Responses of Southeastern
Amphibians and Reptiles
to Forest Management: A Review

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*Abstract—Forest managers in the Southeast
increasingly need information about amphibian
and reptile responses to silvicultural practices
in order to guide sustainable forestry programs.
A review of existing literature indicates that effects
of silvicultural practices on herpetofauna often
are region- and species-specific, with individual
taxa responding positively, negatively, or not at
all in the short term. Responses of herpetofauna
to forestry likely are influenced by adaptations
of taxa to historical disturbance regimes. Few
studies have evaluated long-term population
or landscape-level implications of silvicultural
practices for herpetofauna. Furthermore, many
existing studies lack pretreatment data, replication,
or appropriate reference conditions. We suggest
that future research focus on manipulative and
retrospective studies designed to identify forestry
practices that successfully blend economic
objectives with herpetofaunal conservation.*

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INTRODUCTION

Forests of the Southeastern United States
support a rich diversity of amphibians and
reptiles (herpetofauna). Of the more than
450 species of herpetofauna native to North
America, approximately half occur in the
Southeast and roughly 20 percent, are endemic.
Over 100 species (45 amphibians, 59 reptiles,
excluding sea turtles) have been reported
from the Coastal Plain of South Carolina alone
(Zingmark 1978). Herpetofauna often are the
most abundant vertebrates in forest ecosystems
(Burton and Likens 1975, Congdon and others
1986); in the Southeast, they comprise up to 45
percent of vertebrate species, excluding fish
(Vickers and others 1985).

Several interrelated factors account for
this regional herpetofaunal diversity, including
tremendous variability in habitats related to a
complex matrix of physiography and disturbance
regimes (Sharitz and others 1992). Moreover
many species of southeastern herpetofauna
exhibit biphasic life histories, occupying both
terrestrial and aquatic habitats during annual
cycles (Gibbons and Semlitsch 1991).

Increasingly, forest managers are challenged
to balance production of forest products
with maintenance of environmental quality,
management of wildlife habitat, and conservation
of biodiversity (Moore and Allen 1999, Sharitz
and others 1992). Concerns about even-aged
management, and particularly clearcutting,
have prompted considerable research on effects
of timber harvesting on wildlife. Most research
has focused on mammals and birds, and other
vertebrates such as amphibians and reptiles have
received less attention (deMaynadier and Hunter
1995, Gibbons 1988, Moore and Allen 1999).

Despite their presumed role in forest food webs (Burton and Likens 1975, Congdon and others 1986), potential value as indicators of habitat quality (Dunson and others 1992), and controversy about global amphibian declines (e.g., Pechmann and others 1991), herpetofauna often are not fully considered in forest management decisions (deMaynadier and Hunter 1995).

Questions about the compatibility of forestry and conservation of herpetofaunal biodiversity are driven largely by concerns that both terrestrial and aquatic habitats for many species may be degraded or eliminated in intensively managed forests. In particular, the permeable eggs, gills, and skin of amphibians make them potentially sensitive to changes in both aquatic and terrestrial habitats (Dunson and others 1992). To evaluate these concerns, deMaynadier and Hunter (1995) presented a comprehensive review of available literature about effects of forestry on North American amphibians. Several studies suggested that clearcutting and other forest management prescriptions had short-term impacts on some amphibians, especially salamanders. However, other work indicated that many species (1) were relatively insensitive to forest management, (2) recovered more rapidly after harvesting than previously thought, or (3) responded positively to forestry practices (deMaynadier and Hunter 1995). This literature review revealed that amphibian responses to forest management were complex and often specific to taxa or regions (deMaynadier and Hunter 1995).

Since deMaynadier and Hunter's (1995) review, additional studies have provided new insights about southeastern forestry and herpetofauna. Also deMaynadier and Hunter's (1995) review did not address questions about reptiles, perhaps because of the focus on global amphibian declines (Gibbons and others 2000), or the historical perception that forestry impacts on reptiles generally were neutral or positive (Campbell and Christman 1982, Welsh and Lind 1991). Although evolutionary, morphological, behavioral, and ecological differences between amphibians and reptiles are substantial (Gibbons and others 2000), it is likely that these ectothermic tetrapods will continue to be considered collectively from both conservation and management perspectives (Gibbons and Stangel 1999, Gibbons and others 2000). The purpose of this chapter is to provide an up-to-date overview of information available about responses of amphibian and reptile populations to forestry practices in the Southeastern United States.

OVERVIEW OF LITERATURE ON FORESTRY AND SOUTHEASTERN HERPETOFAUNA

Harvesting and Silviculture

Presumably the microclimatic, vegetational, and structural changes that occur after timber harvesting, and clearcutting in particular, create unsuitable conditions for moisture- and temperature-sensitive amphibians. DeMaynadier and Hunter (1995) reviewed potential negative effects of harvesting on microhabitats correlated with amphibian species richness and abundance. Timber harvesting removes forest canopy, and so causes increased light penetration that results in higher soil temperatures and more evaporative loss of water from the soil and understory. Cover, in the form of leaf litter, coarse woody debris (CWD), and understory vegetation may be reduced following clearcutting and associated site preparation activities (Hunter 1990). Clearcut areas also are subject to greater daily fluctuations in temperature and humidity, and to increased soil surface disturbance during intensive harvest activities (deMaynadier and Hunter 1995). However, it has been suggested by several authors (e.g., Campbell and Christman 1982, Greenberg and others 1994, Welsh and Lind 1991) that clearcutting and other harvesting regimes often create favorable habitats for heliothermic reptiles adapted to early successional habitats.

