover. We centered a 0.5-m^2 PVC frame on the toad and random locations and estimated %
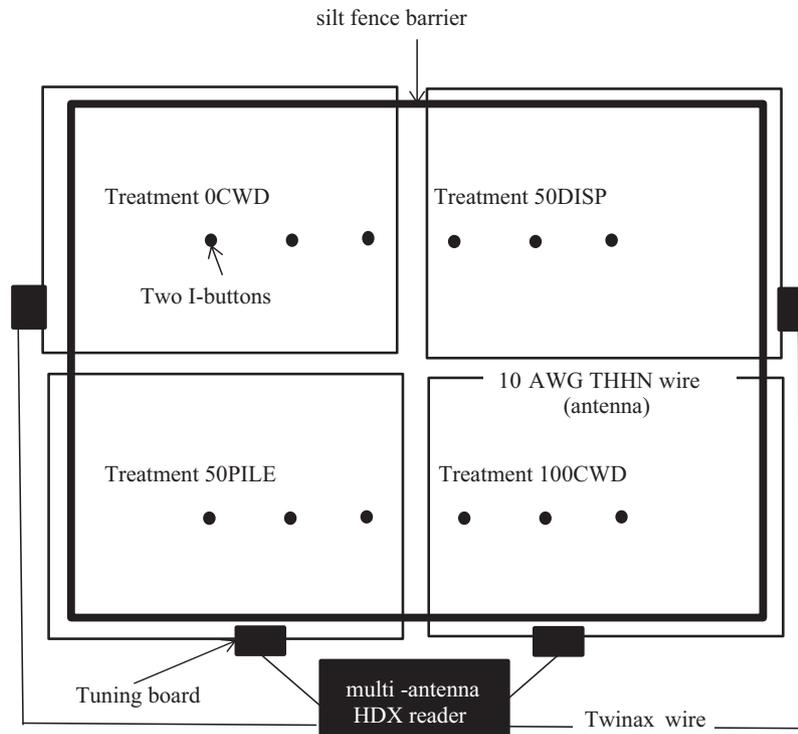
Fig. 1. Schematic of enclosure used to assess southern toad (*Anaxyrus terrestris*) habitat selection in four 16-m² treatments with varying ground areas covered by coarse woody debris (CWD) and spatial allocations of CWD: (1) bare ground with 100% of the area covered by CWD (1.10 m³, 100CWD); (2) bare ground with ≈50% of the area covered with CWD in one large pile (0.60 m³, 50PILE); (3) bare ground with ≈50% of the area covered with CWD dispersed evenly throughout the treatment (0.25 m³, 50DISP); and (4) no CWD (0CWD) in a regenerating loblolly pine (*Pinus taeda*) plantation stand in Beaufort County, North Carolina (not drawn to scale).

groundcover of CWD, fine woody debris (FWD; downed woody debris smaller than CWD), leaf litter, grass, forbs, woody vegetation, bare ground, and water (i.e., puddled rainwater). We checked the belts every 5 days to ensure proper fitting. At the end of the radio-telemetry project, radiotags were removed and toads were released within 100 m of their capture site.

2.3. Statistical analysis

2.3.1. Enclosure trials

Toads are active nocturnally throughout the summer (Lannoo, 2005); therefore, we analyzed nocturnal habitat selection and diurnal refuge site selection separately. We determined nocturnal habitat selection by calculating the proportion of time each toad spent in each treatment during nocturnal hours. We assumed toads remained within a single treatment when there was more than one consecutive hit (i.e., an entrance hit and an exit hit) on the same antenna. We assumed the first hit was when the toad entered the treatment and each subsequent hit was when the toad approached the antenna, but did not cross the antenna to exit the treatment. We assumed toads exited a treatment when the next hit was recorded on a different antenna (i.e., the toad entered a different treatment). When only one hit was recorded on an antenna, we assumed the toad approached the treatment boundary, but did not enter the treatment; therefore we did not use the associated hit in analysis. We calculated time spent in each treatment by subtracting the time of the earliest antenna hit from the time of the latest antenna hit for each consecutive series of hits of the same antenna. We summed the total time spent in each treatment for each toad over the entire trial and calculated the proportion of time each toad spent in each treatment.

We used package adehabitat (Calenge, 2006) in statistical program R (R Core Team, 2012) to conduct a parametric compositional

analysis to determine if the proportion of time spent in each treatment during nocturnal hours differed from treatment availability. We used a matrix of proportion of time each toad spent in each treatment during nocturnal hours with each column representing a treatment and each row representing a toad (i.e., the toad was the unit of replication) compared to a matrix of proportions of time available for each treatment (i.e., time available for each treatment = 25%).

We examined temperatures with three separate analyses. First, we compared temperatures between I-buttons under CWD across all treatments and those in the open across all treatments using one-way Analysis of Variance (ANOVA). Second, we tested for differences in temperatures under CWD among the three treatments with CWD (i.e., 100CWD, 50PILE, and 50DISP) using one-way ANOVA. Last, we averaged temperatures across days and tested for differences among treatments in mean daily temperature using a one-way ANOVA. We used Tukey's Studentized Range criteria to separate treatment means when models were significant at $\alpha = 0.05$.

