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Impacts of Shading on Larval Traits of the Frog *Litoria ewingii* in a Commercial Forest, Tasmania, Australia

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ABSTRACT.—**Removal of vegetation directly surrounding a breeding pond has the potential to significantly alter the environmental conditions experienced by larval amphibians during development and, therefore, may affect the life history of this and subsequent life stages. In this study, we investigated growth, development, and survivorship of *Litoria ewingii* as a result of different shading conditions in a commercially logged forest in Tasmania, Australia. We specifically investigated responses in two types of breeding ponds available to the species: permanent ponds, and smaller ephemeral ponds. Increased shading in permanent ponds resulted in reduced survival. Larval growth and development did not respond significantly to shading treatment in permanent ponds but were significantly affected by pond elevation. In ephemeral ponds, increased shading resulted in decreased developmental rate and a higher coefficient of variation for size at metamorphosis. Our findings suggest that the larval success of *L. ewingii* is not likely to be enhanced by vegetative buffer zones around permanent pond margins but may be enhanced by ensuring heterogeneity of shading conditions around ephemeral ponds.**

The growth of ectothermic animals is controlled predominantly by environmental conditions (Hota, 1994; Sokol, 1984), and amphibian life history, in particular, is known for its extreme plasticity (Wilbur and Collins, 1973). Amphibian larval growth, body size, larval period, and survival vary with numerous factors—temperature, water quality, food availability, predator community, competitors, and pond hydroperiod (for a review of factors affecting larval life history, see Hota, 1994).

Logging drastically alters the local habitat of adult amphibians and produces a heterogeneous landscape in terms of vegetation structure. Although the ecological consequences of logging upon adult amphibians have been the subject of numerous studies (see review by deMaynadier and Hunter, 1995), removal of vegetation directly surrounding a breeding pond also has the potential to significantly alter environmental conditions within breeding sites. The developmental history of larvae has important repercussions on adult traits relating to fitness. For example, increased size at metamorphosis has been positively correlated with increased adult size (Amezquita and Luddecke, 1999), and this may have consequences for fecundity (Kaplan and Salthe, 1979; Ponsero and Joly, 1998), male mating success (Howard, 1980; Berven, 1981), mobility within a landscape (Ponsero and Joly, 1998), desiccation risk (Bellis, 1962), and size-limited predation.

Increases in both shading and coarse woody debris resulting from increased canopy cover may alter both the quality and quantity of tadpole food within ponds. Werner and Glennemeier (1999) and Skelly et al. (2002) both demonstrated that poor resource quality in closed canopy ponds was largely responsible for the poor breeding performance of *Pseudacris crucifer* and *Rana pipiens*. A reduction in solar radiation entering ponds as a result of increased shading may also result in lower water temperatures (Werner and Glennemeier, 1999) and increased size at metamorphosis (Berven, 1982). Increased solar radiation entering less shaded pond waters may increase evaporation rates and decrease pond hydroperiod, and this, in turn, may reduce the duration of the larval period and size at metamorphosis. Increased canopy closure over ponds may also lead to an increase in leaf litter within ponds. Decomposition of this material may decrease dissolved oxygen concentrations in pond waters, affecting amphibian larval life history (Feder and Moran, 1985).

Pond size may also significantly alter the effects of shading because environmental conditions impose different pressures on inhabitants of permanent and ephemeral ponds. Ephemeral

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TABLE 1. Characteristics of permanent ponds used in Experiment 1.

	Pond			
	A	B	C	D
Elevation (m.a.s.l.)	89	177	110	490
Volume (m^3)	37	29	21	78
Max. depth (cm)	100	110	130	130
Surface area (m^2)	88	59	39	144
Shaded	yes	yes	no	no

ponds, for example, are typically less stable with greater temperature ranges, and variations in water quality and quantity. Because of smaller water volumes ephemeral ponds have a higher risk of desiccation, requiring pond inhabitants to develop and reproduce in more condensed time frames (Bonner et al., 1997) and exposing them to much greater competition. However, ephemeral ponds may give species that are adapted to them an advantage as they usually exhibit different predator species and a much lower abundance of predators than permanent ponds (Skelly, 1995). Therefore, the effect of pond shading interacting with pond permanence gradients is expected to impose different selective pressures upon pond residents in these two types of aquatic habitat.

In this study, we investigated the effects of terrestrial habitat structure on larval development, growth, and survival in *Litoria ewingii*. Our purpose was to clarify the response of these traits to biotic and abiotic environmental factors that may vary as a result of different shading conditions at breeding sites. We specifically investigated the responses to shading in two types of breeding ponds that are available to the species: permanent ponds, and smaller, ephemeral ponds.

MATERIALS AND METHODS

The study was conducted within the commercially harvested forests of the Warra Long Term Ecological Research (LTER) site, which is located approximately 60 km southwest of Hobart in Tasmania, Australia (43°3′S; 146°39′E). Vegetation at the site consists predominantly of temperate broad leaf forest (mainly *Eucalyptus obliqua* wet forest), with the remainder of the area consisting of moorland, alpine vegetation, temperate rain forest, riparian forests, conifer forest, and scrub (Brown et al., 2001). Precipitation falls throughout the year, but average monthly rainfall and the number of storms show a strong winter bias, with highest rainfall occurring during July and August (Ringrose et al., 2001). The site has an average annual rainfall of 1080 mm (Hickey et al., 2001).

Two main types of breeding sites were available to the amphibians at the study site. Small- to medium-sized ponds have been constructed adjacent to roads as water supplies for the management of fire by Forestry Tasmania. These ponds provided permanent, incidental breeding sites for amphibians and were the subject of investigation in Experiment 1. There were a total of 28 such permanent ponds in the general study area. Also used as breeding sites are smaller, ephemeral sites formed from natural depressions, table drains associated with road gutters and harvest machinery ruts. We simulated these pond conditions by constructing artificial ponds in Experiment 2. Artificial ponds were used because this allowed us to keep constant variables such as pond dimension that may otherwise have obscured effects of shading in such small bodies of water.

Experiment 1.—This experiment was designed to investigate the factors affecting larval traits in permanent ponds. We used four permanent ponds that had been constructed as water supplies for the management of fire. These ponds represented typical, anthropogenically constructed, permanent breeding sites that are commonly available to the species throughout the commercially harvested forests of southern Tasmania. The four ponds were selected from 28 that were available at the study site. Pond choice was based on minimizing differences between volume, surface area, and maximum depth (thereby minimizing differences in temperature regimes independent of pond shading). Populations of *L. ewingii* occurred naturally in all four. Two shaded and two unshaded ponds were selected. A pond was classed as shaded if it had well-established, overhanging vegetation around at least three sides of the pond (including the north-facing side). Unshaded ponds had no well established, overhanging vegetation around at least three sides of the pond (including the north-facing side). Although no fish species occurred in any of the ponds, invertebrate predators (odonate larvae and dytiscids) were present in each pond. Pond age ranged between 13 and 31 years. Pond characteristics are documented in Table 1.