Amphibians—Several studies in hardwood forests of the Southern Appalachians appear to support the contention that changes in microhabitats and climate after clearcutting reduce amphibian diversity and abundance, with negative effects most pronounced on salamanders (Ash 1988, 1997; Buhlmann and others 1988; Ford and others 2002; Harpole and Haas 1999; Knapp and others 2003; Petranka and others 1993, 1994). In northern Georgia, stand age was an important factor explaining the abundance and community composition of plethodontid salamanders, e.g., *Plethodon* and *Desmognathus* spp., in cove hardwood communities (Ford and others 2002). In North Carolina, populations of plethodontid salamanders in recent clearcuts were 40 percent of those in undisturbed forested plots, and by the fourth year after harvesting, no salamanders could be found on clearcut sites (Ash 1988). Similarly Petranka and others (1993, 1994) found that plethodontid salamanders disappeared from Appalachian forests after clearcutting and that recovery to preharvest population levels took up to 60 years at high-elevation sites. Hyde and Simons (2001) also reported that effects of disturbance on the diversity and abundance of plethodontid

salamanders in the Great Smoky Mountains National Park were still evident after 60 years. Petranka and others (1993) hypothesized that during the last century, clearcutting reduced plethodontid salamander abundance by 70 percent in western North Carolina alone, with current harvest-related losses approaching 14 million salamanders per year.

Three recent studies have evaluated effects of uneven-aged harvesting techniques on Appalachian salamanders. Harpole and Haas (1999) compared abundance of plethodontid salamanders before and after application of seven treatments (understory removal, group selection, two variants of shelterwood, leave tree, clearcutting, reference) in low-elevation hardwood forests in southwest Virginia. They found that salamander numbers were lower after harvesting on the group selection, leave tree, and clearcut sites, but no postharvest differences were detected during the same period on reference or understory removal sites. However, Ford and others (2000) detected no differences in abundance of plethodontid salamanders among group selection treatments, two-aged timber harvests, and uncut control stands in high-elevation, Southern Appalachian hardwood forests of North Carolina. Bartman (1998) did not find that shelterwood harvesting affected salamander populations in the North Carolina Appalachians.

Although it appears likely that diversity and abundance of plethodontid salamanders would decrease after clearcutting, Ash and Bruce (1994) and other authors (Ash 1997, Johnson and others 1993) argue that available data do not indicate that the long-term losses predicted by Petranka and others (1993, 1994) have occurred. For example, Ash (1997) determined that plethodontid salamander populations on previously clearcut sites in the mountains of western North Carolina returned to 100 percent of those in nearby unharvested forests within 24 years of cutting, rather than the 60 years reported by Petranka and others (1993). Harper and Guynn (1999) also reported that plethodontid salamanders appeared to recover relatively quickly from clearcutting, with salamander densities in stands 13 to 39 years old ($\bar{\chi}$ = 21 years) equal to those in older ($\geq$ 40 years) stands.

Responses of amphibians to forest management in other physiographic regions of the Southeast are more complex, with studies reporting individual species increasing, decreasing, or not changing in abundance after clearcutting (Clawson and others 1997, O'Neill 1995, Pais and others

1988, Perison and others 1997, Russell and others 2002b). Perison and others (1997) reported that the overall abundance of amphibians was lower in clearcuts than in forested stands in the upper Coastal Plain of South Carolina, but they found that certain species, such as green treefrogs (*Hyla cinerea* Schneider) and eastern narrowmouth toads (*Gastrophryne carolinensis* Holbrook), were more abundant on clearcut sites. In Alabama, Clawson and others (1997) found that clearcutting of forested floodplains along blackwater streams had little impact on the total abundance of amphibians, but species evenness changed almost immediately after harvesting. Significant declines of two-lined salamanders (*Eurycea cirrigera* Green) and gray treefrogs (*H. chrysocelis* Cope) on clearcut sites were offset by increases of several species, including southern cricket frogs (*Acris gryllus* LeConte), southern toads (*Bufo terrestris* Bonnaterre), and eastern narrowmouth toads. Abundance and richness of several frogs and toads (anurans) increased at temporary wetlands in Florida (O'Neill 1995) and South Carolina (Russell and others 2002b) after clearcutting of surrounding upland pine plantations. Foley (1994) reported that clearcuts in eastern Texas supported fewer marbled salamanders (*Ambystoma opacum* Gravenhorst) than did unharvested controls, but timber harvesting had no effect on numbers of smallmouth salamanders (*A. texanum* Matthes). In a manipulative experiment, Chazal and Niewiarowski (1998) found no significant differences in the number of captures, body mass and length, or clutch size of pond-breeding mole salamanders (*A. talpoideum* Holbrook) after 6 months exposure to a 4-month-old clearcut and a 40-year-old pine stand (animals were captured at an isolated wetland breeding site and placed in 100-m² pens installed after timber harvesting).

Limited evidence suggests that species composition and structure of stands influence diversity and abundance of amphibians in southern forests. Means and others (1996) speculated that conversion of natural longleaf pine (*Pinus palustris* Mill.) stands to slash pine (*P. elliottii* Engelm.) plantations in Florida eliminated populations of flatwoods salamanders (*A. cingulatum* Cope). In the Coastal Plain of South Carolina, Bennett and others (1980) and Hanlin and others (2000) found that the density of amphibians was significantly higher in natural oak-hickory habitats than in previously clearcut even-aged slash pine plantations. Some researchers have speculated that because habitat features which affect the abundance of amphibians, such as soil acidity, leaf litter depth and type, hardwood

shrub abundance, and CWD, may be reduced in conifer plantations, these stand types may be inhospitable for many species of amphibians (Bennett and others 1980, deMaynadier and Hunter 1995, Pough and others 1987). However, Hanlin and others (2000) found that pine plantations actually supported higher amphibian diversity than did hardwood stands. Grant and others (1994) also reported relatively high amphibian diversity in Coastal Plain pine plantations, with intermediate-aged (8 years old) intensively managed loblolly pine (*P. taeda* L.) stands having higher amphibian diversity than recently clearcut (1 to 3 years old) and older stands (26 years old). Grant and others (1994) hypothesized that the greater structural and vegetational complexity of intermediate-aged stands, particularly near ground level, could explain differences in species diversity. They suggested that maintenance of stand structural diversity is critical for sustaining herpetofaunal communities in managed forests of the Southeast, but this hypothesis remains to be tested.

We believe that taxonomic differences among amphibians and habitat differences among physiographic regions largely explain the divergence between results of studies conducted in the Southern Appalachians and those conducted elsewhere in the Southeast. Populations of plethodontid salamanders often decline after timber harvesting, but anurans often respond favorably to harvesting in Coastal Plain forests. Plethodontid salamanders are lungless and entirely terrestrial (Duellman and Trueb 1986) and these traits may make them sensitive to changes in microclimate and microhabitats after harvesting (deMaynadier and Hunter 1995). Results of studies from other regions of North America support the supposition that plethodontids may experience greater population declines after timber harvesting than other groups (deMaynadier and Hunter 1995).