We used four univariate ANOVA tests to determine if mean ground temperature in the enclosure and rain were predictors of nocturnal habitat selection. The dependent variable for each ANOVA was a vector of proportion of time spent in one treatment for each toad during nocturnal hours (Aebischer et al., 1993; Aitchison, 1986). We used rain as a binomial variable because the rain gauge was ≈6 km from the enclosure and we could not estimate exact rainfall at the enclosure site. The independent variables were rain occurrence (1 = rain occurred during the trial and 0 = rain did not occur during the trial) and a vector of mean ground temperature in the enclosure in all treatments during each trial (i.e., mean temperature for each 48-h period, both day and night, estimated over the 24 I-buttons). We included an interaction term between rain and temperature. We considered a covariate as a

predictor of nocturnal habitat selection if the associated *P*-value was $\leqslant 0.05$.

Antennas never received hits after sunrise, so we determined the treatment that toads used for diurnal refuge by identifying the antenna with the last hit of the night (i.e., we assumed the toad was no longer active and seeking refuge for the day). We calculated the proportion of the days toads spent in each treatment by counting the number of days toads spent in each treatment and dividing by the total number of days toads spent in all treatments.

When toads remained in the enclosure, but were unable to be located because they were under piled CWD or buried, we used only the first 48 h of data in the analysis. Further, if a toad was unable to be recovered, we included the total number of toads in the enclosure when determining the number of new toads to place within the enclosure so that the density was never >5 toads.

2.3.2. Radio-telemetry

We analyzed diurnal locations of radio-marked female toads using a global mixed-effects logistic regression model with a binomial response (i.e., 1 = toad location, 0 = random location). We used estimated % groundcover of each cover type (i.e., CWD, fine woody debris, leaf litter, grass, forb, woody vegetation, bare ground, and standing water) as independent continuous covariates. We used the individual toad as a random effect to allow for correlation among observations of the same toad. We used variance inflation factors to assess collinearity among independent variables and dropped a covariate from the analysis if the factor was >3 (Zuur et al., 2009). We did not include data from toads that had only one observation. We ran the global model and considered an estimated groundcover type as a predictor of diurnal refuge selection if it had an associated *P*-value $\leqslant 0.05$.

3. Results

3.1. Enclosure trials

We captured 63 toads (44 females and 19 males) for enclosure trials. We omitted 16 toads from analysis because the toads were not recovered and did not have antenna hits for the complete 48-h trial. Hence, we used 47 adult toads (31 females and 16 males) in the enclosure trial analysis. Eleven of the 47 toads (3 males and 8 females) were not recovered at the end of the trial period, but data from these toads were not deleted from the analysis because we received antenna hits for at least the entire 48-h trial.

Toads did not use treatments randomly during nocturnal hours ($n = 47$, $\Lambda = 0.49$, $P < 0.01$; Table 1). The ranking of nocturnal habitat selection from most selected to least was 0CWD, 100CWD, 50DISP, 50PILE. Overall, temperatures were 2.10 °C cooler under CWD than in the open ($F_{1,83537} = 1997.4$, $P < 0.01$). Temperatures under CWD differed among the three treatments that contained CWD ($F_{2,39545} = 61.05$, $P < 0.01$) and were 0.55 °C cooler in 100CWD than in 50PILE ($P < 0.01$) and 0.70 °C cooler in 100CWD than 50DISP ($P < 0.01$), but temperatures under CWD did not differ between 50PILE and 50DISP ($P = 0.14$). Daily mean ground temperatures across treatments were (mean ± SE) 27.41 °C ± 0.46 °C in 0CWD, 26.12 °C ± 0.37 °C in 50DISP, 25.94 °C ± 0.28 °C in 50PILE, and 25.29 °C ± 0.23 °C in 100CWD. Daily mean ground temperatures differed among treatments ($F_{3,96} = 6.27$, $P < 0.01$) and were 2.13 °C greater in 0CWD than 100CWD ($P < 0.01$), and 1.47 °C greater in 0CWD than 50PILE ($P = 0.02$).

Twenty-two toad trials were omitted from the ANOVA analyses to evaluate effects of weather on nocturnal habitat selection because of missing temperature data; therefore, we performed an ANOVA on 25 toad trials. Mean trial ground temperature did not predict the proportion of time a toad ($n = 25$) spent in 0CWD

Table 1

Ranking matrices, sample size (*n*), lambda (*Λ*), and probability values based on southern toad (*Anaxyrus terrestris*) proportional nocturnal habitat use within an enclosure with four 16-m² treatments with varying ground areas covered by coarse woody debris (CWD) and spatial allocations of CWD: (1) bare ground with 100% of the area covered by CWD (1.10 m³, 100CWD); (2) bare ground with ≈50% of the area covered with CWD in one large pile (0.60 m³, 50PILE); (3) bare ground with ≈50% of the area covered with CWD dispersed evenly throughout the treatment (0.25 m³, 50DISP); and (4) bare ground with no CWD (0CWD). The enclosure was in a regenerating loblolly pine (*Pinus taeda*) plantation stand three years post-clearcut in Beaufort County, North Carolina (May–August 2013). A single sign represents no significant deviation from random at $P \leqslant 0.05$ and a triple sign represents significant deviation from random at $P \leqslant 0.05$.