We used artificial enclosures within the ponds to investigate the effect of shading on growth, development rate, and survival of tadpoles. Our design thereby removed the confounding effect of influx of coarse particulate matter and predators. Experiment 1 took place over the 2000/2001 breeding season.

Cylindrical enclosures were constructed from gauze curtain material (with a mesh size small enough to prevent newly hatched tadpoles passing through). Plastic picnic plates were used to give the top and bottom of the enclosure rigidity (see Fig. 1). Each enclosure had a diameter of 22.5 cm, a height of 25 cm, and a volume of 10 liters. Styrofoam attached to the top of each enclosure allowed them to float at the surface of the water. A lid made from gauze material ensured that the entire enclosure could isolate the amphibian larvae inside from invasion by pond predators and other tadpole competitors.

Late development stage egg clutches were collected from a pond near Hobart, Tasmania. Clutches were allowed to hatch in the laboratory and four clutches were chosen in which all eggs had hatched within a 24-h period, thus removing hatching date as a confounding factor on tadpole growth. Thirty-two tadpoles were selected at random from each clutch and assigned to four groups of eight, each of which was allocated to one of the experimental ponds. Each pond received four enclosures, containing larvae from the four different clutches. Enclosures were anchored using string tied to pond bank vegetation so that they were in close proximity to one another, thus minimizing microhabitat differences between enclosures within ponds. Enclosures were also free to move relative to each other within this limited space, thus mediating temporal variations in environment caused by their relative positions. They were suspended in the middle of the pond so that any drying of the pond between field visits did not expose them.

Tadpoles at stage 25 (Gosner, 1960) were placed within enclosures on 15 October 2001. The experiment was terminated when a tadpole exibed emergence of both front legs in any pond (10 January 2001) so that metamorphs did not drown within the enclosure. At the conclusion of the experiment, all tadpoles were removed from each enclosure and placed in a white tray. The tray contained a minimum quantity of water so that animals were flat against the surface of the tray. A steel ruler was also placed on the bottom of the tray, as a reference length adjacent to the tadpoles. Digital photographs were taken of all tadpoles from each enclosure.

All size measurements and estimates of developmental stage were made from the digital photographs. The reference length of 1 cm was measured three times along the ruler that had been placed on the tray, and the average value was used to estimate the size of each tadpole. Tadpole size was measured as the length from snout–vent length (SVL). Stage was estimated from Gosner (1960). It was difficult to differentiate stages between 25 and 41 from digital photographs so these stages were grouped into the category "< 41." The number of tadpoles surviving within each enclosure was also recorded.

We estimated the primary production within ponds by suspending three microscope slides in each pond, at a depth of 10 cm, for a period of two weeks (see Skelly, 1995). To protect slides from herbivory each was encased in a fine gauze envelope. Upon removal from the pond, each microscope slide was immediately dipped in 70% ethanol to stop further algal growth and then air dried in the laboratory. Once dry, each slide was weighed (± 0.001 mg) and placed in a 500°C muffle furnace to combust all organic matter present. When cool, the slides were reweighed, and the difference in mass (i.e., amount of organic matter) was taken as an indication of pond productivity. Turbidity was measured on three occasions using a HACH turbidity meter.

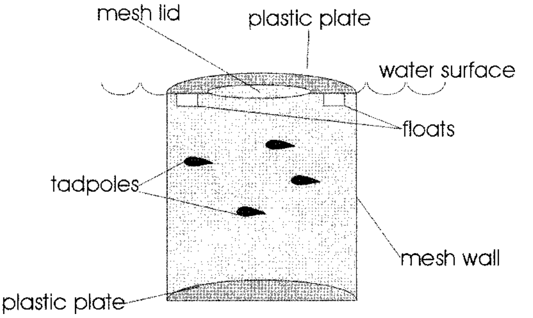

FIG. 1. Cross-section of enclosure used in Experiment 1.

Surface water temperature data were manually collected at two-week intervals throughout the experiment at 28 permanent breeding sites in the general study area, and these data were used to infer temperature regimes influencing tadpole development in the four experimental ponds. There were 19 unshaded ponds and nine shaded ponds. The lengths of temperature records varied from 5–11 records for the unshaded ponds and from 5–12 records for the shaded ponds.

Experiment 2.—This experiment was designed to investigate the factors affecting larval traits in ephemeral ponds. The experiment involved the construction of small, artificial ponds that were open to the environment and represented the lower range of breeding pond size used by *L. ewingii*. These ponds were considered to be more representative of the size of breeding sites naturally available to the species within the study area if anthropogenic construction of fire dams had not occurred. Artificial ponds were used instead of natural ponds to minimize microhabitat differences and to facilitate capture of tadpoles at the conclusion of the experiment. The experimental design isolated cofactors associated with pond shading such as age, pond hydroperiod, temperature (and its covariant elevation), predation and pond productivity for investigation. Experiment 2 took place over the 2001/2002 breeding season.

Twenty-eight artificial ponds were constructed at the site. Of these 14 were unshaded and 14 were shaded. A pond was classed as shaded if it had well-established, overhanging vegetation

TABLE 2. Average productivity and turbidity in ponds used in Experiment 1 (Pond A and B are shaded and B and C are unshaded).

	POND			
	A	B	C	D
Productivity (mg)	3.6	4.4	10.7	4.3
Turbidity (NTU)	124.9	14.4	10.3	2.8

around at least three sides of the pond (including the north facing side). Unshaded ponds had no well-established, overhanging vegetation around at least three sides of the pond (including the north-facing side). Any ponds with competitors present (as a result of natural colonization by other amphibian species) were removed from analysis. For this reason, two shaded ponds were not included in the final analysis.

The dimensions of each pond were 1.0 × 0.8 × 0.3 m. The inside of each excavation was lined with layers of newspaper to protect the pond lining from any sharp rocks or sticks. The pond lining was constructed from 2 × 2 m UV light resistant, clear plastic. The edges of the plastic were buried under soil and/or rocks and logs. Each pond was filled using water collected at a nearby river crossing (*L. ewingii* breeds in standing water so that river water used to fill each pond was unlikely to introduce amphibian larvae or eggs). Substrate from the surrounding area was placed in the bottom of the pond to provide camouflage for tadpoles.

Late developmental stage eggs from several clutches were collected from a permanent pond at the site on 14 November 2001 and were allowed to hatch in the laboratory. Tadpoles hatching on 23 November 2001 were isolated and 26 tadpoles were randomly assigned to each pond. Initial SVL was measured on a microscope slide under a binocular microscope fitted with an eyepiece micrometer. All tadpoles were released into ponds on 28 November 2001.

Primary production was estimated as in Experiment 1. Turbidity levels were recorded for each pond on a scale of 1–3 on 24 January 2002 (1 having no turbidity and 3 being highly turbid). Elevation of each pond was calculated from Geographical Information Systems (GIS) data provided by Forestry Tasmania. Temperature loggers installed in each pond simultaneously recorded hourly temperatures over the 24-h period following tadpole removal.