Anurans have higher operating and tolerance temperatures than do salamanders, and they have the ability to store and reabsorb large quantities of water in the bladder, e.g., 20 to 30 percent of body mass (Duellman and Trueb 1986). These characteristics may explain their tolerance to warmer conditions found in harvested stands (deMaynadier and Hunter 1995). Unlike plethodontid salamanders inhabiting Appalachian forests shaped by relatively small-scale and low-intensity natural disturbances (Brose and others 2001, Sharitz and others 1992), amphibians in the southeastern Coastal Plain presumably are

adapted to the high-intensity natural disturbances, e.g., stand-replacing fires, hurricanes, that characterize this region. In much of the Coastal Plain, elevated water tables, increased soil saturation, and ruts created by tree removal, skidding, and bedding often create standing water in clearcuts (Cromer and others 2002, O'Neill 1995, Perison and others 1997). These fish-free pools, which are often numerous after heavy rains, apparently attract more anurans to clearcuts than are attracted to unharvested stands (Clawson and others 1997, Cromer and others 2002, O'Neill 1995, Perison and others 1997, Russell and others 2002b).

Reptiles—Terrestrial reptiles generally are thought to benefit from the early successional habitats created by forest management (Campbell and Christman 1982, Welsh and Lind 1991), but in reality they do not respond to harvesting as a cohesive assemblage. Studies in Florida sand pine [*P. clausa* (Chapm. ex Engelm.) Vasey ex Sarg.] -scrub habitats have shown that many reptile species respond favorably to even-aged forest management (Campbell and Christman 1982, Greenberg and others 1994), leading these authors to suggest that properly managed clearcutting is sufficiently similar to the effects of historic high-intensity wildfires so that its use can be recommended for maintaining early successional habitats for reptiles. The integrity of these open-scrub reptile communities is diminished by forest maturation, and clearcutting appears to create important microhabitat features such as patches of bare sand (Greenberg and others 1994).

Although numbers of several lizard species increased following clearcutting in eastern Texas, no changes were detected for several other reptiles (Foley 1994). Clearcutting adjacent to bottomland hardwood stands in the upper Coastal Plain of South Carolina generally increased richness and abundance of reptiles relative to richness and abundance in forested stands (Perison and others 1997). However, at least two reptile species, ringneck snakes (*Diadophis punctatus* Linnaeus) and eastern musk turtles (*Sternotherus odoratus* Latreille), were more abundant on unharvested plots (Perison and others 1997). Seldom encountered in habitats lacking cover, ringneck snakes are among those southeastern reptiles associated with deep litter or other surface objects in mesic hardwood or hardwood-pine forests (Gibbons and Semlitsch 1991). Russell and others (2002b) also found that clearcutting adjacent to Coastal Plain isolated

wetlands temporarily reduced numbers of several turtle and snake species, including black racers (*Coluber constrictor* Linnaeus), but no effects were evident by 2 years after harvesting. Although black racers are common in early successional habitats, clearcutting temporarily eliminated or disturbed understory vegetation and woody cover that served as refugia and nest sites.

Although effects of forest management on southeastern reptiles have not received the same attention as those on amphibians, available data suggest that reptile responses also are species- and region-specific. The response of an individual reptile species to harvesting is influenced by a variety of factors including the degree of habitat specificity, the spatial scale at which the organism selects its habitat, the morphology and physiology of the organism, and numerous other biotic and abiotic factors. Thus clearcutting may be sufficient to create the open habitats favored by many southeastern reptiles, but insufficient to create habitat suitable for others unless forested patches or CWD are retained.

Roads and Skidder Ruts

Many forestry operations incidentally create aquatic habitats that are used by herpetofauna for reproduction, foraging, and cover. Examples of such habitats include pools along logging roads and machinery ruts within stands. However, these activities can alter hydrological processes and damage natural aquatic habitats (deMaynadier and Hunter 1995). Because the reproductive strategies, e.g., timing, of many amphibian species are adapted to fluctuating hydrology, an increasing concern is that these artificial aquatic habitats may act as population sinks for amphibians if seasonal drying occurs too rapidly (reproductive failure) or not at all (permanent habitat for predators). To date, only two studies have evaluated effects of roads and harvest skidder ruts on southeastern herpetofauna. Adam and Lacki (1993) documented widespread use of forest road-rut ponds for breeding by eight species of salamanders and anurans in Kentucky. Road-rut use was positively associated with surface area, depth, and water clarity, but negatively associated with detrital coverage. More recently, Cromer and others (2002) compared herpetofaunal communities in recently harvested gaps, skidder trails, and undisturbed depressional wetlands to assess effects of group selection harvesting and skidder traffic on herpetofauna in a South Carolina bottomland hardwood forest. Total species richness and abundance were similar among gaps, skidder trails, and undisturbed bottomland depressions.

However, salamander abundance, especially for pond breeding *Ambystoma* spp., was negatively correlated with pronounced rutting from skidder trails. The characteristic ephemeral hydrology of bottomland depressions was altered in the harvested gaps and along skidder trails to produce perennially flooded ponds. This created permanent habitat for several aquatic and semiaquatic species of amphibians and reptiles that dispersed from bottomland depressions during periods of drought. However, the skidder-trail ruts also supported fish and invertebrate predators whose populations in the natural depressions typically are controlled by annual droughts.

Although selective harvesting techniques have been recommended as an alternative to clearcutting as a means of protecting forest herpetofauna (deMaynadier and Hunter 1995), these approaches may require repeated stand entries with additional ground disturbance and may create more roads and ruts than do even-aged regeneration methods. The artificial aquatic habitats created by these activities may have significant implications for habitat selection, and effects on reproductive success and survival of herpetofauna should be evaluated.