	Treatment				*n*	*Λ*	*P*
	0CWD	50DISP	50PILE	100CWD			
0CWD	0	+++	+++	+	47	0.49	<0.01
50DISP	− − −	0	+++	−			
50PILE	− − −	− − −	0	− − −			
100CWD	−	+	+++	0			

($F_{1,21} = 0.58$, $P = 0.46$), 50DISP ($F_{1,21} = 2.13$, $P = 0.16$), or 50PILE ($F_{1,21} = 0.58$, $P = 0.46$). Rain did not predict the proportion of time a toad spent in 0CWD ($F_{1,21} = 0.08$, $P = 0.78$), 50DIS ($F_{1,21} = 2.10$, $P = 0.16$), or 50PILE ($F_{1,21} = 0.89$, $P = 0.36$). There was an interaction between rain and mean trial ground temperature ($F_{1,21} = 4.86$, $P = 0.04$) for the proportion of time a toad spent in 100CWD (Fig. 2). When rain occurred during the trial (i.e., rain = 1), mean trial ground temperature was not a predictor of the proportion of time toads spent in 100CWD ($\beta = 0.01$, $t = 0.23$, $P = 0.82$). When rain did not occur during the trial (i.e., rain = 0), toads spent a greater proportion of time in 100CWD as mean trial ground temperature increased ($\beta = 0.18$, $t = 2.60$, $P = 0.03$; Fig. 2). Seventy-five percent of diurnal refuge sites were in 100CWD, and each of the other three treatments contained 8.3% of diurnal refuge sites.

3.2. Radio-telemetry

We attached radio transmitters to 40 individual female toads. Three toads were omitted because we located the toad only one time before either the belt slipped ($n = 1$) or the toad died from an undetermined cause ($n = 2$). We acquired between two and 27 locations (mean = 7.10; SE = 1.22) per toad before the toad was depredated, died of other causes, or moved into a ditch or offsite and was unable to be recovered. Toads occasionally traveled into ditches (0.02% of toad locations) that were covered with vegetation, and in these cases we could not estimate groundcover because of the inability to visually locate the toad. The covariance inflation factor for forb groundcover was >3, so we omitted forb groundcover from the model. Toads ($n = 37$) avoided grass ($\beta = -0.02$, $z = -3.40$, $P < 0.01$) and bare ground ($\beta = -0.06$, $z = -5.05$, $P < 0.01$) as diurnal refuge sites. There was no significant relationship with CWD cover ($\beta = 0.02$, $z = 1.59$, $P = 0.11$) or fine woody debris cover ($\beta = -0.01$, $z = -1.41$, $P = 0.16$; Fig. 3). Toad diurnal refuge locations included under CWD (34.94%; including 21.69% of refuges in or under piled CWD and 13.25% of refuges in or under a single piece of CWD), under live vegetation (30.12%), in or under fine woody debris/sawdust (13.25%), in a ditch (13.25%), in the open/not in a refuge (4.82%), and burrowed into soil (3.61%).

4. Discussion

Southern toads used large CWD piles as diurnal refuge sites but selected areas with no CWD during nocturnal hours. Although radio-marked toads often were located under or near CWD in the daytime, toads also used other sources of cover for diurnal refuges,
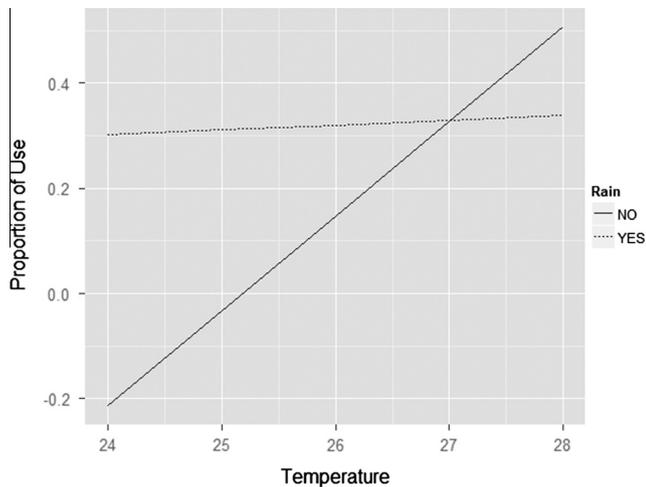
Fig. 2. The interaction between rain (binomial) and temperature (°C) in 100CWD treatment resulting from an analysis of variance of southern toad (*Anaxyrus terrestris*; *n* = 47) proportional nocturnal habitat use within an enclosure with four 16-m² treatments with varying ground areas covered by coarse woody debris (CWD) and spatial allocations of CWD: (1) bare ground with 100% of the area covered by CWD (1.10 m³, 100CWD); (2) bare ground with ≈50% of the area covered with CWD in one large pile (0.60 m³, 50PILE); (3) bare ground with ≈50% of the area covered with CWD dispersed evenly throughout the treatment (0.25 m³, 50DISP); and (4) bare ground with no CWD (0CWD) in a regenerating loblolly pine (*Pinus taeda*) plantation stand three year post-clearcut in Beaufort County, North Carolina (May–August 2013).

