Effects of Prescribed Burning on Amphibian Diversity in a Southeastern U.S. National Forest

JAMIE M. SCHURBON† AND JOHN E. FAUTH*

Department of Biology, College of Charleston, 66 George Street, Charleston, SC 29424-0001, U.S.A.

Abstract: Fire alters the abundance and diversity of many species, but its effects on amphibians are poorly known. We tested whether prescribed burning affected amphibian abundance and diversity within the Francis Marion National Forest, South Carolina, by monitoring assemblages at 15 temporary ponds with five different burn bistories: 0, 1, 3, 5, and 12 years after burns. We also monitored terrestrial and aquatic environmental variables likely to influence amphibian diversity, such as leaf-litter depth, pond water chemistry, and distance to neighboring ponds. Fire had significant negative effects. Immediate effects (burning during the study) explained 12.8% and 10.8% of the variation in anuran and amphibian abundance, respectively, whereas short-term effects explained 31.8% and 24.6% of variation in amphibian species richness and evenness, respectively. Species richness increased and evenness decreased with time since burn, primarily because salamanders were rarely encountered at sites burned within 2 years. These sites had the shallowest leaf litter and bigbest soil temperature variances. Environmental factors unrelated to burning also significantly influenced amphibian diversity. Water chemistry explained 31.1% of variation in species richness, 32.2% of evenness, and >25% of anuran, salamander, and total amphibian abundances. Salamanders were most sensitive to water chemistry factors, particularly pH. Our results suggest that decreasing the frequency of prescribed burns from the current 2-3 years to 3-7 years will better maintain diverse amphibian and plant assemblages. Substituting growing-season burns for the current practice of winter and spring burns would avoid repeatedly interrupting amphibian breeding and would maintain the desired longleaf pine community.

Efectos de Quemas Prescritas sobre la Diversidad de Anfibios en un Parque Nacional en el Sureste de E.U.A.

Resumen: El fuego altera la abundancia y diversidad de muchas especies, pero se conocen poco sus efectos sobre los anfibios. Analizamos el efecto de quemas prescritas sobre la abundancia y diversidad de anfibios en el Parque Nacional Francis Marion, Carolina del Sur, mediante el monitoreo de sus asociaciones en 15 charcas temporales con cinco historias de quema distintas: 0, 1, 2, 3 y 12 años después de las quemas. También monitoreamos variables ambientales terrestres y acuáticas que pudieran influir en la diversidad de anfibios, tales como profundidad de la bojarasca, química del agua de la charca y distancia a charcas vecinas. El fuego tuvo efectos negativos significativos. Los efectos inmediatos (quema durante el estudio) explicaron 12.8% y 10.8% de la variación en la abundancia de anuros y anfibios, respectivamente, mientras que los efectos de corto plazo explicaron 31.8% y 24.6% de la variación en la riqueza de especies de anfibios y su equitabilidad, respectivamente. La riqueza de especies incrementó y la equitabilidad decreció con el tiempo desde la quema, principalmente porque raramente se encontraron salamandras en sitios quemados dos años antes. En estos sitios la bojarasca tenía la menor profundidad y las mayores variaciones en la temperatura del suelo. La diversidad de anfibios también fue influenciada significativamente por factores ambientales no relacionados con la quema. La química del agua explicó 31.1% de la variación de la riqueza de especies, 32.2% de la equitabilidad y >25% de la abundancia de anuros, salamandras y total. Las salamandras fueron más sensibles a factores químicos del agua, particularmente el pH. Nuestros resultados sugieren que una reducción en la frecuencia actual de quemas prescritas cada 2-3 años a quemas cada 3-7 años manten-

[†]Current address: Anoka Conservation District, 16015 Central Avenue NE, Suite 103, Ham Lake, MN 55304-5618, U.S.A. *Current address: Department of Biology, University of Central Florida, 4000 Central Florida Boulevard, Orlando, FL 32816-2368, U.S.A. Paper submitted October 24, 2001; revised manuscript accepted January 21, 2003.

drá mejor las diversas asociaciones de anfibios y plantas. La sustitución de la práctica actual de quemas en invierno y primavera por quemas en épocas de crecimiento evitaría la interrupción reiterada de la reproducción de anfibios y mantendría la comunidad deseada de pinos.

Introduction

Prescribed burning is widely used to maintain native assemblages of fire-dependent plants and avoid destructive wildfires (Malanson 1987). Prescribed burning also affects the life cycles, abundance, and diversity of invertebrates, reptiles, birds, and mammals, but its effects on amphibians are poorly known (for reviews, see Russell et al. 1999; Bury et al. 2000). Amphibians are important components of many fire-maintained communities, particularly in the southeastern United States (e.g., Semlitsch et al. 1996), and declines of fire-adapted species have been linked to fire suppression and resulting vegetation changes (Means & Moler 1979; Palis 1997). Thus, inappropriate prescribed burning practices could cause amphibian declines in a region otherwise little affected by the anthropogenic stresses causing global declines (Wake & Morowitz 1990; Houlahan et al. 2000).

We examined the effects of current prescribed burning practices on amphibian assemblages within the Francis Marion National Forest (FMNF), South Carolina, U.S.A. Twenty anuran and 11 salamander species occur in the FMNF, including several species restricted to firemaintained pine flatwoods (Eason & Fauth 2001). Our analysis explored the immediate and short-term effects of fire on amphibian abundance, species richness, and evenness. We also compared the relative importance of burning versus other environmental factors, including pond water chemistry and terrestrial habitat variables.

Anecdotal evidence suggests that few amphibians are killed directly by fire (Russell et al. 1999). Subterranean lifestyles protect many species from fires, which often leave vegetation intact in wet areas, providing additional refugia (Means & Campbell 1981; Mushinsky 1985; Friend 1993). Treefrogs also escape fire in unburned areas such as tree crowns and beneath bark. The consensus is that behavioral and physiological adaptations of amphibians limit mortality during fires (Russell et al. 1999).

