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Fire and amphibians in North America

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Abstract

Information on amphibian responses to fire and fuel reduction practices is critically needed due to potential declines of species and the prevalence of new, more intensive fire management practices in North American forests. The goals of this review are to summarize the known and potential effects of fire and fuels management on amphibians and their aquatic habitats, and to identify information gaps to help direct future scientific research. Amphibians as a group are taxonomically and ecologically diverse; in turn, responses to fire and associated habitat alteration are expected to vary widely among species and among geographic regions. Available data suggest that amphibian responses to fire are spatially and temporally variable and incompletely understood. Much of the limited research has addressed short-term (1–3 years) effects of prescribed fire on terrestrial life stages of amphibians in the southeastern United States. Information on the long-term negative effects of fire on amphibians and the importance of fire for maintaining amphibian communities is sparse for the majority of taxa in North America. Given the size and severity of recent wildland fires and the national effort to reduce fuels on federal lands, future studies are needed to examine the effects of these landscape disturbances on amphibians. We encourage studies to address population-level responses of amphibians to fire by examining how different life stages are affected by changes in aquatic, riparian, and upland habitats. Research designs need to be credible and provide information that is relevant for fire managers and those responsible for assessing the potential effects of various fuel reduction alternatives on rare, sensitive, and endangered amphibian species.
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1. Introduction

The extensive and damaging fires of 2000 and 2002 that burned across large portions of western and southeastern North America have increased public awareness of the consequences of large fires. This national attention has resulted in fire and forest management policy changes on private, state, and federal lands. In 2001, a National Fire Plan (NFP) was approved by Congress to reduce fire risk and to restore fire-adapted ecosystems on federal lands through proactive fuel reduction (USDA and USDI, 2001). One problem with implementing NFP objectives is that large information gaps exist regarding effects of

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proposed fuel reduction practices (e.g. prescription burning and mechanical fuel reduction) on native flora and fauna. Most fuel-reducing activities on federal lands require ecological assessments, as mandated by the National Environmental Protection Act (NEPA), that require information on potential responses of species to proposed management practices. Until recently, such information has been poorly represented in peer-reviewed literature and has not been summarized.

Amphibians are of particular conservation concern because many species have restricted geographical ranges, occur only in localized microhabitats that may be vulnerable to management activities, or are listed under the Endangered Species Act (Semlitsch, 2000). Many amphibian species have declined across large portions of their range throughout the United States (Corn, 2000). Information on amphibian responses to fire and fuel reduction practices is needed to assist managers in determining whether an event or action is beneficial or harmful. However, most studies of the effects of fire on amphibians have recorded responses of terrestrial species or terrestrial life stages of aquatically breeding species to prescription burning in the southeastern United States (Table 1; see reviews by deMaynadier and Hunter, 1995; Russell et al., 1999). Bury et al. (2002) summarized potential responses of amphibian distribution and abundance to fire in the Pacific Northwest and compared patterns using a chronosequence of forest stands. Few studies to date offer insight into the effects of fire on aquatic habitats of amphibians.

The primary goal of this paper is to extend prior reviews by providing a more detailed summary of observed and potential effects of wildland fires, fuel reduction practices, and associated management activities on aquatic habitats of amphibians and species that breed in aquatic habitats throughout North America. Hence, this review focuses on those species that require water in one or more life stage (which essentially means all species except plethodontid salamanders). Further, we provide new information from recent literature and ongoing studies, and offer a framework for identifying information gaps and directing future scientific research to examine amphibian responses to fire and fire-related habitat changes.

2. Characteristics of amphibians and their habitats that influence responses to fire

Amphibians are a diverse group of animals with complex life cycles and many have evolved and persisted in fire-prone regions, possibly due to adaptations to fire disturbances. Some pond-breeding species in forests with high frequency fire regimes (e.g. southeastern coastal plain) rely on the heterogeneous landscapes and open conditions created and maintained by fire for long-term population stability (Dodd, 1997; Brennan et al., 1998; Greenberg, 2002). Conversely, species that have narrow geographic distributions, are closely tied to specific microhabitat conditions (e.g. soil or water temperatures, or cover types), or occur in

Table 1
Number of peer-reviewed studies on the effects of prescribed and wildland fire on amphibians in eastern and western North America (roughly east and west of the Mississippi River, respectively) and Australia

Region	Fire type	Habitats sampled			
		Terrestrial	Lentic	Lotic	Total
Eastern North America	Prescribed	7	0	0	7
	Wildland	0	0	0	0
Western North America	Prescribed	2	0	0	2
	Wildland	1[a]	1[a]	1	3
Australia	Prescribed	2	0	0	2
	Wildland	1	0	0	1
Total		13	1	1	15

[a] One study sampled both lake margin and adjacent upland habitats. This study was counted twice in corresponding row and column totals.