including woody vegetation, herbaceous groundcover, and fine woody debris, indicating their ability to use what cover was available. Conversely, southern toads in the enclosure used 100CWD for diurnal refuge, likely because we removed other cover sources (e.g., vegetation) as part of the experiment. Therefore, the combination of results indicates toads exhibit behavioral plasticity
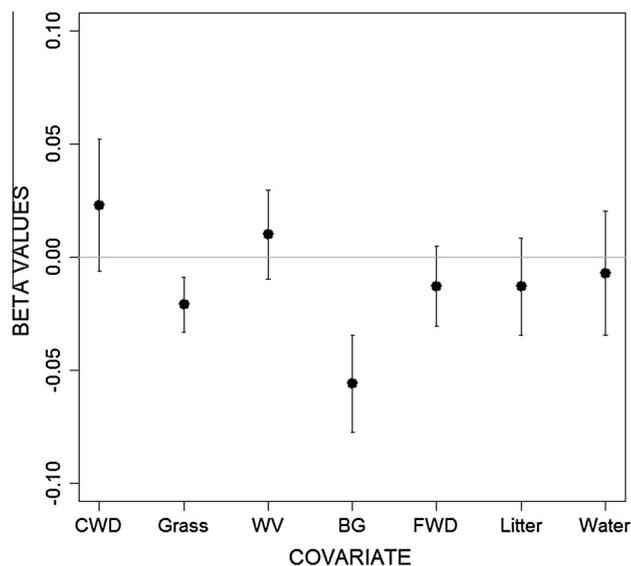

Fig. 3. Beta (*β*) value estimates and 95% confidence intervals of parameters from a global mixed effects logistic regression model of radio-transmitted female southern toad (*Anaxyrus terrestris*; *n* = 37) diurnal refuge selection in a regenerating loblolly pine (*Pinus taeda*) plantation stand three years post-clearcut in Beaufort County, North Carolina (May–August 2013). We considered a covariate significant if $P \leqslant 0.05$. Covariates included CWD = coarse woody debris ($P = 0.11$), grass ($P < 0.01$), WV = woody vegetation ($P = 0.32$), BG = bare ground ($P < 0.01$), FWD = fine woody debris ($P = 0.16$), Litter = leaf litter ($P = 0.24$), and water ($P = 0.60$).

in selecting diurnal refuge sites when a variety of cover sources are available.

Southern toads in the enclosure exhibited thermoregulatory behavior based on temperature and precipitation and used 100CWD more often as temperatures increased and when rain did not occur, presumably to decrease desiccation risk. Amphibians experience rapid water loss through their permeable skin at high temperatures and at low humidity (Vitt and Caldwell, 2009). Behavioral hypothermia in toads reduces water loss (Malvin and Wood, 1991), and southern toads are known to exhibit thermoregulatory behavior based on hydration state (Forster, 2013). Similar to American toads (*A. americanus*), which sought lower temperatures that decrease evaporative water loss when dehydrated (Tracy et al., 1993), southern toads used 100CWD more often when rain did not occur and temperature increased. Radio-marked toads also may have been exhibiting thermoregulatory behavior by avoiding bare ground during daytime hours, likely to minimize water loss. Further, increases in temperature directly affect amphibian metabolic rates and energy expenditure (Pough, 1980; Rome et al., 1992; Homyack et al., 2010), which may encourage ecological trade-offs that influence an individual's fitness, such as growth (Congdon et al., 1982; Sears, 2005; DuRant et al., 2007). For example, newly metamorphosed western toads (*Anaxyrus boreas*) maximize energy ingestion, linear growth, and weight increase at 27 °C and behaviorally thermoregulate to keep their body at that temperature by changes in location (Lillywhite, 1970, 1973). Although we are unsure of the precise motive, southern toads in the enclosure collectively changed their nocturnal locations to use 100CWD more often when temperatures increased. Therefore, cover sources that maintain preferable microclimates, may become more critical to amphibians in a warmer and drier climate as is predicted for the southeastern United States (IPCC, 2013, U.S. Global Change Research Program, 2014). Contrary to our predictions, toads did not select between piled and dispersed CWD in the enclosure experiment (i.e., 50PILE and 50DISP) or radio-telemetry study likely because temperature did not differ despite whether CWD was dispersed or in small piles, as demonstrated by the I-buttons in those two enclosure treatments.