Site Preparation

Mechanical treatments—As deMaynadier and Hunter (1995) noted, generalizations about the effects of clearcutting on herpetofauna can be misleading because a wide range of site preparation techniques are associated with even-aged management. For example, intensive mechanical site preparation is used extensively in the Coastal Plain to expose seedbeds and remove competing vegetation prior to replanting, but is rarely employed in Appalachian forest management. Unfortunately, few studies have specifically examined effects of postharvest mechanical site preparation on southeastern amphibians and reptiles. The available literature suggests that these activities can, at least temporarily, reduce habitat complexity and affect some herpetofauna negatively. Although direct mortality is likely for selected species (Dodd 1991, Russell and others 2002b), mechanical treatments typically are applied only once during stand initiation, and intensive mechanical treatments, such as raking, harrowing, disking, chopping, bedding, probably do greater harm by removing leaf litter, CWD, herbaceous vegetation, root channels, and other important microhabitats for herpetofauna (Enge and Marion 1986, Whiles and Grubaugh 1993).

Enge and Marion (1986) compared herpetofaunal populations of three pine flatwoods stands in Florida: a 40-year-old pine stand and two clearcuts receiving minimum (roller-drum chop, bed, plant) and maximum (stump removal, burn, windrow, harrow, bed, plant) site preparation treatments. After treatment, the maximum site preparation stand had less leaf litter, CWD, and herbaceous vegetation, and had a greater percentage of exposed soil, than did the minimum-treatment or reference stands. Amphibian richness did not vary significantly among the three stands, but amphibian abundance was lower in both site preparation treatment stands than in the reference stand. Intensive site preparation reduced abundance and richness of most reptile species, with the largest impact on fossorial snakes. The authors attributed lower reptile abundance in the maximum site preparation clearcut to elimination of CWD and other cover objects that served as refugia and nesting sites. However, intensive site preparation appeared to benefit at least one species, the six-lined racerunner (*Cnemidophorus sexlineatus* Linnaeus), a lizard that prefers open sandy areas.

A limitation of Enge and Marion's (1986) study is that effects of site preparation were not isolated from those of harvesting. Russell and others (2002b) found that when compared to clearcut-only and reference stands, mechanical site preparation of sites adjacent to isolated wetlands in the South Carolina Coastal Plain did not appear to negatively influence amphibians breeding at the ponds. In fact, bronze frogs (*Rana clamitans* Latreille) migrated into wetlands from site-prepared stands in higher numbers in the second year after treatment. Snakes, including black racers, were less abundant within the first 6 months after treatment, possibly in response to physical disturbance of nest sites and reductions in ground cover. These effects were short lived, however, and no effects of site preparation on reptiles were detected in the second year after application.

In addition to removing surface cover, mechanical site preparation may destroy burrows and other subsurface refugia of fossorial herpetofauna. Several studies have documented destruction of gopher tortoise (*Gopherus polyphemus* Daudin) burrows by chopping and other mechanical treatments (Diemer and Moler 1982, Landers and Buckner 1981, Marshall and others 1992, Tanner and Terry 1981), although Landers and Buckner (1981) and Diemer and Moler (1982) observed tortoises emerging from

destroyed burrows and either reopening them or excavating new sites. Loss of gopher tortoise burrows to site preparation can indirectly affect other species; at least 332 wildlife species are known to use burrows of gopher tortoises, including several rare amphibians and reptiles (Lips 1991). Soil disturbance from site preparation also has been linked to destruction of Red Hills salamander (*Phaeognathus hubrichti* Highton) burrows in Alabama (Dodd 1991).

Prescribed fire—Prescribed burning is used to achieve a variety of silvicultural objectives including controlling heavy fuel accumulation, exposing mineral soil, releasing available nutrients for seedbed preparation, and controlling insects, diseases, and competing vegetation. A detailed literature review of fire effects (and fire exclusion) on southeastern herpetofauna was conducted by Russell and others (1999) and only a brief summary is provided here. Generally, replacing fire-adapted vegetation with fire-intolerant associations, e.g., hardwoods, in the southeastern Coastal Plain leads to concomitant declines in overall herpetofaunal abundance and diversity. However, it may be appropriate to use prescribed fire in combination with other forestry practices to benefit Coastal Plain herpetofauna by restoring an historic mosaic of successional stages, habitat structures, and plant species compositions in both terrestrial and aquatic habitats (citations in Russell and others 1999). For example, in southern Florida, richness and abundance of herpetofauna consistently were higher in slash pine plots subjected to three different burn intervals (1, 2, 7 years) than in a reference plot protected from burning for 20 years (Mushinsky 1985). Based on these results, Mushinsky (1985) recommended a 5- to 7-year prescribed burn cycle to maintain diverse herpetofaunal communities in southern Florida sandhills.

Available evidence suggests that direct mortality of herpetofauna following fire typically is low and presumably outweighed by maintaining desired habitat features (Means and Campbell 1981, Russell and others 1999). Although fire-induced disturbance may temporarily decrease herpetofaunal diversity within a particular stand, a heterogeneous matrix of stand ages and structural conditions should increase diversity on a broader scale (Greenberg 2002, Greenberg and others 1994, Jones and others 2000, Litt and others 2001). Unfortunately, concerns over crop tree productivity, smoke management, air quality standards, and liability have led to fire exclusion

policies that may have significant long-term consequences for herpetofauna in Coastal Plain forests and elsewhere (Russell and others 1999).

Even within fire-adapted southern forests some species of herpetofauna may depend on climax vegetation (Greenberg 2002). Means and Campbell (1981) examined herpetofaunal communities in longleaf pine and shortleaf pine (*P. echinata* Mill.) stands in peninsular Florida that had been burned annually for 60 to 70 years and in an unburned forest that had succeeded to a closed-canopy hardwood association. Three species of amphibians [tiger salamander (*A. tigrinum nebulosum* Holowell), oak toad (*Bufo quercicus* Holbrook), ornate chorus frog (*Pseudacris ornata* Holbrook)] and six-lined racerunners were captured predominantly from the burned pine stands, whereas three amphibian species [marbled salamander, mole salamander, and slimy salamander (*Plethodon glutinosus* Green)] were captured almost exclusively in the hardwood forest. The authors suggested that these differences in distribution reflected adaptations (or lack thereof) of individual species to fire (Means and Campbell 1981).