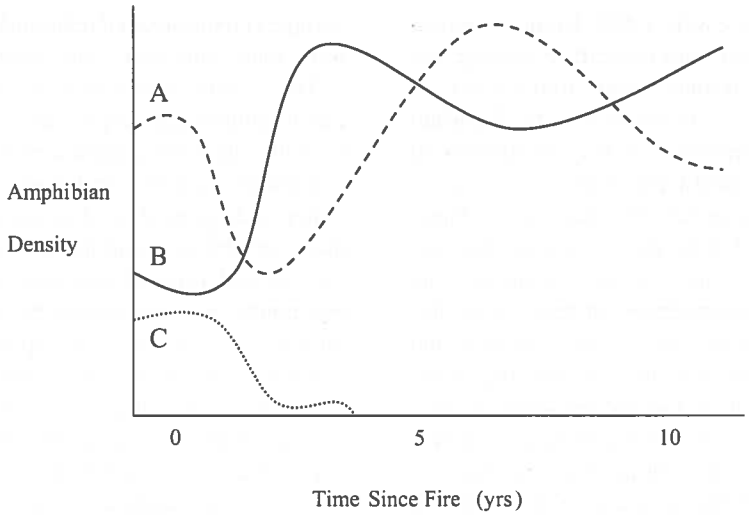

Fig. 1. Predicted responses of different amphibians to fire and fire-related habitat changes over time. Line A represents a possible response to fire for species that are initially sensitive to disturbance but benefit from long-term increases in productivity. Line B represents a possible response to fire for species that benefit from predator release, competitive release, or opening of forest canopy that was closed due to years of fire suppression. Line C represents a possible response to fire for rare, sensitive species (low densities or limited distribution) that are negatively affected by fire.

areas with very long fire-return intervals may be adversely affected by fire (Fig. 1). Factors such as timing of reproduction, duration of larval period, vagility, and resistance to desiccation are characteristics that may determine a species' response to fire. A few species of amphibians remain in water during all life stages (Dodd, 1997). Many species breed in aquatic environments, but juveniles and adults spend some time on land, where they may be particularly vulnerable to fire-related mortality and habitat disturbances. Ecological sensitivity analyses have indicated that mortality of juveniles and adults would likely have the strongest influence on population dynamics of some species of frogs and toads (Biek et al., 2002). Thus, the sensitivity of amphibians to fire disturbances will likely vary among life stages, among populations in different geographic regions, and certainly among species that have evolved under different environmental conditions and fire regimes.

Fire-related disturbances operate across multiple habitats and spatial scales. Individual animals or small populations may respond to disturbances at the microhabitat level, where fires eliminate or alter important amphibian cover through combustion of understory vegetation and surface materials, or filling of interstitial spaces in aquatic substrates with ash and sediment. At the macrohabitat level (e.g. lake, pond, and stream), fires may increase solar radiation and water temperatures, alter hydroperiods and nutrient cycling, and enhance productivity. Landscape attributes such as the spatial distribution of amphibian habitat in a watershed may influence the resistance and resilience of a population to disturbance. For example, many amphibians that breed in isolated water bodies will travel hundreds to thousands of meters away from water seasonally and may be more or less susceptible to fire at these times (Dodd, 1996; Hayes et al., 2001; Pilliod et al., 2002). Moreover, amphibian populations may function as metapopulations, and local fluctuations, extirpations, and dispersal patterns can be linked across a landscape (Marsh and Trenham, 2001).