Indirect effects of fire on amphibians are poorly known but are likely important. Fire alters soil moisture and temperature, vegetation structure, leaf-litter depth, nutrient availability, erosion, and wetland hydroperiod (Langdon 1981; Christensen 1987, 1993; Kirkman 1995; Lugo 1995; Cain et al. 1998); all can affect amphibian assemblages. However, the literature offers no consistent conclusions about fire's indirect or cumulative effects on amphibians (Russell et al. 1999). In seven studies, the effects of fire were positive in three (Means & Moler 1979; Means & Campbell 1981; Kirkland et al. 1996), were negative in two (McLeod & Gates 1998; Papp & Papp 2000), and had no effect on amphibians in two (Bamford 1992; Ford et al. 1999). In another (Mushinsky 1985), effects varied with burn regime, and in two others changes in trophic relationships and community composition were not categorized as positive or negative (Barbault 1976; Kerby & Kats 1998). Thus, the effectiveness of prescribed burning in maintaining amphibian assemblages remains unclear (Russell et al. 1999; Bury et al. 2000).

Burning reduces leaf litter and vegetation structure, which provide terrestrial habitat for many amphibians. Historically, fires that occurred every 2-4 years allowed leaf litter to accumulate but maintained an open understory (Frost 1995). Deviation from historical fire frequencies (including fire suppression in the FMNF after Hurricane Hugo) may be detrimental to amphibians, especially species endemic to southeastern pine forests. Burn season also could be problematic if fires occur at vulnerable stages in the life cycle (Mushinsky 1985). Historically, fires occurred in the dry season (summer) and were intense (Frost 1995), but most prescribed burns are now done in winter and are less intense. Current burn practices and silvicultural methods in the southeastern United States often change the dominant tree from longleaf (Pinus palustris) to loblolly pine (P. taeda) and alter understory composition (Frost 1995), negatively affecting amphibians specialized to southeastern pine flatwoods (Means et al. 1996; Palis 1997).

Fire may affect aquatic stages of amphibians by releasing large quantities of nutrients in a usable, mineralized form. Burning removes organic matter and reduces soil porosity, leading to increased runoff and erosion. Enhanced overland water flow (DeBano et al. 1998) can deliver nutrients to ponds, stimulating plankton and algae, which are grazed by larval anurans. Cations released by fire also reduce water and soil acidity (DeBano et al. 1998), a positive outcome for acid-sensitive species. Many amphibians use both aquatic and terrestrial habitats during their life cycle, so the cumulative effects of burning across life-history stages could be compensatory, additive, or synergistic. Our objective was to determine the relative importance of both immediate (withinyear) and short-term (1- to 12-year) effects of fire on the abundance and diversity of amphibians. We quantified both the direct effects of prescribed burns and indirect effects mediated through altered aquatic and terrestrial conditions, and compared their magnitude using regression techniques.

Methods

Study Sites and Sampling Design

We studied the effects of prescribed burning on amphibians in temporary ponds within the 101,000-ha FMNF, in Charleston and Berkeley Counties, South Carolina. All ponds were small (diameter: 28.3-53.9 m), shallow (maximum depth: 0.29-1.32 m), acidic (mean annual pH: 3.43-5.41), and at low elevations (<15 m above sea level). Additional details about the study sites are provided by Schurbon (2000).

We monitored amphibian assemblages at 15 ponds encompassing five different burn histories: 0, 1, 3, 5, and 12 years after fire. We selected three ponds within each target burn history at random from all available ponds through the use of aerial photographs and U.S. Forest Service burn records. Selecting ponds at random ensured that our conclusions were applicable to the entire universe of temporary ponds within the FMNF and, by extension, to ponds in similar habitats elsewhere. Selecting ponds at random also minimized possible confounding effects, such as pre-Hurricane Hugo (October 1989) fire regimes, for which reliable records were unavailable. Ponds burned more recently were on a more frequent burn cycle, so recent burns were not more intense than earlier burns.

Monitoring Amphibians

We used five standard techniques to sample amphibians: drift fences, treefrog shelters, calling censuses, minnow trapping, and visual surveys (Heyer et al. 1994). We used partial drift fences of aluminum sheeting (7 m long \times 50 cm high, buried 10 cm into soil) with 11-L plastic buckets ($30 \times 24 \times 33$ cm) as pitfall traps to capture terrestrial amphibians. We placed three fences 10 m from and parallel to each pond's margin. Fences were equidistant from one another and overlapped traps, which we covered with lids except during and 48 hours after rainfalls that stimulated amphibian activity. We opened pitfalls 16 times (288 trap nights/pond) during our 1-year study, which commenced 1 July 1999. We identified, measured, weighed, sexed, and released all animals captured.

We used two different shelters to monitor treefrogs, which can climb out of pitfall traps (Moulton et al. 1996). At each pond, we drove 10 75-cm-long polyvinyl chloride (PVC) pipes into the soil and attached 10 25cm-long pipes (with lower end capped) to shrubbery at breast height. All shelters were 1.9 cm (3/4'') diameter. We alternated ground- and shrub-based shelters around each pond and checked them the same days as the pitfall traps (Schurbon 2000).

We conducted anuran calling censuses after major rainfall events, visiting each pond for 5 minutes and recording the species and approximate number of anurans calling. Calling censuses detected species not captured in treefrog shelters or that bypassed drift fences. We deployed 16 unbaited minnow traps (Fauth 1999*a*, 1999*b*) in each pond twice to census aquatic species (i.e., sirens and amphiumas) undetected by other methods. After 24 hours, we removed traps and inventoried their contents. Incidental sightings of amphibians in or near study ponds provided a few additional records.

We did not expect to recapture individuals repeatedly and therefore did not give them unique identifying marks. To avoid counting recaptured individuals more than once, we estimated minimum abundances with mass, length, and sex data from individual captures. Resulting estimates were used to calculate evenness (E), which is independent of species richness and abundance (Bulla 1994).

Environmental Parameters

We monitored three terrestrial environmental parameters (Fig. 1): soil moisture, leaf-litter mass, and soil temperature variance (Schurbon 2000). We measured soil moisture and leaf-litter mass 15, 30, and 45 m from pond margins along a randomly selected compass heading. We pushed a probe 1.9 cm (3/4'') in diameter into the soil for 20 cm and extracted a sample, which we weighed initially and weighed again after drying it for 24 hours at 60° C to determine percent moisture. Similarly, we collected leaf litter within three randomly located 0.5-m² quadrats, dried it, and weighed it to estimate mass. We placed a "Hobo" H8 data logger (Onset Computer Corporation, Bourne, Massachusetts) at a random location 20 m from each pond margin to record temperature at the margin between leaf litter and soil. We also measured four parameters that could affect metapopulation dynamics: distances to the nearest road, ditch, and intermittent and permanent wetlands.