Southern toads in the enclosure used CWD in 100CWD for diurnal refuge presumably because the temperature under CWD in the large pile was cooler than under CWD in the other treatments. Piled CWD has been demonstrated to lower desiccation risk in anurans (Seebacher and Alford, 2002; Rittenhouse et al., 2008). Thus, retaining relatively large piles (i.e., larger than the pile in the 50PILE enclosure treatment) of CWD dispersed throughout the landscape to provide cover during hot and dry weather before vegetation becomes established may limit impacts of woody biomass harvesting on some amphibians, particularly those with high desiccation risk. Although radio-marked toads selected CWD for diurnal refuge mostfrequently even when vegetation was available for cover (i.e., during year three post-clearcut), they also used live vegetation and other material for cover. However, toads may have used CWD more extensively during year one post-clearcut, before vegetation became well established. Clearcut harvesting temporarily can increase soil and air temperatures (Valigura and Messina, 1994), and retaining downed woody debris following timber harvests may mitigate negative effects on amphibians (deMaynadier and Hunter, 1995), particularly before vegetation cover is available. Protective microhabitats have the potential to buffer climate extremes and likely reduce mortality during extreme climate events (Scheffers et al., 2014). Radio-telemetry results suggest that when vegetation or other cover sources are available, CWD may be a less important cover source for adaptable species like southern toads. However, toads still used CWD extensively when vegetation was well-established. These results suggest that sensitive

amphibians, such as some species of terrestrial salamanders, may be more reliant on retained CWD because they are less vagile and typically are more susceptible to desiccation than toads.

Radio-marked southern toads avoided bare ground for diurnal refuge, but toads within the enclosure selected bare ground during nocturnal hours, likely for foraging. Previous research in southeastern U.S. Coastal Plain pine forests found no differences in southern toad diet composition or prey abundance or frequency among forested treatments with CWD experimentally removed, CWD experimentally increased 5-fold, and an unmanipulated control (Moseley et al., 2005). Although abundance of some invertebrate groups can be negatively affected by CWD removal (Harmon et al., 1986; McCay et al., 2002), captures of some ant species (a primary prey of southern toads (Moseley et al., 2005)), such as invasive fire ants (Solenopsis invicta), can be greater in clearcuts with CWD removed than in clearcuts with CWD retained, unharvested forested stands, and thinned forest stands in the southeastern United States Coastal Plain (Todd et al., 2008). Our results agree with Moseley et al. (2005) that downed woody debris in early decay stages may not be important foraging substrate for southern toads in southeastern Coastal Plain pine forests because toads within the enclosure spent the majority of nocturnal hours away from CWD.

Although a tendency to relocate or move toward home or breeding sites after experimental relocation has been observed in many anurans (Bogert, 1947; Dole, 1968; Jameson, 1957), we did not analyze homing behavior because exact capture locations were not linked to individual toads. However, southern toad homing abilities decrease with distance from the home site with nearly 37% returning from ≈420 m, 20% from 690 m, 17% from 930 m, and 19% from 1609 m (Bogert, 1947). A few southern toads used in the enclosure study were captured within 420 m of the study site, but the majority was captured >500 m from the study site. Additionally, it is not known whether southern toads return to their former sites directly or wander in different directions before returning. For example, American toads (A. americanus) are able to return to their former sites after displacement of up to 235 m, but many return by indirect routes (Dole, 1972). We assumed toads returning home indirectly instead of in a straight trajectory would not impact habitat selection results. Further, if homing did occur in toads within the enclosure, we expected the effects to be minimal because we captured toads on roads in all directions surrounding the study site with relatively equal effort.

5. Conclusion

Our results indicated individual southern toads selected downed woody debris under certain conditions; however, further research is needed to understand the effects of operational-scale woody biomass harvests on southern toads and other amphibians at the population level. Current woody biomass harvests on our study sites retained ⩾16.28 m^3/ha of downed woody debris (Fritts et al., 2014). This volume exceeds by over threefold sustainability recommendations set by the Forest Guild (Perschel et al., 2012) and may be above the threshold needed to sustain amphibian populations, if a threshold exists. However, as markets for wood-based energy expand and technological advances in conversion and harvest machinery occur, there may be less downed woody debris, particularly CWD, retained following woody biomass harvests (Haynes, 2003; Perlack et al., 2005; Janowiak and Webster, 2010). We recommend research that quantifies the minimum volume of CWD needed to sustain amphibian populations following timber harvests. This information in conjunction with results from mechanistic studies like ours can be used to guide development of best management practices that ensure sustainability of woody biomass harvests.

References

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74, 1313–1325.

Aitchison, J., 1986. The Statistical Analysis of Compositional Data. Chapman and Hall, London, New York, USA.

Beck, C.W., Congdon, J.D., 1999. Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (Bufo terrestris) metamorphosis. Can. J. Zool. 77, 944–951.