3. Effects of fire on amphibians

Available data suggest that amphibian responses to fire and associated habitat alteration are species-specific, incompletely understood, and variable among habitats and regions. Wildland and prescribed fires may affect amphibian populations either directly (e.g. killing individuals) or indirectly (e.g. habitat alteration), and effects likely vary relative to

time since burning (Gresswell, 1999). Biotic responses to fire can be partitioned into immediate (during and days after a fire), short-term (<1 year), mid-term (1–10 years), and long-term (>10 years) effects (Minshall et al., 1997). Public impressions of fire are often based upon immediate and short-term visible effects associated with news media-covered conflagrations. These effects are usually short in duration, whereas other less dramatic indirect effects can alter ecosystems for years and even decades. Indirect effects of fires on amphibians result from changes in habitat structure and ecosystem function. Most investigations into the effects of fire on amphibians have focused on short- to mid-term responses (Table 2) and few studies have examined the long-term effects of fire on amphibians, with the exception of persistent fire exclusion in the southeast. Long-term fire effects on aquatic ecosystems may be related to a suite of changes in aquatic and upland habitats (Gresswell, 1999) and understanding these complex environmental relationships will likely require more than "time since fire" studies (Table 3).

The season in which a fire occurs can also be a factor influencing amphibian responses. Most wildland fires in North America burn in the summer when conditions are driest, and most amphibian species are either underground or close to water. Even if individuals are able to avoid fire by occupying wet areas or moving underground, migratory routes back to breeding ponds may no longer be suitable. Prescription burning often occurs in the spring and late fall when conditions are moist, the same conditions that are associated with surface activity in many temperate zone amphibians. During the spring, pond- and some stream-breeding amphibians may be migrating to water for reproduction or dispersing from breeding sites, and may be particularly vulnerable to direct mortality from fire. Terrestrial salamanders, which forage extensively near the surface during the spring,

Table 2
Selected references that have quantified amphibian responses to fire in forested watersheds in North America

Source	Time scale[a]	Fire[b]	Location[c]	Comments
Means and Campbell (1981)	−1 to +3	PF	FL	Abundance of three spp. greater in annually burned pine forests, but abundance of three other spp. greater in fire-suppressed hardwood forests
Mushinsky (1985)	0 to +2	PF	FL	Amphibian richness greatest in 5–7-year burn cycle due to increased habitat complexity
Kirkland et al. (1996)	+1	PF	PA	More *Bufo americanus* captured in burned forests, but species richness was similar between burned and unburned stands
Cole et al. (1997)	−1 to +2	PF	OR	Capture rates of *Ensatina* spp. and *Dicamptodon* spp. decreased after logging and burning
Gamradt and Kats (1997)	−1 to +3	WF	CA	Fire-induced landslides and stream siltation reduced breeding habitat for *Taricha torosa*
McLeod and Gates (1998)	0 to +2	PF	MD	More amphibians were captured in hardwood and pine stands than in logged and burned areas
Ford et al. (1999)	0 to +1	PF	NC	Slope position accounted for more variation in amphibian abundance than burning
Jones et al. (2000)	+2 to +3	PF	OK	Amphibian abundance greater in untreated (no burn and no herbicide) and herbicide-only plots relative to herbicide and burned plots
Constible et al. (2001)	+2 to +3	WF	ALB	No significant differences between frog abundance in undisturbed, burned, and logged forests, but logged areas had consistently higher abundance relative to burned and undisturbed areas
Litt et al. (2001)	0 to +3	PF	FL	Two spp. of toads rarely captured in burned plots (burn, herbicide + burn, and felling + burn) compared to unburned controls
Greenberg (2002)	5 years	PF	FA	Frogs and toads used ponds in fire-suppressed hardwood forests, but a newt spp. used ponds in frequently burned pine forests
Vreeland and Tietje (2002)	−2 to +2	PF	CA	*Batrachoseps* spp. abundance was similar in prescribed burn and unburned plots

[a] Time scale is relative to the year of the fire (year of burn = 0).
[b] Fire: PF—prescribed fire; WF—wildland fire.
[c] Location: ALB—Alberta, Canada; CA—California; FL—Florida; MD—Maryland; NC—North Carolina; OR—Oregon; PA—Pennsylvania.