We monitored three aquatic environmental parameters during each visit: turbidity, pH, and dissolved oxygen (Fig. 1). We measured pond depth 2–3 times/month to assess hydroperiod. In addition, water samples drawn on 5 March 2000 were analyzed for K^+ , Ca^{2+} , Mg^+ , Fe, Na⁺, Cl⁻, and total dissolved solids (Schurbon 2000).

Statistical Analyses

We tested the null hypotheses of no effects of time since burn or of terrestrial and aquatic environmental variables on amphibian diversity with backward stepwise regression. Amphibian species richness (S), evenness (E), and minimum amphibian, anuran, and caudate abundance were response variables. Ponds (n = 15) were the independent units of statistical analysis. Independent variables included number of months since last burn and a "burned during study" dummy variable to account for prescribed burns conducted at four sites. Distances to



Figure 1. Mean (\pm 1 SE) terrestrial and aquatic environmental parameters as a function of years since last burn for 15 temporary ponds within the Francis Marion National Forest, U.S.A.: (a) terrestrial environmental variables; (b) aquatic variables. Pond diameter and distances to the nearest permanent and ephemeral wetlands and to ditches are given in meters; leaf-litter mass in grams per square meter; soil moisture as a percentage; and soil temperature variance in degrees Celsius squared. Turbidity is in nepholometric turbidity units (NTU); dissolved oxygen (DO) as a percentage, and total dissolved solids (TDS) and concentrations of all ions in ppm.

the nearest intermittent wetland and road were logtransformed to meet assumptions of multiple regression (Draper & Smith 1981).

We used principal components (PCs) analysis to condense our 10 aquatic environmental factors into four components, which retained approximately 95% of the original variation (Table 1). Using PCs instead of raw variates allowed us to include environmental factors and effects of burning in fully parameterized, initial regression models.

Soil temperature variance failed regression assumptions even after transformation and was excluded from models. Instead, we used a Kruskal-Wallis Test (Sokal &

Table 1. Results of principal components analysis of aquaticenvironmental parameters monitored at 15 ponds in the FrancisMarion National Forest, South Carolina, U.S.A.

| | P | rincipal c | componer | nt |
|---------------------------------|--------|------------|----------|--------|
| Eigenvalues and eigenvectors | 1 | 2 | 3 | 4 |
| Eigenvalue | 6.70 | 1.11 | 0.97 | 0.69 |
| % variation | 67.03 | 11.10 | 9.70 | 6.93 |
| cumulative % variation | 67.03 | 78.14 | 87.84 | 94.77 |
| Eigenvectors* | | | | |
| mean turbidity | 0.328 | -0.212 | 0.215 | -0.385 |
| mean pH | 0.371 | -0.005 | -0.070 | -0.224 |
| mean dissolved oxygen | -0.128 | 0.514 | 0.740 | 0.279 |
| potassium | 0.298 | 0.292 | 0.284 | -0.423 |
| calcium | 0.372 | -0.063 | 0.105 | -0.044 |
| magnesium | 0.356 | 0.269 | -0.172 | 0.120 |
| iron | 0.204 | 0.642 | -0.487 | 0.144 |
| sodium | 0.359 | -0.075 | -0.022 | 0.321 |
| chloride | 0.286 | -0.318 | 0.118 | 0.634 |
| total dissolved solids | 0.363 | -0.099 | 0.169 | 0.050 |

* Eigenvector magnitudes are weightings of original variates on a principal component. Eigenvector signs indicate the direction of relationships between original variates and principal components.

Rohlf 1995) to examine differences in soil temperature variance among burn categories. We used one-way analysis of variance (ANOVA) to test for differences in leaflitter mass, soil moisture, and water-chemistry principal components among ponds based on time since last burn. We performed statistical analyses using JMP version 3.2.2 (SAS Institute 1998), with $\alpha = 0.05$ for all hypothesis tests.

Results

Abundance and Diversity of Amphibians

We recorded 1495 amphibians comprising 25 species (Fig. 2). *Pseudacris ocularis* (little grass frog), *Rana sphenocephela* (southern leopard frog), and *Bufo terrestris* (southern toad) were the most common species, comprising 21%, 19%, and 12% of records, respectively. These and three other species—*Gastrophryne carolinensis* (eastern narrowmouth toad), *Hyla femoralis* (pine woods treefrog), and *R. clamitans* (green frog)—were encountered in every burn category. With the exception of *Ambystoma talpoideum* (mole salamander) and a single *Pletbodon variolatus* (South Carolina slimy salamander), salamanders were not encountered at sites burned within 2 years (Schurbon 2000).

Amphibians used as management indicator species were recorded from ponds in all burn categories. Pinewoods treefrogs (*H. femoralis*) were found at all but one site, which was burned 3 years before. Southern chorus frogs (*P. nigrita*) were detected at five ponds: two burned during the study's first year (including one



Figure 2. Mean $(\pm 1 \text{ SE})$ amphibian responses as a function of years since last burn for15 temporary ponds within the Francis Marion National Forest: (a) total number of individuals recorded for each species; (b) total number of amphibians observed, minimum amphibian abundance (no. individuals), species richness (S), and evenness (E). Abbreviations: SHOL, Scaphiopus holbrooki; BTER, Bufo terrestris; BQUE, B. quercicus; AGRY, Acris gryllus; HCIN, Hyla cinerea; HFEM, H. femoralis; HSQU, H. squirella; HCHR, H. chrysoscelis; PCRU, Pseudacris crucifer; PNIG, Pseudacris nigrita; PORN, Pseudacris ornata; POCU, Pseudacris ocularis; GCAR, Gastrophryne carolinensis; RCAT, Rana catesbeiana; RVIR, R. virgatipes; RCLA, R. clamitans; RSPH, R. sphenocephala; AMEA, Amphiuma means; SINT, Siren intermedia; ATAL, Ambystoma talpoideum; AOPA, Ambystoma opacum; AMAB, Ambystoma mabeei; AMAC, Ambystoma maculatum; NVIR, Notophthalmus viridescens; PVAR, Plethodon variolatus.

individual captured immediately after a burn) and the others 1, 5, and 12 years after a burn. Mabee's salamander (*A. mabeei*) was encountered at only two sites, in the 5- and 12- year post-burn categories. We encountered no proposed, endangered, threatened, or sensitive amphibian species (Carolina gopher frog [*Rana capito*], flatwoods salamander [*Ambystoma cingulatum*], or eastern tiger salamander [*A. tigrinum*]) during our study. Carolina gopher frogs and flatwoods salamanders are known from <10 sites in the FMNF, and eastern tiger salamanders have not been recorded for >12 years (J. F., personal observation; J. R. Harrison III, personal communication).