Ponds were inspected weekly for the presence of predators. All tadpoles were removed on 24 January 2002 when the emergence of front legs was first noticed (i.e., before the animals moved into the terrestrial environment). The SVL of each tadpole from each pond was measured (as for Experiment 1) and developmental stage recorded.

Statistical analyses were conducted using SPSS™ 8.0 for Windows Student Version. Assumptions for all statistical tests were confirmed for all data sets. No transformation of data was required.

RESULTS

Experiment 1.—Each enclosure was monitored for the presence of any predators that may have entered inadvertently. No tadpole predators were found within the enclosures. Furthermore, the number of tadpoles within each enclosure never exceeded the initial number of tadpoles originally assigned to each enclosure. The size of tadpoles within enclosures was relatively consistent with each measurement (i.e., no very large or very small tadpoles whose size was inconsistent with tadpoles within the experiment were ever found). From these data, we made the presumption that any decrease in tadpole numbers in enclosures over the study period was attributed to death of tadpoles and not to escape or predation.

Although it was not possible to analyze caused by to insufficient residual degrees of freedom), there appeared to be no relationship between mean primary production and mean turbidity and no consistent difference in these factors between shaded and unshaded ponds (see Table 2). Temperature records taken every two weeks from the 28 ponds inevitably had missing values that necessitated the use of model fitting procedures using maximum likelihood (Pinheiro and Bates, 2000; Crawley, 2002). Because temperature follows a periodic cosine function over an annual cycle, linear periodic regression (Batschelet, 1981) was used to describe the differences between shaded and unshaded ponds, with each pond being treated as a subject in the resulting mixed-model analysis (Pinheiro and Bates, 2000). For each pond, linear periodic regression describes the relationship between temperature, y, and time, t, as follows:

$$y_i = M + A\cos(t - \phi) + \varepsilon_i$$

where y_i denotes the ith observation of temperature, M is the mean level of temperature over the annual cycle, A is the amplitude of the oscillation of about the mean temperature, t is the time in days since the summer solstice at which the redox observation was taken, ϕ is the acrophase angle which describes the time over the cycle at which the maximum amplitude is reached, and ε_i is the residual associated with observation y_i. Time was converted to radians for the purposes of model-fitting but was converted back to days relative to the austral summer

TABLE 3. Results from linear periodic regression examining the relationship between pond shading and water temperature in Experiment 1.

	Shaded	Unshaded
N (no. of temperature records)	77	168
M, Mean (°C)	10.82 ± 1.74	10.89 ± 1.71
A, Amplitude (°C)	5.65 ± 1.75	11.35 ± 1.95
ϕ, Acrophase (days relative to summer solstice)	13.8 ± 18.0	6.9 ± 9.7

TABLE 4. Results from ANCOVAs examining influence of shading upon SVL and stage and ANOVA examining influence of shading on survival in Experiment 1 (df = 1,15 for all sources).

Trait	Source	*F*	*P*
SVL	Shade	2.948	0.112
	Elevation	30.397	<0.001
Stage	Shade	0.016	0.901
	Elevation	66.502	<0.001
No. survived	Shade	12.185	0.004

solstice when reporting the results. The significant interaction between shading treatment and the periodic parameters representing time (likelihood ratio [LR] = 6.745 on 2 df, $P = 0.034$) showed that the two shading treatments did not have parallel profiles of temperature over time. Accordingly separate regressions were fitted to shaded ponds and unshaded ponds, and confidence intervals computed for the parameter estimates using restricted maximum likelihood (REML) for the final regressions after heteroscedasticity in the data has been accounted for by inclusion of a power function of time (Pinheiro and Bates, 2000). These analyses were carried out in R version 1.8.1 (R Development Core Team, Vienna, Austria, 2003).

The periodic regressions for both types of pond were highly significant (likelihood ratios with $P <$ 0.0001; Table 3). Both shaded and unshaded ponds had similar mean temperature over the year, but the amplitude of temperature fluctuations for unshaded ponds was nearly double that of shaded ponds (i.e., at the maximum temperature unshaded ponds on average were at ~22.2°C, whereas shaded ponds on average achieved ~ 16.5°C). The date at which the maximum temperature was achieved was later in shaded ponds than in unshaded ponds, although the 95% confidence intervals for the acrophase overlapped for the two pond types.

Growth, development and survival data were analyzed using average data for each enclosure. Model I analysis of variance (ANOVA) showed that there was no significant difference in the average SVL of tadpoles between ponds ($F_{3,127} =$ 1.397, $P = 0.247$) at the time of installation. All tadpoles were at Gosner stage 25 (Gosner, 1960).

Numerous studies have highlighted the systematic variation of temperature with elevation and the subsequent influence of elevation on larval growth and development (e.g., Berven and Gill, 1983). Site selection criteria imposed a restriction on the number of sites suitable for the study and meant that altitude could not be controlled. The elevation of the four breeding ponds varied over a range of 400 m. To confirm the influence of elevation on larval growth and development, we conducted linear regressions of elevation against SVL, stage, and survivorship. Significant relationships were found between elevation and SVL ($r^2 = 0.953$, $F_{1,2} = 40.197$, $P = 0.024$), stage ($r^2 = 0.959$, $F_{1,2} = 47.216$, $P =$ 0.021), but not survivorship ($r^2 = 0.553$, $F_{1,2} =$ 2.470, $P = 0.257$).

To remove the confounding effect of elevation on subsequent analysis involving SVL and stage, we conducted analysis of covariance (ANCOVA) using elevation as the covariate. ANOVA was used to investigate survivorship data.

SVL and stage did not differ significantly between shaded and unshaded ponds (Table 4). Survivorship was lower in shaded ponds than in unshaded ponds (mean ± SE = 5.6 ± 1.0 compared to 7.2 ± 0.7 larvae, respectively).

Experiment 2.—Initial data analysis investigated any relationships between pond habitat variables. As well as revealing the physical consequences of shading on pond conditions and important interactions between habitat variables, these analyses were used to ensure independence of covariates should they be required in the subsequent analysis of larval traits. Linear regression between biologically relevant habitat variables (selected a priori) was undertaken and the results are presented in Table 5.

TABLE 5. Results from linear regressions examining the relationship between pond habitat variables in Experiment 2.

Parameters	r^2	df	*F*	*P*
Midday water temps vs. elevation	0.15	1,24	0.968	0.058
Sunrise water temps vs. elevation	0.57	1,24	29.98	<0.001
Midday water temps vs. productivity	0.19	1,18	4.139	0.057
Productivity vs. no. tadpoles surviving	0.00	1,19	0.008	0.928
Turbidity vs. primary production	0.00	1,19	0.008	0.929

TABLE 6. Results from ANOVAs examining influence of shading upon larval traits in Experiment 2 (df = 1,24 for all traits).