Becker, C.G., Fonseca, C.R., Haddad, C.F.B., Batista, R.F., Prado, P.I., 2007. Habitat split and the global decline of amphibians. Science 318, 1775–1777.

Berteaux, D., Duhamel, R., Bergenson, J.M., 1994. Can radio collars affect dominance relationships in Microtus? Can. J. Zool. 72, 785–789.

Bogert, C.M., 1947. Results of the Archbold Expeditions No. 57. A field study of homing in the Carolina toad. Am. Mus. Novit. 1355, 1–24.

Butts, S.R., McComb, W.C., 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. J. Wildl. Manage. 64, 95–104.

Calenge, C., 2006. The package adehabitat for the R software, a tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519.

Christy, M.T., 1996. The efficacy of using Passive Integrated Transponder (PIT) tags without anaesthetic in free-living frogs. Aus. Zool. 30, 139–142.

Congdon, J.D., Dunham, A.E., Tinkle, D.W., 1982. Energy budgets and life histories of reptiles. In: Gans, C. (Ed.), Biology of the Reptilia. Academic Press, New York, USA, pp. 233–271.

Davidson, C., Shaffer, H.B., Jennings, M.R., 2002. Spatial tests of the pesticide drift, habitat destruction, UB-B, and climate change hypothesis for California amphibian declines. Conserv. Biol. 16, 1588–1601.

Davis, J.C., Castleberry, S.B., Kilgo, J.C., 2010. Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. For. Ecol. Manage. 259, 1111–1117.

Delis, P., Hushinsky, H., McCoy, E., 1996. Decline of some west-central Florida anuran populations in response to habitat degradation. Biodivers. Conserv. 5, 1579–1595.

deMaynadier, P.G., Hunter Jr, M.L., 1995. The relationship between forest management and amphibian ecology, a review of the North American literature. Environ. Rev. 3, 230–261.

Dole, J.W., 1968. Homin in leopard frogs Rana pipiens. Ecology 49, 386–399.

Dole, J.W., 1972. Homing and orientation of displaced toads, Bufo americanus, to their home sites. Copeia 1972, 151–158.

DuRant, S.E., Hopkins, W.A., Talent, L.E., 2007. Energy acquisition and allocation in an ectothermic predator exposed to a common environmental stressor. Comp. Biochem. Physiol. Part C 145, 442–448.

Evans, J.M., Fletcher Jr., R.J., Alavalapati, J.R.R., Smith, A.L., Geller, D., Lal, P., Vasudev, D., Acevedo, M., Calabria, F., Upadhyay, T., 2013. Forestry Bioenergy in the Southeast United States. Implications for Wildlife Habitat and Biodiversity. National Wildlife Federation, Merrifield, Virginia, USA.

Forster, C.E., 2013. Dehydration in Southern Toads (Anaxyrus terrestris), Metabolic Costs and Effects of Temperature Selection. Scripps Senior Thesis. Paper 161.

Fritts, S.R., 2014. Can biomass harvesting guidelines sustain Herpetofauna following harvests of logging residues for renewable energy? In: Implementing Woody Biomass Harvesting Guidelines that Sustain Reptile, Amphibian, and Shrew Populations (Doctoral Dissertation). North Carolina State University, pp. 34–87.

Fritts, S.R., Moorman, C.E., Hazel, D.W., Jackson, B.D., 2014. Biomass harvesting guidelines affect downed woody debris retention. Biomass Bioenergy 70, 382–391.

Gatten, R.E., Miller, K., Full, R.J., 1992. Energetics at rest, during locomotion. In: Feder, M.E., Burggren, W.W. (Eds.), Environmental Physiology of the Amphibians. University of Chicago Press, Chicago, Illinois, USA, pp. 314–377.

Gibbs, J.P., 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. J. Wildl. Manage. 62, 584–589.

Goh, C.S., Junginger, M., Cocchi, M., Marchal, D., Thran, D., Hannig, C., Heinimo, J., Nikolaisen, L., Schouwenberg, P.P., Bradley, D., Hess, R., Jacobson, J., Ovard, L., Deutmeyer, M., 2013. Wood pellet market and trade, A global perspective. Biofuels, Bioprod. Biorefin. 7, 24–42.

Graeter, G.J., Rothermel, B.B., Gibbons, J.W., 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. J. Wildl. Manage. 72, 473–482.

Graham, S.A., 1925. The felled tree trunk as an ecological unit. Ecology 6, 397–416.

Haddad, N.M., 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. 153, 215–227.

Hanson, C., Yonavjak, L., Clarke, C., Minnemeyer, S., Boisrobert, L., Leach, A., Schleeweis, K., 2010. Southern Forests for the Future. World Resources Institute, Washington, DC, USA.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Harper, E.B., Rittenhouse, T.A.G., Semlitsch, R.D., 2008. Demographic consequences of terrestrial habitat loss for pool-breeding amphibians, predicting extinction risks associated with inadequate size of buffer zones. Conserv. Biol. 22, 1205–1215.