Principal Components Analysis

All water-chemistry parameters except dissolved oxygen loaded positively and approximately equally onto PC1 (Table 1). Thus, ponds with high scores on PC1 were turbid and oxygen-poor; had high concentrations of all ions and high total dissolved solids; and were the least acidic. These attributes were typical of ponds in hardwood stands. Iron and dissolved oxygen loaded strongly and positively onto PC2, but chloride and turbidity loaded negatively. Thus, ponds with high scores on PC2 were nonturbid, acidic, and rich in oxygen and iron but low in chloride. These attributes were typical of ponds in pine stands and of ponds that held water most of the year. In contrast, dissolved oxygen loaded strongly and positively on PC3, but iron loaded negatively. Thus, ponds with high scores on PC3 were oxygen-rich but low in iron. In general, these ponds also were located in pine stands but had shorter hydroperiods, holding water approximately half the year. Dissolved oxygen, sodium, and especially chloride loaded strongly and positively on PC4, whereas turbidity, pH, and potassium loaded negatively. Thus, ponds with high scores on PC4 (Table 1) were relatively clear, acidic, oxygen-rich, and slightly saline. These ponds had the shortest hydroperiods and were near the Wambaw Swamp Wilderness, a river-bottom hardwood swamp bordered by small pine stands.

Effects of Fire on Environmental Factors

Prescribed burning affected terrestrial but not aquatic environmental factors. Leaf-litter mass was significantly higher at sites burned 12 years before (mean ± 1 SE: 704.5 ± 189.01 g/quadrat) than those burned during the study and 1 year before (157.6 ± 33.1 g/quadrat; $F_{4,14} = 5.81$, p = 0.011). Soil temperature variance was higher at sites burned during the study (60.0 $\pm 68.4^{\circ}$ C²) than those unburned (15.3 $\pm 14.9^{\circ}$ C²; Kruskal-Wallis $\chi^2 = 4.93$, df = 1, p = 0.027), but mean soil moisture did not vary significantly with time since burn ($F_{4,14} =$ 0.67, p = 0.63). Mean PC1 score was four times higher in the 12-year burn category than in all others, but this difference was not significant ($F_{4,14} = 8.09$, p = 0.067). Remaining PCs did not vary significantly among burn categories (all $F_{4,14} < 1.12$, p > 0.39).

Determinants of Amphibian Species Richness and Evenness

The final regression model accounted for 93.7% of the total variation in S, with months since burning responsi-

| Table 2. | Results of | f backward stepv | vise regression | ı on amphibiar | n species richness | and evenness. ^a |
|----------|------------|------------------|-----------------|----------------|--------------------|----------------------------|
|----------|------------|------------------|-----------------|----------------|--------------------|----------------------------|

| | Am | pbibian species ri | chness ^b | | Ampbibian evenr | iess ^b |
|--|------------------|--------------------|---------------------|----------------|-------------------|-------------------|
| Source | \mathbf{F}^{c} | standardized β | variation (%) | F ^c | standardized β | variation (%) |
| P1 – months since burn | 87.5**** | 1.51 | 31.8 | 38.2*** | -1.62 | 24.6 |
| P2 - soil moisture | | | | 18.7** | 0.53 | 12.0 |
| P3 - distance to permanent wetland | 16.2** | -0.57 | 5.6 | | - | |
| $P4 - log_{10}$ (distance to intermittent wetland) | 36.8*** | -1.10 | 13.4 | 26.2*** | 0.81 | 16.8 |
| $P5 - \log_{10}$ (distance to nearest road) | 9.9* | -0.43 | 3.6 | | | |
| P6 - distance to nearest ditch | 22.4** | 0.64 | 8.2 | | | |
| P7 - water chemistry PC1 | | | | 20.2** | 0.93 | 13.0 |
| P8 - water chemistry PC2 | 32.3*** | -0.99 | 11.8 | 29.8*** | 1.19 | 19.2 |
| P9 - water chemistry PC3 | 53.2*** | 1.18 | 19.3 | - | - | - |
| Residual (totals sum to 100%) | | | 6.3 | | | 14.3 |

^a Table entries are parameters remaining in model, F ratios, standardized betas (which indicate strength and direction of effect), and percentage of total variation explained.

^b Regression equations: number of amphibian species = $24.822 + 0.084 \cdot P1 - 0.006 \cdot P3 - 7.803 \cdot P4 - 3.108 \cdot P5 + 0.092 \cdot P6 - 2.725 \cdot P8 + 3.517 \cdot P9$; evenness = $-0.180 - 0.005 \cdot P1 + 0.016 \cdot P2 + 0.336 \cdot P4 + 0.064 \cdot P7 + 0.193 \cdot P8$. ^c Significance levels: *p < 0.05; **p < 0.01; ****p < 0.001;

ble for the greatest variation (Table 2). Species richness increased significantly with time since burning (Fig. 3) and when permanent and intermittent wetlands were nearby but decreased with nearby ditches. Species richness also varied significantly with PCs 2 and 3, which were heavily influenced by dissolved oxygen and iron (Table 1). Low iron (i.e., low PC2 scores and high PC3 scores) was associated with increased S (Fig. 3). Nonsignificant factors removed by stepwise regression included the "burned during study" dummy variable, indicating no immediate effect of spring burns.

The final regression model accounted for 85.7% of the variation in E, with months since burning responsible for the greatest variation (Table 2). Evenness decreased significantly with time since last burn (Fig. 3); burning during the study did not alter this result. Evenness also increased significantly with distance to the nearest intermittent wetland, soil moisture, and PCs 1 and 2 (Table 2).