Trait	F	P
SVL	1.550	0.225
Stage	8.034	0.009
Survivorship	0.008	0.931
CV SVL	10.889	0.003
CV stage	1.500	0.233

Midday water temperatures were not correlated with elevation but were lower in shaded than in unshaded ponds (mean of 14.3 ± 2°C compared to 16.9 ± 2°C, respectively, $F_{1,23}$ = 8.469, P = 0.008), indicating that solar radiation was more important in determining water temperature during the day than elevation. In contrast, water temperature before sunrise was significantly related to elevation, showing that once the sun went down the water volume within ponds was insufficient to retain heat accumulated from the previous day's solar input and water temperatures equilibrated to surrounding air temperatures.

Light availability may influence the algal biomass within lentic systems (Holomuzki, 1998). Noon water temperatures were used as an indicator of solar radiation entering the ponds; however, no significant correlation was found with primary production. Similarly, no significant difference between productivity in shaded and unshaded ponds was found ($F_{1,19}$ = 0.144, P = 0.709). The investigation of tadpole density (i.e., number of tadpoles surviving at the completion of the experiment) and primary production showed no significant relationship, indicating that tadpole herbivory was not a determinant of algal biomass. Turbidity may also limit the amount of solar radiation entering water and may subsequently influence the amount of photosynthesis; however, no relationship between turbidity and pond productivity was found.

Analysis of variance was used to investigate effects of shading on larval traits. There was no significant difference in SVL between enclosures at the time of allocation to shaded and unshaded ponds ($F_{2,537}$ = 0.612, P = 0.936). All tadpoles were at Gosner stage 25 (Gosner, 1960).

Once again, the systematic variation of temperature with elevation may have had a confounding effect on tadpole growth and development. This was tested with linear regressions between elevation and larval traits (SVL, stage, and survival). Elevation did not significantly affect larval traits and was, therefore, not considered in subsequent analyses.

Linear regression was used to investigate the influence of primary production on larval traits. There was no influence of primary production on SVL (r^2 = 0.061, $F_{1,19}$ = 1.234, P = 0.281), stage (r^2 = 0.044, $F_{1,19}$ = 0.882, P = 0.359), or survivorship (r^2 = 0.000, $F_{1,19}$ = 0.008, P = 0.928).

One-way analysis of variance was used to test differences in larval traits between shaded and unshaded ponds (Table 6). Shading did not significantly influence final tadpole SVL or survival. Developmental stage was higher in unshaded ponds than shaded ponds (mean ± SE = 37.3 ± 1.2 compared to 33.1 ± 1.2, respectively). The coefficient of variation of SVL was higher in shaded compared to unshaded ponds (mean ± SE = 0.29 ± 0.018 compared to 0.20 ± 0.019, respectively).

It should be noted that the two different experiments were conducted in different years and that pond age differed with shading treatment (ephemeral ponds were constructed at the commencement of the experiment, whereas permanent ponds had been established for a number of years). This may have confounded pond type effect with a year and/or pond age effect. Keeping this limitation in mind, we discuss our experimental findings below.

DISCUSSION

We found that primary production in permanent ponds was not affected by pond shading conditions. This may have been a function of the small sample size in this experiment as principle components analysis of pond environmental variables for 28 permanent ponds in the study area grouped pond age, shading and productivity into a single component (Lauck et al., in press). Furthermore, linear regression of pond age against productivity (using the same 28 ponds) showed a highly significant negative relationship with more shaded, older ponds more likely to have low levels of productivity (since ponds are often constructed as part of the logging process and vegetation causing shading becomes more established around the pond as the forest regenerates). As a result, shading is expected to reduce solar radiation entering ponds, thus reducing algal growth.

Similarly, we did not find a difference between the quantity of algal growth in shaded and unshaded ephemeral ponds. The relationship between productivity and midday water temperatures almost reached significance, and midday water temperatures, in turn, were higher in unshaded ponds. This is indicative of some association, but the lack of a strong relationship between pond productivity and shading may mean that limiting factors other than shading influenced pond productivity. For example, the rather cold and cloudy season in which the ephemeral pond experiment took place may indicate that light is a limiting factor. Alternatively, the low nutrient status of pond water or the limited time since pond construction may also have limited algal growth.

In ephemeral ponds, productivity was independent of grazing pressure from tadpoles and in both experiments turbidity levels did not influence productivity. In contrast to the studies of Werner and Glennemeier (1999) and Skelly et al. (2002), food availability was not a significant mechanism regulating the growth of *L. ewingii* larvae in ephemeral and permanent ponds. This may have been because shading conditions in our study were not as intense as in the aforementioned studies that required complete canopy cover over the entire pond for it to be classed as shaded. At our study site, the canopy never completely covered entire ponds and as a consequence the effect of shading on algal growth may have been less severe.

Amphibian larval growth data also imply different temperature regimes between permanent and ephemeral ponds. In permanent ponds, final tadpole SVL was strongly influenced by altitudinally mediated temperatures. In ephemeral ponds, this relationship was not significant. The larger size of permanent ponds means that larger water volumes would have buffered diurnal temperature changes; thus, we would expect the influence of factors with little diurnal variation (such as elevation) to be more important in regulating the temperatures in these ponds. Furthermore, in permanent ponds, the sun heated only the very shallow upper layer of water (BL, pers. obs.). The body of colder water beneath this layer would have largely buffered diurnal variation in water temperatures. Temperatures in smaller ephemeral ponds are expected to have higher diurnal variability than those of larger ponds. In smaller ponds, the water was shallow enough for the entire water volume to be warmed during daylight hours (as demonstrated by the strong relationship between midday water temperatures and shading), but accumulated heat was lost at night when temperatures equilibrated to surrounding air temperatures (as indicated by the relationship between water temperatures at sunrise and elevation).

We found that some larval traits responded differently to shading as a result of different pond conditions in permanent and ephemeral ponds. In permanent ponds, tadpole size at the onset of emergence did not differ with shading treatment. Skelly et al. (2002) considered temperature to be the fundamental mechanistic influence of shading on amphibian growth rates. In our study, however, mean water temperatures in the 28 permanent ponds in the study area did not differ with shading treatment. A greater temperature range was achieved sooner in unshaded ponds (for example, the maximum temperature was almost 6°C higher), but tadpoles may have behaviourally mediated such variations in temperature by using the lower part of the enclosure with more stable temperatures than those experienced at surface waters.

An effect of shade on SVL was also not evident in ephemeral ponds. Given the rather cold, rainy and cloudy weather in 2002, temperature differences between shaded and unshaded ponds are likely to have been less than expected in an average season. The difference in midday water temperatures between ponds was only 2°C and was maintained for a small part of the day only.

Interestingly, we found a higher coefficient of variation in tadpole SVL from ephemeral shaded ponds than unshaded ponds. Crump (1984) argued that, under crowded conditions and limited resources, larger hatchlings coming from larger eggs would maintain their initial size advantage, whereas in productive habitats or those with high per capita resources, individuals may vary little in size at metamorphosis or developmental period. The coefficient of variation of developmental stage did not differ between shaded and unshaded ponds, demonstrating that the rate of development was relatively consistent and irrespective of treatment.