Almost all studies of fire effects on southeastern herpetofauna have been conducted in Coastal Plain forests (Russell and others 1999), and caution must be exercised when extending conclusions to other areas. Until recently, fire was not considered an important or desirable disturbance regime in mixed-hardwood forests of the Appalachian and Piedmont regions (Brose and others 2001). However, it has been hypothesized that periodic, low-intensity surface fires were crucial for perpetuating these oak-dominated forests for millennia and are necessary to restore such forests (Brose and others 2001). To date, only two studies have investigated prescribed fire-herpetofauna relationships in these areas. Ford and others (1999) found that prescribed fires in the Southern Appalachians had little effect on herpetofauna and concluded that concerns about negative effects of prescribed burning on plethodontid salamanders probably were unwarranted. An ongoing study evaluating the use of prescribed fire to restore oak forests in the South Carolina Piedmont also has not found dramatic negative impacts (Floyd and others 2002).

Other topics needing attention include (1) the combined effects of fire frequency, intensity, and seasonality on herpetofauna; (2) the use of herbicides as a substitute for prescribed fire (Litt and others 2001); and (3) the use of prescribed fire to restore and maintain aquatic habitats of herpetofauna threatened by hardwood succession (Russell and others 1999).

Herbicides—In forestry, herbicides are used for site preparation, for release of crop trees from herbaceous and woody plants, for managing species composition and structure, and for timber stand improvement (Miller and Mitchell 1994). Herbicides may be broadcast across a stand, sprayed in bands centered on rows of trees, or applied to individual woody stems. Individual stems usually are treated by directly spraying foliage, applying the herbicide to the tree bole (or to wounds on the bole), or applying a soil-active herbicide to the ground near the tree.

Documented adverse effects of herbicides on some herpetofaunal life stages include mortality, reduced body mass, failure to metamorphose, decreased stimulatory response of neuroepithelial synapses, chromosomal fragmentation, deformities, and DNA profile abnormalities (citations in Pauli and others 2000). It has been suggested that herbicides are among the causative factors explaining global declines of amphibian populations (citations in Fellers and others 2001). However, these effects generally have occurred at exposure levels above those likely to occur in normal forestry operations. Furthermore, several literature reviews have concluded that commonly used forestry herbicides are not acutely toxic to wildlife because they have relatively low mutagenicity, have no or very weak oncogenetic effects, are rapidly eliminated by animals, do not bioaccumulate, and have a short environmental half life (McComb and Hurst 1987, Miller and Witt 1991). Forestry herbicides also are used infrequently, i.e., many even-aged stands receive only one or two applications during a typical rotation, and most herpetofauna likely are shielded from direct exposure, i.e., by being underground or under vegetation, leaf litter, or CWD.

Because herbicides are designed to kill vegetation, they can affect herpetofauna indirectly by altering habitat. Herbicide effects on habitat vary with soils, structure of the pretreatment plant community, herbicide product used, application rates, timing of application, weather conditions, and other factors. However, herbicide application to individual trees in midrotation or maturing stands often promotes canopy gaps and understory biomass production (McComb and Hurst 1987). When broadcast in regenerating stands, herbicides often temporarily reduce biomass production for one to several growing

seasons, and shift the dominant understory vegetation from woody to herbaceous plants (Miller and Witt 1991).

Few studies have documented herpetofaunal response to herbicide-induced habitat changes. Results of those studies, and studies for other wildlife taxa, suggest that herpetofaunal responses are species-specific (Howell and others 1996, Lautenschlager 1993, McComb and Hurst 1987), with individual species increasing, decreasing, or not changing in abundance at the stand level (Cole and others 1997, Harpole and Haas 1999, Lautenschlager and others 1998, Yahner and others 2001). Landscape-level responses of herpetofaunal species to herbicide applications probably depend on the productivity and natural disturbance regime of the landscape (Huston 1999), the extent of the area simultaneously treated with herbicides, the vegetation structure of treated stands and the broader landscape, and other factors previously described.

Whether used alone or with other management practices, e.g., prescribed fire, herbicides may be applied to meet selected management objectives for herpetofauna and other wildlife species. For example, Brooks and others (1993) concluded that any of the three herbicide treatments they evaluated (hexazinone, imazapyr, and picloram + triclopyr) were compatible with the goal of maintaining quality habitat for gopher tortoises. Managers can use herbicides to control nonnative plant species; create snags; manipulate the species composition and structure of understory, midstory, and overstory vegetation; manage the spatial and temporal availability of habitat; and for other purposes (Wigley and others 2002).

Riparian Buffers, Isolated Wetlands, and Terrestrial Corridors

Riparian buffers—Retention of streamside management zones (SMZs or buffers) as a means of conserving biodiversity continues to be a widely debated strategy (Harrison and Voller 1998). Some studies conducted in the Pacific Northwest suggest that unharvested riparian buffers are important for protecting stream- and riparian-associated amphibians from effects of timber harvesting (Corn and Bury 1989, Welsh and Lind 1991). Riparian buffers presumably lessen accumulation of fine sediments in stream substrates, limit increases in water temperatures, and mitigate other negative impacts of soil transport and solar radiation on stream habitats (deMaynadier and Hunter 1995). Little information is available, however, about effects of riparian logging on

southeastern stream amphibian communities (Pauley and others 2000). In the Southern Appalachians, salamanders were 50 percent more abundant in SMZs than in adjacent harvested areas (Petranka and others 1993). In the western Piedmont of North Carolina, Willson and Dorcas (2003) found that the relative abundance of stream-dwelling salamanders was inversely proportional to the percentage of disturbed habitat at the watershed scale, but they found no relationship between the relative abundance of salamanders and the percentage of disturbed habitat within riparian buffer zones. Stiven and Bruce (1988) speculated that stream-dwelling blackbelly salamanders (*Desmognathus quadramaculatus* Holbrook) were less abundant in recently logged Appalachian watersheds, and that harvesting also might alter genetic diversity of the affected populations.