Table 3
Predicted effects of fire on amphibians and their aquatic habitats relative to time since burning[a]

Condition	Predicted effects			Examples
	Short-term	Mid-term	Long-term	
Combustion	−			Mortality of all life stages
Decreased cover	−	−/+	+	Mortality from desiccation, increased vulnerability to predators (−); increased temperatures, longer hydroperiods (+)
Increased temperature	−	−/+	+	Mortality, habitat loss (−); increased food supply and rates of growth and development (+)
Increased nutrients	−	+		Mortality (−); increased food supply and rates of growth and development (+)
Sedimentation	−	−	−	Mortality of eggs, habitat loss, changes in stream channel morphology
Debris flow and woody debris inputs	−	−/+	+	Mortality, habitat loss (−); increased habitat complexity (+)
Channel scour	−	−	−	Mortality, habitat loss
Hydroperiod	+	+		Increased surface water

A blank cell indicates a neutral response or return to prefire conditions.
[a] Time periods are short-term (during and days after a fire up to 1 year), mid-term (>1 to 10 years after fire), and long-term (>10 years after fire).

may be negatively affected by spring burning, either directly by mortality or indirectly by loss of habitat or prey. Fall burning and late-summer wildland fires may be problematic for those amphibians that are migrating to water or settling under leaf litter to overwinter.

3.1. Direct effects

3.1.1. Mortality

Along with habitat loss, direct mortality of animals is the most publicly recognized consequence of fire. However, mortality of amphibians during prescribed and wildland fires is thought to occur rarely and be of relatively minor importance to most populations (Lyon et al., 1978; Means and Campbell, 1981; Russell et al., 1999; Smith, 2000). Based on the presence of living amphibians in burned areas immediately after a fire, at least some terrestrial stages of amphibians are apparently able to retreat to underground burrows or find moist refugia as protection from burning (Vogl, 1973; Main, 1981; Bamford, 1992; Friend, 1993). However, some fires may move too quickly for amphibians to reach refugia, and more experimental evidence on the ability of amphibians to avoid fire is needed. Grafe et al. (2002) reported that one anuran (*Hyperolius nitidulus*) in Australia can detect the sound of fire and respond by moving toward cover. Frogs, toads, and salamanders moved up to 20 m to avoid a small (~1.0 ha) prescribed fire in a short grass prairie in Iowa (EJH, personal observation). Immediately after the burn, American toads (*Bufo americanus*) were found partially burrowed into the soil with superficial burns on their dorsal skin. Following a prescribed fire in Florida, researchers found partly burned leopard frogs (*Rana sphenocephala*) and bullfrogs (*Rana catesbeiana*) near a wetland (Vogl, 1973).

Mortality of aquatic life stages such as eggs and larval amphibians are rarely reported and may be inconsequential (Lyon et al., 1978; Driscoll and Roberts, 1997). Although aquatic life stages may be more protected from direct contact with fire compared to terrestrial life stages, mortality of some species in ponds or streams could result from thermal stress or rapid changes in water chemistry (Table 3; Spencer and Hauer, 1991). Within days after a 1998 wildfire and a 2001 wildfire burned across several third-order streams in northwestern Montana, Forest Service biologists observed numerous dead adult and larval tailed frogs (*Ascaphus montanus*) in the water along with dead westslope cutthroat trout (*Oncorhynchus clarki lewisi*) (P. Van Eimeren, USDA Forest Service, personal communication). The causes of these mortality events are unknown, but they may be associated with ammonium toxicity in the water resulting from smoke diffusion (Spencer and Hauer, 1991). Based on these

observations, we suspect that mortality of aquatic life stages of some species of amphibians may occur on occasion.

Documenting mortality of the various life stages of amphibians is problematic under field conditions. Dead animals can be incinerated, retreat underground and then die, or get washed downstream and, thus, mortalities are difficult to find. Likewise, inferring mortality from the apparent absence of individuals from formerly occupied habitats is questionable, because failure to find an animal does not necessarily mean it is dead. For example, Driscoll and Roberts (1997) suggested that a spring prescribed burn in Australia may have killed up to 29% of male Nornalup frogs (*Geocrinia lutea*), but this estimate was based on the post-fire absence of male frogs that were calling from small burrows before the fire. They justified their assumption that absent frogs were killed in the fire by the continuous occupancy of all burrows in unburned areas and the discovery of a burned body of one male *G. lutea* about 10 cm from its burrow after the fire (Driscoll and Roberts, 1997).