Determinants of Amphibian Abundance

The final backward-regression model accounted for 98.4% of the variation in minimum anuran abundance (Table 3), which increased significantly with time since last burn and decreased significantly at sites burned during the study (Fig. 4). Collectively, these two factors accounted for 16.4% of the variation in minimum anuran abundance. However, distance to the nearest ditch accounted for most variation in minimum abundance (26.7%), which was significantly higher with ditches nearby. Minimum anuran abundance also increased significantly with increasing soil moisture and decreased with increasing scores on PCs 1-3 (Table 3). Anurans comprised 93.7% of all amphibians recorded, so minimum amphibian abundance had the same pattern (Table 3).

In contrast, time since burning and burning during the study had no significant effects on minimum salamander abundance (Table 3). Instead, PCs 1-3 accounted for 82.2% of the total variation, with PC1 explaining the most (67.3%; Table 3). Minimum salamander abundance increased with increasing PC1 scores. Principle components 2 and 3 explained considerable variation, with minimum salamander abundance decreasing with PC2 and increasing with PC3 (Fig. 4). Distances to the nearest ditch and intermittent wetland explained smaller but significant amounts of variation (Table 3). Salamander abundance was highest at sites with nearby ditches but isolated from other wetlands.

Discussion

Immediate and Short-Term Effects of Prescribed Burns

We found negative immediate and short-term effects of prescribed burning on amphibian abundance and diversity in the Francis Marion National Forest. Both anuran and total amphibian abundance were lower at sites burned during the study than at unburned sites. Previously, direct effects of fire were considered negligible because most amphibians reside in wet, unburned areas, underground, or in the forest canopy (Means & Campbell 1981; Mushinsky 1985; Friend 1993; Ford et al. 1999; Russell et al. 1999). Immediately after fire, however, leaf-litter cover was lowest, resulting in higher soil-temperature variance than at unburned sites. Risks of desiccation and predation presumably were high, and amphibians may have been killed, migrated to unburned areas, or entered refugia until favorable conditions returned.

Our results contradict the hypothesis that intermediate burning frequencies maximize species richness (in-



Figure 3. Leverage plot of amphibian species richness and evenness for ponds in the Francis Marion National Forest: (a) amphibian species richness versus months since burn; (b) amphibian species richness versus waterchemistry principal component 2; (c) amphibian species richness versus water-chemistry principal component 3; (d) evenness versus months since burn; (e) evenness versus water-chemistry principal component 2; and (f) evenness versus water-chemistry principal component 1. A leverage plot shows one effect in the model after variation explained by all other effects has been removed. The solid line is the regression line, the beavy, dashed horizontal line is the mean number of species per study site, and the finely dashed lines enclose 95% confidence intervals. Abbreviations: TDS, total dissolved solids; DO, dissolved oxygen.

termediate disturbance hypothesis; Connell 1978), at least on the time scale we considered. Instead, amphibian species richness increased linearly with time since last burn, largely because additional species were found at sites not recently burned. In addition, low salamander abundance reduced evenness at recently burned sites. Fire likely had linear short-term effects on species richness and evenness because deep leaf-litter accumulations and other cool, moist microenvironments that amphibians require take years to recover from prescribed burns.

Minimum salamander abundance did not vary significantly between burned and unburned sites, but this result should be interpreted with caution. We captured most (76%) salamanders during winter breeding migrations that preceded prescribed burns. Adult salamanders could suffer acute effects from burning if fire were to precede or coincide with the breeding season, which often occurs in the FMNF. Salamanders migrating across recently burned areas would be exposed to greater risks of desiccation and predation than those migrating on or through moist leaf litter. Determining whether amphibian breeding migrations are directly affected by prescribed burns should be a research priority.

Influence of Terrestrial Variables

Amphibian species richness decreased significantly with increasing distance to the nearest intermittent and per-

| | | Anurans ^b | | | Salamanders ^b | | | Total amphibian | PP AS1 |
|---|--------------------|----------------------------------|----------------------|-----------------|--------------------------|------------------|-------------|----------------------|------------------|
| Source | Ъc | standardized β | variation (%) | Ъ ^c | standardized β | variation (%) | Ъ | standardized β | variation (%) |
| P1 – months since burn | 18.0** | 0.84 | 5.6 | | | | 14.5* | 0.82 | 6.2 |
| P2 – burned during study | 34.8** | -0.37 | 10.8 | 5.0 | 0.13 | 2.2 | 29.8** | 0.37 | 12.8 |
| P3 – pond diameter | 47.2** | -0.76 | 14.6 | | | | 32.5** | -0.68 | 13.9 |
| P4 – soil moisture | 31.6** | 0.41 | 9.8 | | | | 19.3** | 0.35 | 8.3 |
| P5 – leaf-litter mass | 5.6 | -0.40 | 1.7 | | | | 4.3 | -0.38 | 1.8 |
| P6 – distance to permanent wetland | | | | 6.2 | -0.25 | 2.8 | | | |
| $P7 - log_{10}$ (distance to intermittent wetland) | | | | 6.9* | 0.23 | 3.1 | | | |
| $P8 - log_{10}$ (distance to nearest road) | | | | 5.3 | 0.17 | 2.4 | | | |
| P9 – distance to nearest ditch | 86.2*** | -0.66 | 26.7 | 8.2* | -0.20 | 3.7 | 70.2*** | -0.65 | 30.1 |
| P10 – water chemistry PC1 | 33.0** | -0.68 | 10.2 | 150.2**** | 0.75 | 67.3 | 16.9** | -0.53 | 7.2 |
| P11 – water chemistry PC2 | 33.42** | -0.56 | 10.4 | 9.8* | -0.25 | 4.4 | 29.2** | -0.57 | 12.5 |
| P12 – water chemistry PC3 | 27.30** | -0.35 | 8.5 | 23.5** | 0.38 | 10.5 | 12.5* | -0.25 | 5.4 |
| P13 – water chemistry PC4 | | | | 4.8 | -0.16 | 2.2 | | | |
| Residual (totals sum to 100%) | | | 1.6 | | | 1.5 | | | 1.9 |
| ^a Entries are as in Table 2. | | | | | | | | | |
| ^b Regression equations: minimum anuran abunda | nce = 309.4 | $+ 14 \cdot 691.1 + 62$ | 28.917 • P2 - | 7.214 • P3 + 4. | $747 \cdot P4 - 2.354$ | • P9 - 19.863 | • P10 - 38 | .777 • P11 – 25.846 | • P12; mini |
| mum salamander abundance = $-12.289 + 6.893$ | $3 \cdot P7 - 0.1$ | $25 \cdot P9 + 3.77 \cdot P$ | $10 - 2.993 \cdot 1$ | P11 + 4.882 • 1 | P12; and minimu | m total amphit | pian abundo | nce = 314.595 + . | 1.223 • PI + |
| 51.249 • P2 = 0.98/ • P3 + 4.523 • P4 = 2.480 • I ^c Sionificance levels: * h < 0.05. ** h < 0.01 ^{, ***} h < 0 | P9 - 10.012 | * • P10 – 42.281 • P < 0.0001 | 11 - 20.439 • | P12. | | | | | |
| Digitificance reverses. p > 0.01, p > 0.01, p > 0 | 1 (1001) | > 0.0001. | | | | | | | |