In eastern Texas, Foley (1994) found that SMZs retained in clearcuts actually supported higher diversity of herpetofauna than did unharvested reference stands. He and others (deMaynadier and Hunter 1995) have suggested that in addition to protecting aquatic amphibians, riparian buffer strips could also provide an intact strip of forested habitat capable of harboring populations for future recolonization of adjacent disturbed areas. Bowers and others (2000) examined herpetofaunal response to different planting regimes in the Pen Branch corridor, which is associated with a third-order stream on the Savannah River Site in South Carolina. This stream received thermal effluents from a nuclear reactor for over 30 years, and this resulted in the destruction of most riparian vegetation in a portion of the stream's floodplain. Subsequent erosion created a braided stream system with a greatly expanded delta, and restoration of the area began with planting of bottomland hardwood species in 1993. Species diversity of herpetofauna in the unaffected riparian zone was significantly higher than on vegetated islands located between stream braids within the impacted floodplain corridor, and there were also significantly more species and individuals within the riparian zone than in the corridor. According to Bowers and others (2000), these results highlight the importance of the unaffected riparian zone in the faunal recovery of the floodplain.

Recommended streamside buffer widths for herpetofauna in other regions of North America range from 30 to over 100 m (McComb and others 1993, Rudolph and Dickson 1990).

It has been recommended that riparian buffer widths be adjusted proportionally with stream width, intensity of adjacent harvest, and slope (deMaynadier and Hunter 1995). However, we agree with Wigley and Melchiors (1993) that we know too little about empirical relationships between forest management effects and riparian habitat functions to justify our recommending specific stream buffer widths for southeastern herpetofauna.

Isolated wetlands—Although little effort has been devoted to research and management of stream-associated herpetofauna in southern forests, protection of isolated wetland habitats in the southeastern Coastal Plain has received increasing attention. Carolina bays, cypress ponds, and other isolated wetlands, i.e., those with no permanent connections to aboveground stream or river systems, are critical habitats for herpetofauna adapted to seasonal hydroperiods and the absence of predatory fish. Of 29 anuran species native to the southeastern Coastal Plain, 20 breed primarily or exclusively in isolated wetlands (Moler and Franz 1987). Several species of salamanders, e.g., *Ambystoma* spp., also migrate to isolated wetlands for mating and egg deposition but return to upland habitats for the remainder of the year (Gibbons and Semlitsch 1991). In contrast, many Coastal Plain turtles and snakes seek food and cover in isolated wetlands or their peripheries but migrate to adjacent uplands for egg laying and hibernation (Gibbons and Semlitsch 1991, Russell and Hanlin 1999).

Most species of herpetofauna associated with isolated wetlands in the Coastal Plain also use adjacent upland forests, and several authors have recommended, on the basis of anecdotal or retrospective data, that closed-canopy forested buffers or complete exclusion of upland forest management activity is necessary to protect these aquatic habitats and maintain landscape connectivity among wetlands (see citations in Russell and others 2002b). For example, Pechmann and others (1991) speculated that the initial absence and then presence of marbled salamanders at an isolated wetland in South Carolina resulted from regeneration of surrounding upland forests that previously were clearcut and burned. Raymond and Hardy (1991) reported that a clearcut 156 m away from a breeding pond in Louisiana appeared to influence the migratory movements and survivorship of the pond's breeding population of mole salamanders. On the strength of data on movements of several

salamander species from isolated wetlands to adjacent upland forests, Semlitsch (1998) hypothesized that a buffer zone encompassing 95 percent of the populations using those upland stands would extend approximately 164 m from the wetland's edge. Burke and Gibbons (1995) estimated that an upland buffer 275 m in width would be necessary to protect 100 percent of the nest and hibernation sites of two aquatic turtle species associated with isolated wetlands.

In contrast, Wigley (1999) reported that retention of an adjacent forested buffer was correlated with the presence of only 1 of 40 amphibian species and 37 reptile species sampled from 444 temporary isolated wetlands across the southeastern Coastal Plain—the pine woods treefrog (*Hyla femoralis* Bosc). Russell and others (2002a) also found that 5 small isolated wetlands (0.38 to 1.06 ha) surrounded by 18- to 25-year-old loblolly pine plantations in the Coastal Plain of South Carolina were used by at least 56 species of herpetofauna, suggesting that these aquatic habitats within managed forests are capable of supporting high herpetofaunal diversity. Although retaining forested buffers around isolated wetlands is widely recommended, to date only Russell and others (2002b) have experimentally evaluated management of upland forest buffers on southeastern wetland herpetofauna. They examined immigration and emigration of herpetofauna from isolated wetlands in the South Carolina Coastal Plain before and after clearcutting and mechanical site preparation of adjacent upland forests. Although harvest treatments significantly altered overstory and ground cover characteristics of upland stands, no treatment-related changes in the overall richness, abundance, or community similarity of amphibian and reptile communities at the wetlands were observed. Only short-term negative effects were observed for turtles and snakes. These taxa were less abundant only within the first 6 months after clearcutting and site preparation, possibly in response to physical disturbance of nest sites and temporary changes in ground cover. No amphibian species showed negative responses to treatments, and the number of bronze frogs at the wetlands increased after treatments. The authors noted that although it is premature to suggest that upland forested buffers surrounding southern isolated wetlands are unnecessary, assumptions about effects of forestry operations on isolated wetland herpetofauna, and management based on such assumptions (Semlitsch 1998, 2000), must be tested in the field.

Corridors—Preston (1962) was among the first to suggest possible conservation benefits of upland habitat corridors. Preston speculated that habitat preserves would become isolated, and that the only remedy was to maintain continuous corridors that would link reserves. Most studies of corridors have examined movement patterns of mammals and birds (Bennett 1990, Wegner and Merriam 1979). The function and conservation value of upland corridors is still debated widely (citations in Harrison and Voller 1998, Ford and others 2000). Although use of corridors to manage amphibians has been advocated (Semlitsch 2000), we are aware of only one study of the effects of retaining upland forest corridors for herpetofauna in the Southeast or elsewhere (Baughman 2000). In this study from South Carolina, three sites were randomly selected for retention of a 100-m wide unharvested forest corridor traversing the length of a clearcut, and one site was assigned as an unharvested reference. Baughman (2000) found that mean numbers of herpetofauna captured entering or within corridors did not differ from mean numbers of herpetofauna captured in harvested areas, and that herpetofauna assemblages and movement rates for corridors were similar to those for the stands from which the corridors were created. Although corridors provided a continuous web of closed-canopy forest across the study landscape, Baughman (2000) emphasized that long-term monitoring is needed before potential benefits of terrestrial corridors for herpetofauna in managed forests of the Southeast can be determined.