3.2. Indirect effects

3.2.1. Solar radiation and temperature

Limited data exist on specific fluctuations in daily and seasonal water temperatures following fire, but variation across landscapes is likely. Water temperatures can increase during a fire from the intense heat of combustion or after a fire from increased solar radiation due to the loss of riparian vegetation. After the 1988 fires in Yellowstone National Park, summer water temperatures in first- and second-order streams exceeded 20 °C, but in nearby unburned streams, water temperatures never exceeded 15 °C (Minshall et al., 1997). Similar differences were recorded in summer water temperatures in seven streams in central Idaho flowing through watersheds that had burned 10 months prior (daily temperatures ranging from 10 to 21 °C) relative to seven nearby unburned reference streams (daily temperatures ranging from 7 to 15 °C) (DSP, unpublished data). Other streams in this region have demonstrated either little change or more moderate increases (Minshall et al., 2001a). Thermal profiles are thus likely to respond on a stream-by-stream basis, depending on elevation, survival or regrowth of riparian trees, groundwater inputs, and land management in the watershed (e.g. cattle grazing) (Isaak and Hubert, 2001). Stream temperatures may remain elevated for 15 years after canopy removal from timber harvesting, and similar responses may be expected after fire (Johnson and Jones, 2000).

Changes in daily and seasonal water temperature profiles can have negative effects on amphibian development and survival, particularly for cold-adapted stream species. The thermal tolerance of cold-adapted amphibians is mostly unknown except for a few species in the Pacific Northwest (see Table 4). Although streams may not always reach these critical temperatures during or after a fire, sublethal or lethal stress may result from exposure to elevated temperatures over time (e.g. the number of hours in a day that stream temperature is at a stressful level). For example, tailed frog (*Ascaphus truei*) tadpoles held at a constant 22 °C died after 24–48 h, and adults died when held for 18–30 h at this temperature (Metter, 1966). Like salmonid fishes, tailed frogs and torrent salamanders of the Pacific Northwest rarely occur in streams that have maximum water temperatures above 16 °C (Franz and Lee, 1970; Welsh, 1990; Welsh et al., 2001; Welsh and Lind, 2002). Some tailed frogs have been found in streams with water temperatures up to 21 °C where groundwater seeps create cold pockets and spatially complex thermal environments (Adams and Frissell, 2001). The upper temperature for successful embryonic development of tailed frog eggs is about 18.5 °C (Brown, 1975), the lowest temperature for any cold-adapted amphibian. In contrast, many amphibian species that breed or occur in ponds do not show altered behavior or physiological function at temperatures approaching 30 °C (Rome et al., 1992).

Where fire consumes riparian vegetation, loss of shade may result in increased ultraviolet-B (UV-B) exposure to all amphibian life stages. However, not all species or life stages are equally affected by UV-B exposure (Adams et al., 2001). Embryos of California newts (*Taricha torosa*) and California treefrogs (*Pseudacris cadaverina*) suffered increased mortality when exposed to ambient UV-B, and Anzalone et al. (1998) speculated that increased fire frequency in coastal California chaparral may have resulted in increased UV-B exposure and declines of these species. Initially, increased dissolved organic matter is likely to attenuate UV-B effects on amphibians

Table 4
Critical thermal max and tolerance ranges of stream amphibians in the Pacific Northwest

Species	Acclimation[a] (°C)	CT_{max}[b] (°C)	Range (°C)	Source
Tailed frog, *Ascaphus truei*				
Larvae	10	ca. 29		Metter (1966)
	5	ca. 29.6	28.9–30.1	deVlaming and Bury (1970)
Adults	10	ca. 29		Metter (1966)
			23.4–24.1[c]	Claussen (1973)
Torrent salamander, *Rhyacotriton* spp.				
Larvae		ca. 28.3		Brattstrom (1963)
	10	ca. 26.7	25.6–27.4	Bury and Nebeker (unpublished data)
Adults	11	ca. 27.9	26.3–29.3	Bury and Nebeker (unpublished data)
Pacific giant salamander, *Dicamptodon tenebrosus*				
Larvae	11	ca. 29.1	28.7–29.3	Bury and Nebeker (unpublished data)

[a] Acclimation is the temperature at which animals were held at prior to the experiment. This temperature approximates stream temperatures found in the Pacific Northwest.
[b] Critical thermal maxima (CT_{max}) is the temperature where individuals would perish if not removed immediately.
[c] Incipient lethal temperature: temperature at which 50% mortality occurs.