manent wetlands, suggesting that movement between aquatic habitats is important for maintaining local populations. Independent evidence suggests that several amphibian species have difficulty dispersing more than a few hundred meters from their natal ponds (Semlitsch 1998, 2000; Fauth 1999b). Differential colonization ability also may explain why evenness was low when a temporary wetland was nearby: weak dispersers are generally good competitors and often dominate the communities they colonize (Hubbell 2001).

Amphibian species richness decreased significantly when ponds had ditches nearby, which provide routes by which predatory fish can colonize ephemeral ponds (Snodgrass et al. 1996; Semlitsch 2000; Eason & Fauth 2001). Fish are important predators of amphibians and can severely reduce the abundance and distribution of palatable species (Kats et al. 1988; Semlitsch 2000; Eason & Fauth 2001). Unpalatable species benefit indirectly from fish predation (Werner & McPeek 1994). Anuran, salamander, and total amphibian abundance all increased when ditches were nearby, but this was not attributable only to increases in unpalatable species (i.e., bullfrogs and toads).

Influence of Aquatic Variables

Water-chemistry parameters significantly affected every response variable we examined, but PC scores were uncorrelated with time since burning. We found high PC scores and high salamander abundance at ponds with hardwood vegetation. All were located in stands burned 5-12 years previously. Current FMNF management plans prioritize the burning of pine stands over hardwoods (U.S. Forest Service 1996a, 1996b). When we removed hardwood ponds from stepwise regression models, water chemistry PCs and distances to intermittent wetland and ditch no longer affected minimum salamander abundances, but all other results remained unchanged. Amphibians often are more abundant in hardwood than in pine stands (Bennett et al. 1980; Hanlin et al. 2000), and many amphibian species select sites based on soil pH (Wyman & Hawksley-Lescault 1987; Wyman 1988). Hardwood litter generally has a higher pH than needle-dominated leaf litter and therefore is favored by species adapted to hardwood forests (Wyman & Jancola 1992; deMaynadier & Hunter 1995).

In our study, mean species richness and minimum salamander abundance both increased with increasing pond pH. Other studies conducted in the FMNF (Fauth 1999*a*; Eason & Fauth 2001) and elsewhere (Freda & Dunson 1986; Sadinski & Dunson 1992; Jung & Jagoe 1995; Hecnar & M'Closkey 1996) document amphibian sensitivity to low pH. In addition to providing tolerable acidity conditions, hardwood leaf litter also may enrich ponds, creating conditions favorable for larval stages of acid-sensitive amphibians. Although hardwood stands



Figure 4. Leverage plots of minimum amphibian and salamander abundance in ponds in the Francis Marion National Forest: (a) minimum amphibian abundance versus months since burn; (b) minimum amphibian abundance versus sites burned during the study; (c) minimum salamander abundance versus aquatic principal component 2; (d) minimum salamander abundance versus aquatic principal component 3. Lines are as in Fig. 3. Abbreviation: DO, dissolved oxygen.

may be important for maintaining diverse amphibian assemblages, they do not support species adapted to pine flatwoods (Means & Campbell 1981), including most management indicator species and proposed, endangered, threatened, and sensitive amphibian species in the FMNF.

Management Implications

Our findings suggest that extensive and frequent prescribed burns are not beneficial to all members of fireadapted southeastern pine communities. Amphibian species richness increased linearly with time since the last fire, and anuran abundance was lowest at sites burned during our study. We suggest that decreasing burn cycles to 3-5 years would maintain amphibian assemblages without sacrificing native vegetation. At this frequency, fires burn incompletely because they are not extremely intense, leaving refugia for amphibians and other taxa (Friend 1993). Our data suggest that even longer intervals will benefit amphibians. Mushinsky (1986) also recommended a 5- to 7-year prescribed-burn cycle to maintain herpetofaunal assemblages in similar Florida sandhill communities. In general, burn cycles of <5 years adversely affect longleaf pine ecosystems (Cain et al. 1998), whereas fire frequencies of >3-5 years can generate more-intense fires, which can damage the entire community (McCullough et al. 1998). A prescribedburn cycle approaching 5 years should balance the conflicting needs of amphibians and longleaf pines without placing the entire community in danger of catastrophic fire.

Maintaining spatial heterogeneity by burning small patches and varying fire intensity across the landscape should minimize the negative effects of frequent fires on amphibians. Recolonization of burned sites may be delayed if the nearest unburned wetland is >200 m away (Semlitsch 1998; Fauth 1999*a*; this study). Some areas should be protected from frequent fires, which in the FMNF is consistent with U.S. Forest Service goals to promote hardwood growth (U.S. Forest Service 1996*a*, 1996*c*). This protection may prove especially beneficial for salamanders, which do not disperse as readily as frogs. Burning small areas rather than large tracts also meets the management goals of using fire to create a mosaic of habitats that complement wildlife objectives (U.S. Forest Service 1996*a*).

Varying burn season will benefit amphibian populations by introducing temporal heterogeneity. We found lower amphibian and anuran abundances immediately after burns, which occurred after salamander breeding migrations at our sites. Fires may hinder breeding migrations, and repeated interruption could cause localized extinctions (Semlitsch 2000). Palis (1997) attributed declines of flatwoods salamanders (A. cingulatum) in part to infrequent growing-season burns and resulting vegetation changes. Traditionally, prescribed burning is done in winter to minimize damage to pine flatwoods. Recent evidence shows that growing-season burns are more effective than winter burns in controlling hardwoods and sprouts (Langdon 1981; Streng et al. 1993; Sparks et al. 1999) and are less likely to damage pines (reviewed by Streng et al. 1993). Growing-season burns also reduce fatal infections of longleaf pine seedlings by brown spot fungus (Streng et al. 1993). Although U.S. Forest Service management goals reflect this new knowledge, more than 80% of prescribed burning in the FMNF still occurs in the dormant season (U.S. Forest Service 1996a, 1996b).