Hassinger, J.D., 1989. Dead wood for wildlife. In: Proceedings of the 1989 Penn State Forest Resources Issues Conference, April 4–6 1989. University Park, Pennsylvania, USA, pp. 171–184.

Haynes, R.W., 2003. An analysis of the timber situation in the United States, 1952 to 2050. United States Department of Agriculture Forest Service, PNW-GTR-560. Pacific Northwest Research Station, USA.

Hillyard, S.D., 1999. Behavioral, molecular and integrative mechanisms of amphibian osmoregulation. J. Exp. Zool. 283, 662–674.

Homyack, J.A., Haas, C.A., Hopkins, W.A., 2010. Influence of temperature and body mass on standard metabolic rate of eastern red-backed salamanders (Plethodon cinereus). J. Therm. Biol. 35, 143–146.

Homyack, J.A., Aardweg, A., Gorman, T.A., Chalcraft, D.R., 2013. Initial effects of woody biomass removal and intercropping of switchgrass (Panicum virgatum) on herpetofauna in eastern North Carolina. Wildl. Soc. Bull. 37, 327–335.

Horan III, R.V., 2007. Evaluation and Application of Novel Telemetry Methods for the Study of Movements and Ecology of Tropical Hylids. M.S. Thesis. University of Georgia.

Huey, R.B., 1991. Physiological consequences of habitat selection. Am. Nat. 137, 91–115.

Intergovernmental Panel on Climate Change (IPCC), Climate Change, 2013. The physical science basis. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA.

International Union for Conservation of Nature (IUCN). 2013. The IUCN Red List of Threatened Species, Amphibians on the IUCN Red List, Geographic Patterns, Version 2013.2.

Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia 2, 265–268.

Jameson, D.L., 1957. Population structure and homing responses in the Pacific tree frog. Copeia 3, 221–228.

Janowiak, M.K., Webster, C.R., 2010. Promoting ecological sustainability in woody biomass harvesting. J. For. 108, 16–23.

Jørgensen, C.B., 1997. 200 years of amphibian water economy, from Robert Townsend to the present. Biol. Rev. 72, 153–237.

Kluber, M.R., Olson, D.H., Puettmann, K.J., 2009. Downed wood microclimates and their potential impact on Plethodontid salamander habitat in the Oregon coast range. Northwest Sci. 83, 25–34.

Lannoo, M. (Ed.), 2005. Amphibian Declines, The Conservation Status of United States Species. University of California Press, Berkeley and Los Angeles, California, USA.

Lillywhite, H.B., 1970. Behavioral temperature regulation in bullfrog, Rana catesbeiana. Copeia 1970, 158–168.

Lillywhite, H.B., 1973. Role of thermoregulation in growth energetics of toad, Bufo boreas. Ecology 54, 375–383.

Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11, 131–135.

Malvin, G.M., Wood, S.C., 1991. Behavioral thermoregulation of the toad, Bufo marinus, Effects of air humidity. J. Exp. Zool. 258, 322–326.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody debris. In: J.W. Thomas (Ed.), Wildlife Habitats in Managed Forests, the Blue Mountains of Oregon and Washington. United States Department of Agriculture Forest Service Agricultural Handbook No. 553, pp 78–95.

McCay, T.S., Hanula, J.L., Loeb, S.C., Lohr, S.M., McMinn, J.W., Wright-Miley, B.D., 2002. The role of coarse woody debris in southeastern pine forests: preliminary results from a large-scale experiment. In: W.F. Laudenslayer, Jr., P.J. Shea, B.E. Valentine, C.P. Weatherspoon, T.E. Lisle (Eds.). Proc. Symp. The Ecology and Management of Dead Woody in Western Forests. United States Department of Agriculture Forest Service Gen. Tech. Rep. PSW-181, pp. 135–144 [949p].

Mendell, B.C., Lang, A.H. 2012. Wood for Bioenergy, Forests as a Resource for Biomass and Biofuels. Forest History Society.

Minnesota Forest Resources Council (MFRC), 2007. Biomass harvesting guidelines for forestlands, brushlands, and open lands. Minnesota Forest Resources Council. St. Paul, Minnesota, USA.

Moseley, K.R., Castleberry, S.B., Hanula, J.L., Ford, W.M., 2005. Diet of southern toads (Bufo terrestris) in loblolly pine (Pinus taeda) stands subject to coarse woody debris manipulations. Am. Midl. Nat. 153, 327–337.

Muths, E. Gallant, A.L., Grant, E.H.C., Battaglin, W.A., Grmckieen, D.E., Staiger, J.S., Walls, S.C., Gunzburger, M.S., Kearney, R.F., 2006. The Amphibian Research and Monitoring Initiative (ARMI): 5-Year Report. Scientific Investigations Report

2006–5224, U.S. Department of the Interior U.S. Geological Survey, Reston, Virginia.