Demographic Responses to Management

Although short-term measures of richness and abundance may not be affected by forest management, such measures often are not good predictors of habitat quality (Van Horne 1983), and changes in habitats could have longer term consequences for reproductive success, survival, and dispersal of herpetofauna. Few studies have collected demographic data to determine whether responses to forestry practices are age- or sex-specific. Enge and Marion (1986) reported that although there was no difference between overall frog biomass in forested plots, in clearcut plots, fewer juvenile frogs were captured on harvested sites. Raymond and Hardy (1991) suggested that survival of female mole salamanders was lower than survival of males following clearcutting, whereas Ash (1988) reported that sex and age classes of plethodontid salamanders declined at the same rate after clearcutting. Also, without appropriate marking and recapturing techniques, it is difficult to collect data indicative of true

population sizes or to monitor movements of herpetofauna in response to forestry practices (Ash and Bruce 1994). For example, estimates by Petranka and others (1993) of plethodontid salamander mortality resulting from clearcutting are based on the assumption that these salamanders exhibit poor dispersal capabilities and strong site fidelity. Bartman (1998) did not observe dispersal of plethodontid salamanders immediately after logging in North Carolina Appalachian forests, but fates (death vs. dispersal) of herpetofauna after clearcutting and other forestry activities remain poorly known (Ash and Bruce 1994, deMaynadier and Hunter 1995).

Landscape-Level Responses

Although characterizing stand-level responses of herpetofauna to forest management is important, perhaps the most pressing questions are at larger scales (Guerry and Hunter 2002). Some recent studies have characterized herpetofaunal communities at the landscape level. Leiden and others (1999) conducted a broad survey of herpetofauna across an industry-managed landscape in South Carolina. The landscape contained stands in various stand structural classes, including pine plantations. Leiden and others (1999) confirmed the presence of 73 of 102 species of amphibians and reptiles potentially occurring in the landscape (based on range maps). This represented the highest recorded richness of amphibians and reptiles in South Carolina, with the exception of the Savannah River Site, where continuous sampling has occurred since the 1950s (Gibbons and others 1997).

Responses of herpetofauna to forest fragmentation have not been studied as often as have responses of other vertebrates, such as birds. However, a limited number of field studies suggest that isolation of forest patches may influence occupancy of terrestrial habitat in such patches by adult amphibians (citations in Guerry and Hunter 2002). Fox and others (2004) and Shipman and others (2004) censused amphibians and reptiles in four forested watersheds (1500 to 4000 ha each) in the Ouachita Mountains that were managed at different intensities, and thus levels of "fragmentation," ranging from largely unmanaged to intensive even-aged management. Watershed-to-watershed differences in amphibian richness were negligible, and community similarities were high (Fox and others 2004). The watersheds had similar reptile communities, but the least intensively managed watershed had lower
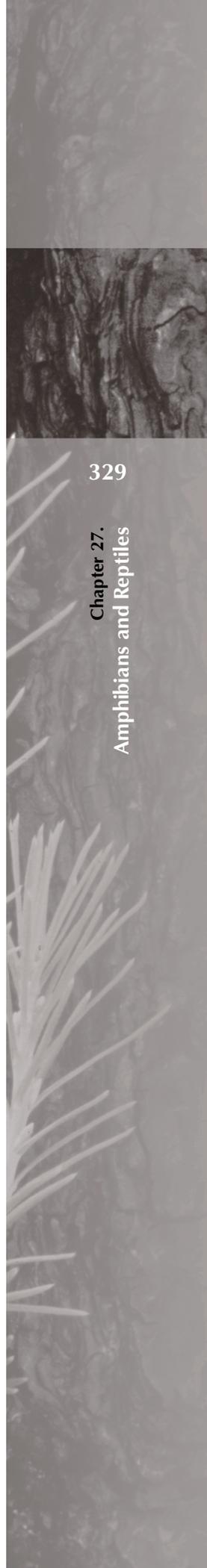
per-plot abundance, species richness, and diversity of reptiles than the others (Shipman and others 2004). This was attributed to dominance by two reptile species in the least intensively managed watershed.

Because many aquatic and semiaquatic herpetofauna use adjacent terrestrial habitats for dispersal, foraging, and refuge, both the proximity of wetlands to terrestrial habitat and the area of terrestrial habitat may influence habitat occupancy. If populations of wetland-associated herpetofauna exhibit metapopulation structure, reduced immigration and emigration rates resulting from disconnection of habitat patches may negatively influence viability (Guerry and Hunter 2002, Joyal and others 2001). In Maine, Guerry and Hunter (2002) found species-specific responses of pond-breeding amphibians to area and proximity of adjacent terrestrial forests. Although the presence and abundance of some species were positively related to forest area and pond-forest adjacency, other species exhibited negative or no associations with one or both of these factors. However, we are unaware of any studies that explicitly evaluate effects of forest fragmentation on either terrestrial or aquatic amphibians in the Southeast.

MANAGEMENT IMPLICATIONS OF NATURAL DISTURBANCE REGIMES

Currently available evidence suggests that southeastern herpetofauna respond in a complex manner to changes in climatic, vegetational, and structural features of stands and landscapes after the implementation or exclusion of specific management practices (such as fire suppression). DeMaynadier and Hunter (1995) argue that herpetofauna generally benefit when forest management prescriptions retain sufficient microhabitat and microclimate elements within stands, and ensure a diversity of habitat types across larger areas. They also suggest that identifying and then minimizing differences between forest management practices and historic patterns of natural disturbance, e.g., retention or creation of microhabitats, will improve conservation of herpetofauna in our managed forests.