In contrast to permanent ponds, where shading treatment did not significantly influence final developmental stage, shading did influence developmental rate in ephemeral ponds. Developmental rate was found to be higher in unshaded, than in shaded ponds. This result is consistent with literature relating to the effect of hydroperiod on larval traits. To reduce the risk of mortality as a result of complete pond drying, some species of amphibian larvae are able to accelerate the rate of development to metamorphose earlier into a terrestrial environment that is less harsh than the aquatic habitat.

In permanent ponds, survivorship of tadpoles in shaded ponds was lower than in unshaded ponds (70% vs. 90% survivorship, respectively). These findings corroborate with those of Skelly et al. (2002) for *Rana sylvatica*, which also demonstrated greater survival in shaded ponds (although *Pseudacris crucifer* showed no effect of shading treatment on survival). Interestingly, Werner and Glennemeir (1999) found no difference is survivorship with shading treatment for *R. sylvatica* but found lower survivorship in shaded ponds for *Rana pipiens* and *Bufo americanus*. Survivorship of *L. ewingii* did not differ in shaded and unshaded ephemeral ponds, but this may not have been the case had ponds dried completely before metamorphosis could be completed (thus, highlighting the importance of hydroperiod for small bodies of water).

Indeed, this raises an important point that must be highlighted to discuss the implications of the experimental findings for vegetation management around ponds. Both experiments were conducted in different years, and the climatic conditions in these years were different. The first year had average annual rainfall and solar radiation, whereas the second was atypically cold, cloudy and rainy. This makes direct comparisons between the experiments more difficult but raises an important issue with respect to the interpretation of data. Had 2001 (when the permanent pond experiment was conducted) been colder and cloudier, shading conditions may not have resulted in significant differences in survival between shaded and unshaded ponds since shading effects may not have been as great. Similarly, had 2002 (when the ephemeral pond experiment was conducted) been warmer and sunnier, desiccation rates may have been higher, especially in unshaded ponds, such that metamorphosis could not be completed before complete pond drying, resulting in the mortality of cohorts within ponds.

Conclusions.—Although growth and developmental rates seem unaffected, increased shading around permanent ponds is at the expense of larval survival. Larval success of *L. ewingii*, therefore, may not necessarily be enhanced by vegetative buffer zones in the immediate margins of ponds located within the managed forest. The management of vegetation around ponds at the study site (which is incidental to other forest management objectives) has resulted in 19 of 28 ponds classed as unshaded.

Changes in elevation had a more significant affect on growth and develop rate at permanent ponds than shading effects. Given that the majority of ponds within the commercially managed forest are anthropogenically constructed, decisions relating to pond location have a greater significance for larval growth and development than those relating to the vegetation management around pond margins.

Larval success in ephemeral ponds is likely to be enhanced by heterogeneity of shading conditions around pond margins. This may allow a compromise between accelerated developmental rates in unshaded ponds and the risk of premature pond desiccation that may be delayed by increased pond shading. Such conditions may allow populations to "hedge their bets" with respect to stochastic environmental variability.

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Arboreal Habitat Use by the Green Salamander, *Aneides aeneus*, in South Carolina

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Abstract.—**Green Salamander (*Aneides aeneus*) habitat has been described traditionally as rock outcrop formations that contain moist, but not wet, crevices. Early studies of Green Salamander natural history claimed arboreal habitat was used secondarily to rock outcrops and in situations where more suitable habitat was unavailable. Although arboreal behavior of western *Aneides* has been well established, arboreal habitat has been deemed "not typical" for Green Salamanders. This study examined the extent to which Green Salamanders use arboreal habitat. Surveys were conducted between August 2001 and July 2004 at a study area in Pickens County, South Carolina. Salamander size influenced arboreal habitat use, but gender and reproductive condition did not. There was a positive relationship between tree diameter at breast height (DBH) and Green Salamander observations and a negative relationship between tree distance to rock outcrop and salamander observations. Tree selection did not reflect tree species relative dominance, and salamanders favored hardwoods over conifers. Seasonal use of arboreal habitat was distinct, implying that salamanders overwinter in rock outcrops and move into trees and logs at the onset of spring. Salamanders observed during summer were primarily arboreal, but they returned to rock outcrops in late fall. Researchers have largely overlooked arboreal habitat use by Green Salamanders, and consequently, the importance of arboreal habitat near rock outcrops has been underestimated. Arboreal habitat appears to be an important component of the life history of this declining species, and future survey and monitoring efforts should include searches of arboreal habitat.**

Given its unique habitat requirements and natural history, the Green Salamander (*Aneides aeneus*) is listed as a "species at risk" by the U. S. Fish and Wildlife Service. It is listed as critically imperiled, imperiled, or vulnerable in 10 of the 13 states in which it occurs. Interest in conservation of Green Salamanders piqued following a publication by Corser (2001), which reported a 98% decline of some populations within the Blue Ridge Escarpment since 1970. Speculation about why these populations declined has centered on synergistic effects of overcollection by researchers, fungal pathogens, climate change, and habitat loss (Corser, 2001). It is the latter component of such speculation that is of interest to this study.

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Green Salamander habitat has been described traditionally as limestone (Walker and Goodpaster, 1941), sandstone, granite, and schist formations (Netting and Richmond, 1932; Gordon and Smith, 1949; Schwartz, 1954; Bruce, 1968; Mount, 1975) that contain crevices that are moist but not wet. Petranka (1998) suggested that Green Salamanders have a patchy distribution caused by their dependence on rock outcrops. However, morphological and ecological traits of members of the genus *Aneides* suggest an arboreal lifestyle (Wake, 1963, 1966). Arboreal behavior by western *Aneides* has been well documented (Ritter, 1903; Fitch, 1936; Stebbins, 1951; Stelmock and Harestad, 1979; Whitaker et al., 1986; Davis, 2002), and there are numerous reports of Green Salamanders in arboreal or woody habitat (Brimley, 1927; Bishop, 1928; Pope, 1928; Welter and Barbour, 1940; Brimley, 1941; Fowler, 1947; Gordon and Smith, 1949; Gordon, 1952; Schwartz, 1954; Canterbury, 1991). Barbour (1971) described an arboreal observation in Kentucky, stating "They [Green Salamanders] sometimes reach a high population in logged-over areas where dead tree tops were left. They reached tremendous populations in the 1930s under the bark of the millions of dead chestnut trees in eastern Kentucky."

Other scientific literature suggested that Green Salamanders are not closely associated with arboreal habitat, and they are described as being "weakly" arboreal (Bishop, 1928). In the most extensive summary of Green Salamander life history, Gordon (1952) stated that Green Salamanders were only occasionally arboreal in the Blue Ridge Escarpment, and there has been little evidence to suggest that arboreal habitat is essential to healthy population structure for the species. Bruce (1968) suggested that arboreal habitat use is restricted to mixed-mesophytic forests of the Appalachian Plateau Province, where arboreal observations have been noted (Barbour, 1971). Currently, arboreal habitat is deemed "not typical" over most of the range of the species (Snyder, 1991).