The prescribed burning regime most effective for maintaining amphibian assemblages is likely to vary among regions and habitats. Prescribed burns in the southern Appalachians, U.S.A., apparently have little effect on amphibians, which are largely sheltered by moist coves (Ford et al. 1999). Preliminary results from Oregon, U.S.A., also indicate that fire has little effect on terrestrial amphibians (Bury et al. 2000). In comparison, fires are vital for maintaining the longleaf pine savannas that harbor diverse amphibian assemblages along the southeastern U.S. coastal plain and sandhills (Means & Campbell 1981; Mushinsky 1985; Means et al. 1996; Palis 1997). Determining how fire affects amphibian species with different life-history traits should enhance understanding of the trade-offs associated with different prescribed-burning regimes.

Acknowledgments

We thank K. Johnson, E. Levesque, and H. Schurbon for help constructing drift-fence arrays and J. A. Herbert, B. Ott, K. Owens, L. Sanfratello, and the Fall 1999 herpetology class at the College of Charleston for help with fieldwork. G. Eason, A. Halfacre, A. Herbert, P. Marino, B. Scholtens, and two anonymous reviewers provided guidance and/or made helpful comments on the manuscript. Special thanks go to the Francis Marion National Forest staff, especially D. Carlson, B. Twomey, and M. Butler. This research was funded by grants to J.M.S. from the American Wildlife Research Foundation and Sigma Xi, The Scientific Research Society, and to J.E.F. from the National Science Foundation (DEB 9727039), the Environmental Protection Agency (R825795), and the National Fish and Wildlife Foundation (Challenge Grant 97-231). The University of Illinois, the Illinois Natural History Survey, the Ethel Jane Bunting Foundation, and the Gaylord and Dorothy Donnelly Foundation generously provided matching funds. The views and conclusions contained in this document are those of the authors and should not be interpreted as representing the opinions or policies of the U.S. Government. Mention of trade names or commercial products does not constitute their endorsement by the U.S. Government.

Literature Cited

- Bamford, M. J. 1992. The impact of fire and increasing time since fire upon *Heleioporus eyre I*, *Lymnodynastes dorsalis*, and *Myobatrachus gouldii* (Anura: Leptodactylidae) in *Banksia* woodland near Perth, Western Australia. Wildlife Research 19:169-178.
- Barbault, R. 1976. Structure et dynamique d'um peuplement d'Amphibiens en savane protegee du feu (Lamto, cote-d'Ivoire). Terre Vie 30:246-263.
- Bennett, S. H., J. W. Gibbons, and J. Glanville. 1980. Terrestrial activity, abundance, and diversity of amphibians in differently managed forest types. American Midland Naturalist 103:412-416.
- Bulla, L. 1994. An index of evenness and its associated diversity measure. Oikos 70:167-171.
- Bury, R. B., D. J. Major, and D. Pilliod. 2000. Responses of amphibians to fire disturbance in Pacific Northwest forests: a review. Pages 34-42 in W. M. Ford, K. R. Russell, and C. E. Moorman, editors. The role of fire in nongame wildlife management and community restoration: traditional uses and new directions. Proceedings of a special workshop. General technical report NE-288. U.S. Forest Service, Northeastern Research Station, Newton Square, Pennsylvania.
- Cain, M. D., T. B. Wigley, and D. J. Reed. 1998. Prescribed fire effects on structure in uneven-aged stands of loblolly and shortleaf pines. Wildlife Society Bulletin 26:209-218.
- Christensen, N. L. 1987. The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of the southeastern United States. Pages 1-21 in L. Trabaud, editor. The role of fire in ecological systems. Academic Publishing, Dordrecht, The Netherlands.
- Christensen, N. L. 1993. The effects of fire on nutrient cycles in longleaf pine ecosystems. Pages 205-214 in S. Herman, editor. Proceedings of 18th Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.
- DeBano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. Fire's effects on ecosystems. Wiley, New York.
- deMaynadier, P. G., and M. H. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Review **3**:230-261.
- Draper, N. R., and H. Smith. 1981. Applied regression analysis. Wiley, New York.
- Eason, G. E., and J. E. Fauth. 2001. Ecological correlates of anuran diversity in temporary ponds: a field study in South Carolina, USA. Israel Journal of Zoology 47:347-365.
- Fauth, J. E. 1999a. Identifying potential keystone species from field data: an example from temporary ponds. Ecology Letters 2:36-43.
- Fauth, J. E. 1999b. Interactions between branchiate mole salamanders (*Ambystoma talpoideum*) and lesser sirens (*Siren intermedia*): asymmetrical competition and intraguild predation. Amphibia-Reptilia 20:119-132.
- Ford, W. M., M. A. Menzel, D. W. McGill, J. Laerm, and T. S. McCay. 1999. Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. Forest Ecology and Management 14:233-243.
- Freda, J., and W. A. Dunson. 1986. Effects of low pH and other chemi-

Schurbon & Fauth

cal variables on the local distribution of amphibians. Copeia **986:** 454-466.