Owens, A.K., Moseley, K.R., McCay, T.S., Castleberry, S.B., Kilgo, J.C., Ford, W.M., 2008. Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (Pinus taeda) forests. For. Ecol. Manage. 256, 2078–2083.

Pennsylvania Department of Conservation and Natural Resources (PA DCNR), 2008. Harvesting Woody Biomass for Energy. Pennsylvania Department of Conservation and Natural Resources. Harrisburg, Pennsylvania, USA.

Perlack, R.D., Wright, L.L., Turhollow, A.F., Graham, R.L., Stokes, B.J., Erback, D.C., 2005. Biomass as Feedstock for a Bioenergy and Bioproducts Industry, The Technical Feasibility of a Billion-ton Annual Supply. United States Department of Energy. Oak Ridge National Laboratory. Oak Ridge, Tennessee, USA.

Perschel, B., Evans, A., DeBonis, M., 2012. Forest biomass retention and harvesting guidelines for the Southeast. Forest Guild Southeast Biomass Working Group. Forest Guild. Sante Fe, New Mexico, USA.

Pough, F.H., 1980. The advantages of ectothermy for tetrapods. Am. Nat. 115, 92–112.

Puttock, G.D., 1987. The economics of collecting and processing whole-tree chips and logging residues for energy. For. Products J. 37, 15–20.

R Core Team, 2012. R, A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

REN21, 2013. Renewables 2013 Global Status Report. Renewables Energy Policy Network for the 21st Century. Paris, France.

Rittenhouse, T.A., Harper, E.B., Rehard, L.R., Semlitsch, R.D., 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak-hickory forest. Copeia 2008, 807–814.

Rome, L.C., Stevens, E.D., John-Alder, H.B., 1992. The influence of temperature and thermal acclimation on physiological function. In: Feder, M.E., Burggren, W.W. (Eds.), Environmental Physiology of the Amphibians. University of Chicago Press, Chicago, Illinois, USA.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. Global Change Biol. 20, 495–503.

Schmidt, B.R., 2003. Count data, detection probabilities, and the demography, dynamics, distribution and decline of amphibians. C.R. Biol. 326, 119–124.

Sears, M.W., 2005. Resting metabolic expenditure as a potential source of variation in growth rates of the sagebrush lizard. Comp. Biochem. Physiol. Part A 140, 171–172.

Seebacher, F., Alford, R.A., 2002. Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (Bufo marinus). J. Herpetol. 36, 69–75.

Spotila, J.R., Standora, E.A., 1985. Energy budgets of ectothermic vertebrates. Am. Zool. 25, 95–125.

Stuart, W.B., Porter, C.D., Walbridge, T.A., Oderwald, R.G., 1981. Economics of modifying harvesting systems to recover energy wood. For. Products J. 31, 37–42.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.

Thorson, T., Svihla, A., 1943. Correlation of the habitats of amphibians with their ability to survive the loss of body water. Ecology 24, 374–381.

Todd, B.D., Rothermel, B.B., 2006. Assessing quality of clearcut habitats for amphibians, effects on abundances versus vital rates in the southern toad (Bufo terrestris). Biol. Cons. 133, 178–185.

Todd, B.D., Rothermel, B.B., Reed, R.N., 2008. Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles. Biol. Invasions 10, 539–546.

Tracy, C.R., Christian, K.A., O-Connor, M.P., Tracy, C.R., 1993. Behavioral thermoregulation by Bufo americanus, the importance of the hydric environment. Herpetologica 49, 375–382.

United States Global Change Research Program, 2014. Climate change impacts in the United States. United State National Climate Assessment, Washington, DC, USA.

Valigura, R.A., Messina, M.G., 1994. Modification of Texas clearcut environments with loblolly pine shelterwoods. J. Environ. Manage. 40, 283–295.

Vitt, L.J., Caldwell, J.P., 2009. Thermoregulation, Performance, and Energetics. In: Vitt, L.J., Caldwell, J.P. (Eds.), Herpetology, An Introductory Biology of Amphibians and Reptiles. Academic Press, San Diego, California, USA, pp. 191–216.

Watson, W.F., Stokes, B.J., Savelle, I.W., 1986. Comparisons of two methods of harvesting biomass for energy. For. Prod. J. 36, 63–68.

Whiles, M.R., Grubaugh, J.W., 1996. Importance of coarse woody debris to southern forest herpetofauna. In: McMinn, J.W., Crossley, D.A., Jr. (Eds.), Biodiversity and Coarse Woody Debris in Southern Forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests, Effects on Biodiversity. United States Department of Agriculture Forest Service General Technical Report SE-94, pp 94–100.

White, G.C., Garrott, R.A., 1990. Analysis of Wildlife Radio-tracking Data. Academic Press, San Diego, California, USA.

Woodall, C.W., Monleon, V.J., 2008. Sampling Protocol, Estimation, and Analysis Procedures for the Down Woody Debris Indicator of the FIA Program. United States Department of Agriculture Forest Service. Newtown Square, Pennsylvania, USA. NRS-GTR-22.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York, USA.