Historically, search efforts for Green Salamanders focused on rock outcrops, although arboreal surveys occasionally were conducted. In such surveys, researchers focused on dead or dying trees (standing or fallen) with loose bark, rather than on live trees, and few studies yielded arboreal observations. Consequently, arboreal habitat was deemed secondary to rock outcrops as preferred habitat and in situations where more suitable habitat was not available (Gordon and Smith, 1949; Gordon, 1952; Woods, 1968; Barbour, 1971; Mount, 1975). Rock outcrops are still thought of as harboring the majority of salamanders within a given population. Evidence of reproduction or nesting in standing arboreal habitat is lacking, and there are few records of Green Salamanders nesting in logs.

In August 2001, we discovered nine Green Salamanders on a single American Beech (*Fagus grandifolia*) at a South Carolina study site and observed 14 individuals on 14 different trees during a subsequent survey of the area. Thus, we began a study on the arboreal habits of Green Salamanders. Specifically, we addressed four questions. (1) How does habitat use (arboreal vs. rock outcrop) vary by size-class and gender of salamanders? (2) Do Green Salamanders favor specific tree species over others? (3) Does tree diameter and distance to rock outcrop influence arboreal habitat use? (4) Does arboreal habitat use vary seasonally?

Materials and Methods

Study Area.—The study area was surveyed between August 2001 and July 2004. The exact location of the study area is not reported because of a history of overcollection leading to population declines at sites reported in previously published papers. The study area was located at the base of the Blue Ridge Escarpment (elevation = 300 m) in Pickens County, South Carolina. Mixed pine-hardwood forest dominated the lower portion of the study site, and more xeric species (e.g., Virginia Pine) dominated the area above the main outcrop. Twelve species of trees (> 5 cm Diameter at Breast Height [DBH]) were documented within the study area. Rhododendron was numerous, although it had a low relative dominance because of the size of its stems. Cores extracted from a Red Oak (*Quercus ruber*), Tulip Poplar (*Lirodendroan tulipifera*), and Eastern Hemlock (*Tsuga canadensis*) indicated the stand was uneven-aged, with larger trees ranging from 85–100 yr. Several granite rock outcrops exposed along the floodplain of a medium-sized stream characterized the site. The main rock outcrop was approximately 80 m long and 10 m high, with numerous crevices and fissures. The stream created a boundary that limited searches to approximately 20 m from the main rock outcrop. The area between the main rock outcrop and the stream was approximately 25 × 72 m (0.18 ha).

Surveys.—We attempted to conduct surveys during optimal weather conditions (i.e., overcast and/or drizzling), but time constraints and logistical problems often meant that the study area was surveyed during what would be considered suboptimal conditions (i.e., sunny and dry). Surveys were timed and involved searching all available habitat within the study area, including the ground, trees, logs, and rock outcrops. Flashlights were used during both day and night searches to scan crevices and faces of emergent rock outcrops, trees, and logs. Even during daytime searches, light from the flashlights reflected off of the skin of salamanders and made them easier to observe on trees. Inaccessible individuals were coaxed from their crevice using a wire or stick with a hook and blunt tip in order to measure age classes.

Tree searches were conducted from the ground, although it was difficult to observe salamanders above approximately 10 m; salamanders could sometimes be seen easily with binoculars. Ground searches involved searching the ground surface for active salamanders, but leaf litter searches (sifting through leaf litter and turning of logs) were not conducted. When a salamander was observed, we recorded whether it was within a crevice or active on the substrate surface. Captured individuals were placed in a plastic bag, sexed, and measured for snout–vent length (SVL), total length (TL), and the salamander was released at the exact capture location. The dorsal pattern of each salamander was photographed for individual recognition as part of a concurrent mark-recapture and movement study. Individual identification allowed for observations of the number of individual salamanders found on trees. However, not all individuals counted during surveys were accessible for capture and individual recognition. Therefore, unless specified, data are presented as the number of salamander observations.

Salamanders were placed into one of three age classes according to SVL, including adults ($>$ 44.5 mm), subadults (29.5–44.4 mm), and juveniles ($<$ 29.4 mm). Sex was determined based on the presence of mental glands in males and eggs in gravid females. When neither mental glands nor eggs were observed in individuals greater than 44.5 mm SVL during the breeding season, we assumed they were nongravid females. Sex could not be determined when dimorphic characters were not present outside of the breeding season. Measurements taken at each capture location included substrate type (rock, tree, or log), height, tree or log diameter, and distance to nearest rock outcrop. Tree Diameter was measured at breast height, and log diameter was measured at the center of each log. The "distance to nearest rock outcrop" measurements were made to one particular rock where salamanders appeared to overwinter (unpubl. data).

Data Analysis.—All statistical analyses were performed using SAS (SAS Institute Inc., Cary, NC, 2002). Negative binomial Poisson regression (PROC GENMOD) was used to examine the relationship between the number of salamander observations, tree size (DBH), and distance to the nearest rock outcrop. Because salamanders had different levels of detectability on logs and trees, observations on logs were excluded from the Poisson regression analysis. However, observations made on logs and trees were clumped for most other analyses. One-way frequency tables were used to examine the distribution of salamanders on rocks and arboreal habitat (trees and logs) throughout the year. Chi-square analysis was used to examine differences in size class, gender, and reproductive condition with respect to arboreal habitat use. Only active season (April through October) observations were used for descriptions of tree and log use patterns. Because salamanders were only observed in rocks during the winter, we assumed they were overwintering in rock outcrops. Therefore, we classified the active season as between April and October, when salamanders were found on rocks, trees, and logs. Seasonal activity patterns were described and referenced to the number of adjusted person hours spent searching for salamanders. We assumed that it took at least five minutes to process individuals based on the length of time required to handle salamanders during early surveys. Therefore, person hours were adjusted so that five minutes were subtracted for each salamander captured from the total number of minutes spent searching the study area.

Results

We recorded 491 Green Salamander observations within the study area during 71 surveys. Of 345 salamander observations during the active season, 143 were found on rocks (113 individuals), 150 on trees (71 individuals), and 52 on logs (11 individuals).

Habitat Use by Size-Class and Sex.—More adults (N = 228) were observed than subadults (N = 108) and juveniles (N = 115) during this study. Use of rocks, trees, and logs differed among salamander size classes ($\chi^2 = 20.61$, df = 4, $P <$ 0.001). Juveniles were observed most often on trees, whereas adults and subadults were more frequently observed on rocks (Fig. 1A). Trees, logs, and rock outcrops were used in proportion to the number of males (N = 54) and females (N = 41) observed ($\chi^2 = 4.50$, df = 2, $P > 0.05$, Fig. 1B). Both gravid (N = 16) and nongravid (N = 21) females were observed on rocks, trees, and logs (Fig. 1B), although low sample size on logs only allowed for comparisons between rock outcrops and trees. Trees and rock outcrops were used in proportion to the number of gravid and nongravid females observed ($\chi^2 = 2.89$, df = 1, $P > 0.05$, Fig. 1B). Evidence of arboreal nesting was observed on one occasion in October 2003, when hatchlings were seen descending a Black Walnut (*Juglans nigra*) during a fall survey.