- Friend, G. R. 1993. Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia: a review. Biological Conservation **65**:99-114.
- Frost, C. C. 1995. Presettlement fire regimes in southeastern marshes, peatlands, and swamps. Pages 39-60 in S. Cerulean and R. Engstrom, editors. Proceedings of the 19th Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.
- Hanlin, H. G., M. F. Douglas, L. D. Wike, and S. H. Bennett. 2000. Terrestrial activity, abundance and species richness of amphibians in managed forests in South Carolina. American Midland Naturalist 143:70-83.
- Hecnar, S. J., and R. T. M'Closkey. 1996. Amphibian species richness and distribution in relation to pond water chemistry in south-western Ontario, Canada. Freshwater Biology 36:7-15.
- Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster, editors. 1994. Measuring and monitoring biological diversity; standard methods for amphibians. Smithsonian Institution Press, Washington, D.C.
- Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyers, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404:752-755.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, New Jersey.
- Jung, R. E., and C. H. Jagoe. 1995. Effects of low pH and aluminum on body size, swimming performance, and susceptibility to predation of green treefrog (*Hyla cinerea*) tadpoles. Canadian Journal of Zoology 73:2171-2183.
- Kats, L. B., J. W. Petranka, and A. Sih. 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1865– 1870.
- Kerby, J. L., and L. B. Kats. 1998. Modified interactions between salamander life stages caused by wildfire-induced sedimentation. Ecology 79:740-745.
- Kirkland, G. L., H. W. Snoddy, and T. L. Amsler. 1996. Impact of fire on small mammals and amphibians in a central Appalachian deciduous forest. American Midland Naturalist 135:253–260.
- Kirkman, L. K. 1995. Impacts of fire and hydrological regimes on vegetation in depression wetlands of Southeastern USA. Pages 10-20 in S. Cerulean, and R. Engstrom, editors. Proceedings of the 19th Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.
- Langdon, O. G. 1981. Some effects of prescribed fire on understory vegetation in loblolly pine stands. Pages 143-153 in G. W. Wood, editor. Prescribed fire and wildfire in southern forests: symposium proceedings. Belle W. Baruch Forest Science Institute, Georgetown, South Carolina.
- Lugo, A. E. 1995. Fire and wetland management. Pages 1-9 in S. Cerulean and R. Engstrom, editors. Proceedings of the 19th Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.
- Malanson, G. P. 1987. Diversity, stability, and resilience: effects of fire regime. Pages 49-63 in L. Trabaud, editor. The role of fire in ecological systems. Academic Publishing, Dordrecht, The Netherlands.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annual Review of Entomology 43:107–127.
- McLeod, R. F., and J. E. Gates. 1998. Response of herpetofaunal communities to forest cutting and burning at Chesapeake Farms, Maryland. American Midland Naturalist 139:164–177.
- Means, D. B., and H. W. Campbell. 1981. Effects of prescribed burning on amphibians and reptiles. Pages 89-97 in Prescribed fire and wildfire in southern forests: symposium proceedings. Belle W. Baruch Forest Science Institute, Georgetown, South Carolina.
- Means, D. B., and P. E. Moler. 1979. The pine barrens treefrog: fire,

seepage bogs, and management implications. Pages 77-83 in R. R. Odum and L. Landers, editors. Proceedings of the rare and endangered wildlife symposium. Technical bulletin WL-4. Georgia Department of Natural Resources, Game and Fish Division, Atlanta.

- Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander (*Ambystoma cingulatum*). Conservation Biology 10:426-437.
- Moulton, C. A., W. J. Fleming, and B. R. Nerney. 1996. The use of PVC pipes to capture hylid frogs. Herpetological Review 27:186-187.
- Mushinsky, H. R. 1985. Fire and the Florida sandhill herpetofaunal community. Herpetologica **41:**333-342.
- Mushinsky, H. R. 1986. Fire, vegetation structure, and herpetofaunal communities. Pages 383–388 in Z. Rocek, editor. Studies in herpetology: proceedings of the third European herpetological meeting. Charles University, Prague, Czechoslovakia.
- Palis, J. G. 1997. Distribution, habitat, and status of the flatwoods salamander (*Ambystoma cingulatum*) in Florida, USA. Herpetological Natural History 5:53-65.
- Papp, M. G., and C. O. Papp. 2000. Decline in a population of the treefrog *Phyllodytes luteolus* after fire. Herpetological Review 31: 93-95.
- Russell, K. R., D. H. Van Lear, and D. C. Guynn. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 27:374-384.
- SAS Institute. 1998. JMP statistics and graphics guide. Version 3.1. SAS Institute, Cary, North Carolina.
- Sadinski, W. J., and W. A. Dunson. 1992. A multilevel study of effects of low pH on amphibians of temporary ponds. Journal of Herpetology 26:413-422.
- Schurbon, J. M. 2000. Effects of prescribed burning on amphibian diversity in the Francis Marion National Forest, South Carolina. M.S. thesis. University of Charleston, Charleston, South Carolina.
- Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones of pond-breeding salamanders. Conservation Biology 12:1113-1119.
- Semlitsch, R. D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631.
- Semlitsch, R. D., D. E. Scott, J. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217-248 in M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, New York.
- Snodgrass, J. W., B. A. Lawrence, R. F. Lide, and G. M. Smith. 1996. Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 53:443-454.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd edition. W.H. Freeman, New York.
- Sparks, J. C., R. E. Masters, D. M. Engle, M. E. Payton, and G. A. Bukenhofer. 1999. Influence of fire season and fire behavior on woody plants in Red-cockaded Woodpecker clusters. Wildlife Society Bulletin 27:124–133.
- Streng, D. R., J. S. Glitzenstein, and W. J. Platt. 1993. Evaluating effects of season of burn in longleaf pine forests: a critical literature review and some results from an ongoing long-term study. Pages 227-263 in S. M. Hermann, editor. Proceedings of the 18th Tall Timbers fire ecology conference. Tall Timbers Research Station, Tallahassee, Florida.
- U.S. Forest Service. 1996a. Francis Marion National Forest record of decision for the revised land and resource management plan. U.S. Department of Agriculture, Washington, D.C.
- U.S. Forest Service. 1996b. Francis Marion National Forest revised land and resource management plan. U.S. Department of Agriculture, Washington, D.C.
- U.S. Forest Service. 1996c. Francis Marion National Forest final environmental impact statement for the revised land and resource management plan. U.S. Department of Agriculture, Washington, D.C.

- Wake, D. B., and H. J. Morowitz. 1990. Report to Board on Biology, National Research Council, on workshop on declining amphibian populations, Irvine, California, 19–20 February 1990. National Research Council, Irvine, California.
- Werner, E. E., and M. A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368-1382.
- Wyman, R. L. 1988. Soil acidity and moisture and the distribution of

amphibians in five forests of southcentral New York. Copeia 988: 394-399.

- Wyman, R. L., and J. Jancola. 1992. Degree and scale of terrestrial acidification and amphibian community structure. Journal of Herpetology **26:**392-401.
- Wyman, R. L., and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Pletbodon cinereus*. Ecology 68:1819–1827.