We suggest this historic context has often been overlooked by those considering the effects of forest management on southeastern herpetofauna. Current forest management regimes are only the latest in a continuum of forest clearing, intensive agriculture, prescribed burning, forest regrowth, and timber harvesting across the Southeast

(Sharitz and others 1992). Prior to human influence, natural disturbances, e.g., fire, hurricanes, windthrow, ice storms, occurring at different frequencies, intensities, and extents depending on physiographic region, controlled the character of southern forests and maintained the stand and landscape diversity essential to support the flora and fauna of the region (Brose and others 2001, Myers and Van Lear 1998, Sharitz and others 1992). Unmanaged southern forests were not a homogeneous blanket of "intact" or "continuous" closed-canopy forest, but rather a heterogeneous mixture of stands of different ages and structural types. Many vertebrates in the South, including herpetofauna, have tolerated and adapted to disturbance events throughout much of their evolutionary histories (Campbell and Christman 1982, Greenberg and others 1994, Russell and others 1999). Thus the complexity and regional nature of herpetofaunal responses to forest management should not be surprising. As Means and Campbell (1981) point out, it is illogical to conclude that herpetofauna associated with southeastern forests are not themselves adapted to local patterns of disturbance. We have found, however, that few studies or management recommendations (Semlitsch 2000) involving responses of herpetofauna to forest management have fully considered the spatial and temporal complexity of forest habitats, including disturbance scales and intensities that species and communities are adapted to. It is absolutely necessary that we understand this context if we are to predict how southeastern herpetofauna will respond to forest management, and if we are to develop efficacious and cost-effective conservation strategies. For example, are recommendations for closed-canopy buffers around isolated wetlands consistent with the existence of the exposed and sparsely vegetated nest sites selected by many turtle species (Kolbe and Janzen 2002)? Management and recovery strategies for herpetofauna that do not recognize the dynamic rather than static nature of southern forests, or those that provide one-size-fits-all solutions, are likely to fail.

CONSIDERATIONS FOR FUTURE RESEARCH

Increasingly, researchers and resource managers are recognizing the importance of herpetofauna within the context of forest management (deMaynadier and Hunter 1995, Dunson and others 1992). However, much remains to be learned concerning effects of forestry practices on southeastern herpetofauna. Currently available data suggest that herpetofauna are

influenced both positively and negatively (and occasionally not at all) by management of southern forests, and responses are specific to individual regions, taxa, and management prescriptions. The population and community effects of forest management activities on southeastern herpetofauna are still difficult to assess, though, because of methodological limitations and because a variety of study designs have been employed (deMaynadier and Hunter 1995).

The absence of pretreatment data, replication, and true reference conditions in many studies has limited conclusions about impacts of forestry on herpetofauna (Ash and Pollock 1999, deMaynadier and Hunter 1995, Petranka 1999, Russell and others 1999). Most studies have inferred management effects on the strength of retrospective comparisons of herpetofaunal attributes of harvested and unharvested sites. This approach assumes that the herpetofaunal populations of harvested sites once exhibited characteristics, e.g., abundance, identical with those of populations present on forested reference sites. Baseline data on habitat parameters are necessary if we are to assess the comparability of sites and the extent of postharvest changes. Only six studies investigating effects of forest management on southeastern herpetofauna have employed manipulative designs with pretreatment and posttreatment data, treatment replication, or true spatial and temporal references (Ash 1997, Chazal and Niewiarowski 1998, Clawson and others 1997, Harpole and Haas 1999, Knapp and others 2003, Russell and others 2002b). Also needed are longer-term studies that separate immediate population responses to harvesting from long-term effects on fitness.

The challenge for future studies of herpetofauna-forestry relationships has moved beyond simply documenting the range of harvest effects to successfully blending economic and cultural objectives with those for conservation of herpetofauna by identifying silvicultural prescriptions that retain significant natural components of regenerating stands (deMaynadier and Hunter 1995, Grant and others 1994). Although documentation of the magnitude of silvicultural effects on herpetofauna is increasing, the causal factors that shape the distribution and abundance of herpetofauna in southern forests remain poorly understood. Pioneering work by MacArthur and MacArthur (1961) demonstrated the importance of vegetational structural diversity to avian communities. However, quantitative studies that explicitly examine relationships

among structural attributes of forests and herpetofaunal populations in the Southeastern United States are lacking (Grant and others 1994). Studies from the Pacific Northwest and Northeast suggest that structural characteristics and components of forests, particularly those at ground level, e.g., CWD, leaf litter depth and moisture, understory vegetation, are important correlates of herpetofaunal abundance and diversity (Aubry 2000, deMaynadier and Hunter 1995, McComb and others 1993, Pough and others 1987).

Although microhabitat variables such as CWD and leaf-litter depth often increase with stand age, there is a great deal of stand-specific variability related to natural and silvicultural disturbance history, climate, soils, elevation, proximity to aquatic habitats, and other influences (Oliver and Larson 1996). For example, intensive site preparation treatments, e.g., bedding or windrowing, may retard development of stand structure by eliminating cull trees, snags, CWD, and understory species, whereas less-intensive applications that only slightly disturb the soil, e.g., roller chopping, or occasional prescribed burning, may increase diversity and biomass of understory species (Hunter 1990). Thus stand age may not be an accurate delimiter of transitions in stand structural development (deMaynadier and Hunter 1995, Hunter 1990, Oliver and Larson 1996), particularly across regions and ownerships with different methods of harvesting or site preparation.

Approximately 90 percent of southeastern forests are privately owned (U.S. Department of Agriculture, Forest Service 1988), and most of these forests will continue to be managed for economic benefit. We think that information obtained by means of retrospective and manipulative studies that elucidate relationships among stand structural diversity, forest management practices, and herpetofaunal communities can be used to integrate management of these forests with the protection and promotion of herpetofaunal biodiversity. This will be accomplished by approximating the range of natural disturbance events that historically shaped the region's forests. One research approach is to inventory the distribution and abundance of herpetofauna in forest stands with variable structural characteristics and management histories within larger landscapes (Gibbons and others 1997, Wigley and others 2000). Then quantitative models can be developed that relate distribution, abundance,

and demographic characteristics of species to specific habitat elements found in managed forests, and eventually integrated into sustainable landscape models that would predict herpetofauna responses to different management scenarios (Wigley and others 2001).

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