Tree Selection: Relative Dominance, Size, and Distance from Rock Outcrop.—Green Salamanders were observed on 35 of the 63 trees regularly

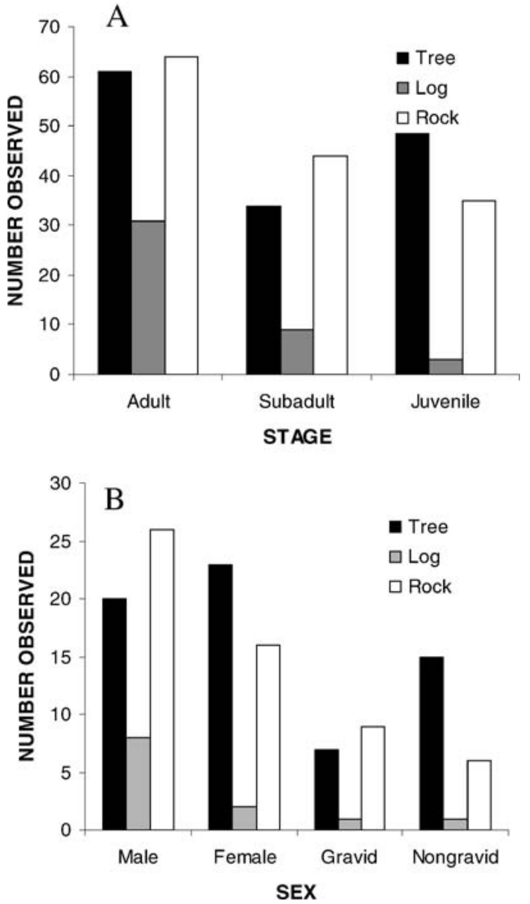

FIG. 1. (A) Number of observations of Green Salamanders in rock outcrops, trees, and logs during the active season (April through October). (B) Number of observations of male and female (gravid and nongravid) Green Salamanders on trees, logs, and rock outcrops during the active season within the study area.

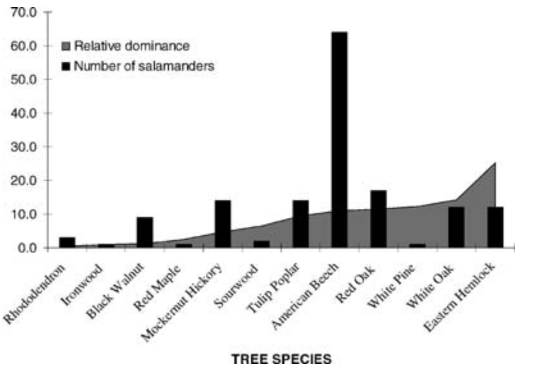

FIG. 2. Number of observations of Green Salamanders in tree species that occurred within the study area. Numbers are presented with respect to the relative dominance of each tree species within the study area.

surveyed during the study, including all 12 of the tree species available within the area. Only one individual was found beneath the bark of a dead tree; all other arboreal observations, with the exception of those on logs, occurred on living trees. Observations of arboreal salamanders were not proportional to the relative dominance of tree species (χ^2 = 234.26, df = 11, $P < 0.0001$, Fig. 2). Although two of the three most dominant tree species were conifers (Fig. 2), Green Salamanders were observed more often on hardwood trees (N = 137) than coniferous trees (N = 13), and salamanders used hardwoods disproportionally to their abundance (χ^2 = 102.51, df = 1, $P <$ 0.0001). Multiple salamanders were sometimes found together on the same tree. For instance, as many as nine individuals were observed on a single American Beech at the same time.

On average, salamanders were observed 1.3 m high (N = 182, SD = 0.61, range = 0.1–3.6) on rocks, and 2.3 m high (N = 137, SD = 2.67, range = 0.25–21) on trees. The number of observations of adults, subadults, and juveniles was proportional on rocks and trees (χ^2 = 5.29, df = 2, $P > 0.05$), and they were combined in the negative binomial Poisson regression model. The original Poisson model included the y-intercept and predictor variables DBH and distance to rock outcrop, but the y-intercept was not significant (estimate = –0.1975, SE = 0.43, χ^2 = 0.21, $P > 0.05$), and there was a problem with overdispersion (Pearson χ^2 = 89.38). Therefore, we used a negative binomial linear model to predict the number of Green Salamander observations in trees with respect to DBH and distance, without the inclusion of the y-intercept. The model indicated a positive relationship between DBH (estimate = 0.1203, SE = 0.01, χ^2 = 73.56, $P < 0.0001$) and salamander observations (Pearson χ^2 = 32.40), and a negative relationship between distance to rock outcrop and the number of salamander observations (estimate = –0.0744, SE = 0.03, χ^2 = 6.02, P = 0.01).

Seasonal Habitat Use.—Strong seasonal activity patterns on rock outcrop and arboreal habitat were evident without regard to sampling effort (Fig. 3). Seasonal shifts in habitat use suggest salamanders overwinter in rock outcrops and move into woody or arboreal habitat beginning in March, where they appear to remain throughout the breeding/nesting season before returning to rock outcrops in October and November (Fig. 3). Fluctuations in activity on rock outcrops were pronounced (χ^2 = 21.39, df = 10, $P < 0.05$), because few individuals were observed on the rocks during summer months (Fig. 3). However, when arboreal and rock outcrop observations were combined for analysis, salamander obser-

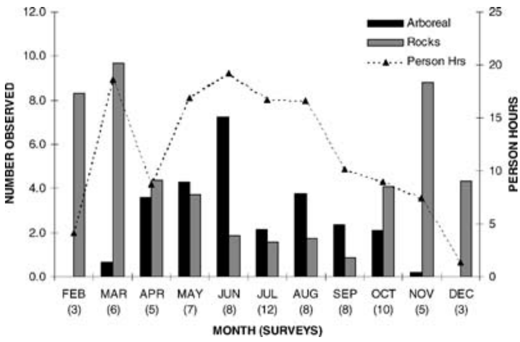

FIG. 3. Seasonal use of arboreal and rock outcrop habitat by Green Salamanders. Numbers in parentheses below each month refer to the number of surveys conducted during the respective month between August 2001 and July 2004. Number observed refers to the number of Green Salamanders observed per survey, per month.

vations remained constant throughout the year ($\chi^2 = 8.26$, df = 10, $P > 0.05$).

DISCUSSION

Sampling bias toward rock outcrops and dead trees probably caused researchers to overlook Green Salamanders in arboreal habitat during the active season in previous studies. Until now, scientific literature has been devoid of information suggesting trees (live or dead) and logs play a major role in the behavior and population ecology of Green Salamanders. Unlike early reports of Green Salamander habitat use, where arboreal searches were uncommon and focused on dead or dying trees, we suggest that dead trees are not necessary for Green Salamander activity in arboreal habitat. To the contrary, only one Green Salamander was observed on a dead tree during this study. The presence of Green Salamanders of all size classes and both sexes (regardless of reproductive condition) on trees and logs throughout the active season, along with evidence of nesting in trees, clearly suggests that arboreal structure is at least as important as rock outcrops to the natural history of Green Salamanders.

Habitat Use by Size-Class and Sex.—The frequency at which adults, subadults and juveniles were observed did not necessarily reflect population demographics. A plausible explanation for the observed bias toward adults is that smaller salamanders were more difficult to detect. Therefore, the frequency of size class observations is likely the result of sampling bias.

Our observations suggest gravid females select both arboreal and rock outcrop habitats for breeding and nesting. Gravid females were found on trees and logs throughout the breeding season and just prior to the onset of nesting season (mid-July). Although no females were observed with nests in trees, it seems unlikely that gravid females would be far from desired nesting habitat just prior to depositing eggs. In addition, sexually mature males with mental glands were observed in high numbers on trees throughout the breeding season, which suggests that they were defending nesting habitat (Cupp, 1980) and attempting to breed with females that were in trees.

Only three nests (all in rock crevices) were discovered during the study period, but two failed before hatching. Nevertheless, hatchlings were abundant at the site. The observation of a cluster of hatchlings in a tree in October infers that the individuals were dispersing from a nest within the tree. The tree on which the hatchlings were observed had numerous tree holes that appeared suitable for nesting. Whether nesting in trees is common, preferred, or related to a lack of suitable nesting crevices in rock outcrops is unknown.

Tree Selection: Relative Dominance, Size, and Distance from Rock Outcrop.—The observation that Green Salamanders did not use tree species based on tree relative dominance and that salamanders were disproportionately found on hardwoods, indicated that salamanders were selecting hardwood tree species. Although not quantified, the major similarity among hardwood trees selected by Green Salamanders was that they were large trees with holes of various shapes and sizes on the main stem. Regression analysis further elucidated why Green Salamanders selected specific trees. The effect of tree size and distance from rock outcrops offered insight into why 58 Green Salamander observations were made on a single American beech. This tree had a 75 cm DBH, and was located within 2 m of the rock outcrop.

Trees used by Green Salamanders appeared to provide cover through a series of bark characteristics. During dry days, individuals were often seen under flaps of bark on various tree species. Red Oak, Tulip Poplar, and White Oak have bark that tends to become flaky and furrowed enough for an adult salamander to hide beneath as the tree becomes older and larger. Green Salamanders were well camouflaged on older American Beech trees, despite their smooth bark, because the bark was often lichen-covered. Further, large beeches are oftentimes hollow and have numerous holes formed by fallen branches. One adult Green Salamander was observed halfway out of a tree hole in an American Beech at a height of 21 m (viewed with binoculars). These large, lichen-covered trees with numerous tree holes appeared to provide extensive habitat for Green Salamanders.

Seasonal Habitat Use.—The extent to which Green Salamanders disperse from rock outcrops is poorly understood. Researchers have suggested that Green Salamanders are likely to disperse from rock outcrops when suitable crevices for breeding and nesting are not available (Gordon, 1952; Woods, 1968). This implies that salamanders overwintering in rock outcrops that lack suitable breeding crevices have to travel to find nesting habitat. Green Salamanders did not appear to disperse from rock outcrops solely for breeding and nesting opportunities. Rather, individuals began dispersing from rock outcrops as soon as environmental conditions were suitable in the spring. Breeding was clearly not the only reason salamanders used trees, as evidenced by observations of juveniles and subadults in arboreal habitat throughout the active season.

Seasonal use of arboreal habitat was distinct. Green Salamanders migrated from their winter refugia in the rock outcrop to trees and logs as soon as the threat of freezing weather ceased (late March through early April), and individuals returned to the rock outcrops as colder weather approached (late October through early November). Green Salamanders have been historically difficult to detect during summer months, whereas spring and fall surveys have been more successful at detecting salamanders. Because the number of observations was low during summer months, researchers have speculated that salamanders retreated into crevices to avoid hot summer conditions and that salamander activity decreased during summer months. Specifically, Gordon (1952) reported an annual cycle of Green Salamander activity in the Blue Ridge Escarpment that included a "pre-hibernation dispersal and aggregation period" (late April through May) and a fall "post-hibernation aggregation and dispersal period" (late September through November). These aggregations consisted of numerous adult salamanders and hatchlings that were thought to be gathering on the rock outcrop just prior to and just after winter months; other studies have reported similar results (Woods, 1968; Cupp, 1991). Our study showed a similar trend with regard to salamander observations on rock outcrops. However, when arboreal habitat was included in analysis, the number of Green Salamander observations was not significantly different among months. Our results suggest that spring and fall peaks of salamander observations on rock outcrops do not reflect seasonal salamander activity as outlined by Gordon (1952). Rather, there appears to be a seasonal shift in habitat use. This habitat shift is only evident when arboreal habitats are surveyed. Although not significant, the number of salamander observations decreased in July, even though search hours remained high. Given the seasonal shift toward arboreal habitat, we believe the lower number of observations in July was caused by salamanders climbing into the tree canopy, where they were not detectible.

Conservation Implications.—Researchers have largely overlooked Green Salamander arboreal habitat use, and consequently, the importance of arboreal habitat near rock outcrops has been underestimated. Because tree canopies were not searched during the study, and because of difficulty in observing salamanders above 10 m, our results present an underestimation of the importance of arboreal habitat to Green Salamanders. It is clear that Green Salamanders can be highly arboreal, and we present conservative estimates of the importance of, and the extent to which, Green Salamanders use arboreal habitat. In addition to our study area in South Carolina, we have observed numerous Green Salamanders in arboreal habitat in the Allegheny Mountains, Appalachian Plateau, and Blue Ridge Provinces within the states of West Virginia, Ohio, Georgia, and other areas of South Carolina (unpubl. data).

Forest management around rock outcrops may directly affect movements and habitat use by Green Salamanders. We believe sampling bias toward rock outcrops has led to inaccurate descriptions of Green Salamander habitat requirements. Consequently, managers have had no indication that leaving trees around rock outcrops may prove important for this sensitive species, aside from providing shade for outcrops. Future research efforts should examine the benefits of leaving tree buffers around rock outcrops in managed landscapes, and determine how far Green Salamanders disperse within an active season. Our most distant Green Salamander observation was 42 m from the nearest rock outcrop at a study site in Georgia (Unpubl. data). Efforts to survey and monitor Green Salamander populations should incorporate arboreal habitat, including canopy searches. Tree climbing will greatly benefit arboreal searches and increase the probability of encountering nests in trees. Finally, certain species of large diameter trees appear to be favored by Green Salamanders, and these issues should be considered in forest planning within the range of this unique salamander.

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