(Palen et al., 2002). Over time, however, it is unknown how UV-B may act synergistically with other fire-related parameters including pH (see Dodd, 1997; Pahkala et al., 2002), dissolved organic matter (Palen et al., 2002), and water level (Corn and Muths, 2002).

3.2.2. Sedimentation and substrate composition

Fires often result in accelerated erosion of exposed mineral soils from raindrop impact, fire-induced soil hydrophobicity, and overland flow, particularly on steeper slopes in the first year after a high-severity fire (Robichaud and Brown, 1999). During snowmelt, winter storms, and summer thunderstorms, considerable loads of sediments are washed into streams, altering the substratum and channel morphology with which many amphibians are closely tied (Newcombe and MacDonald, 1991). Fire-induced erosion and sedimentation rates are usually comparable to those resulting from logging (Murphy et al., 1981; Triska et al., 1982), but short-term sedimentation of small streams following fires can be dramatic, reaching 10 to 100 times natural levels for at least 10 years (Megahan, 1980; Megahan et al., 1995). For example, fish-killing sediment pulses were observed 2 years after the 1988 Yellowstone fires (Bozek and Young, 1994).

Sedimentation from post-fire runoff has resulted in adverse effects on amphibian populations, particularly in streams. Stream amphibians use the interstitial spaces between rocks in a streambed to lay eggs, forage, and hide. Stream amphibians in the Pacific Northwest decrease in abundance with increasing inputs of fine sediments after logging (Corn and Bury, 1989; Welsh and Ollivier, 1998; Wilkins and Peterson, 2000; Adams and Bury, 2002). Similarly, the spring salamander (*Gyrinophyilus porphoryticus*) is associated with low sediment levels in New Hampshire (Lowe and Bolger, 2002). In controlled experiments, increasing levels of in-stream sediment resulted in decreased growth and development of tadpoles of the Australian spotted treefrog (*Litoria spenceri*) (Gillespie, 2002). Gamradt and Kats (1997) found that sedimentation of a California stream 1–2 years after a wildfire burned surrounding chaparral hillsides resulted in a 20–30% reduction in pool and run habitats that are favored by California newts. Associated with burn-induced habitat modification was a 33% reduction in egg mass numbers following the fire. The effects of increased sedimentation on amphibian breeding habitats in lakes and ponds have yet to be studied and may be inconsequential except for rare occasions (e.g. in reservoirs downstream from a high-severity fire).

3.2.3. Hydroperiods

Fire-induced vegetation changes can alter the water holding capacity of plants and soils, the rate of snow melt, and local water tables, and these factors can lead to changes in the timing of peak and low-water events and the formation of small forest pools (Means and Moler, 1979; Rieman and Clayton, 1997). Means and Moler (1979) argued that increased evapotranspiration from woody plant invasion of herb bogs in Florida decreased local water tables and thus breeding pools of the pine barrens treefrog (*Hyla andersonii*). Small pools often form after loss of vegetation (from logging or fire) because decreased evapotranspiration results in elevated water tables and increased soil saturation (Shepard, 1994; Perison et al., 1997). In the coastal plain of South Carolina, removal of trees in a loblolly pine forest resulted in increased standing water and higher numbers of bronze frogs (*Rana clamitans*) in cleared versus reference (unharvested) stands (Russell et al., 2002a). Small isolated wetlands are particularly important amphibian habitats (Dodd, 1992; Semlitsch and Brodie, 1998; Russell et al., 2002b), and their formation in burned forests may benefit some amphibians.

3.2.4. Nutrient pulses, loading, and productivity

Post-fire surface runoff can result in nutrient pulses in streams or longer-term loading in lakes and ponds. Intense fire in watersheds can result in increased concentrations of nutrients such as soluble reactive phosphorus, ammonium, nitrate, and nitrite in streams (Tiedemann et al., 1978; Schlindler et al., 1980; Neary and Currier, 1982; Knoepp and Swank, 1993; Minshall et al., 2001a) and ponds (Dodd, 1997; Semlitsch, 2000). High nutrient loads immediately following a fire result from mobilization of phosphorus and nitrogenous compounds, generally stored in vegetation, from leaching of ash deposited directly into the water and from diffusion of smoke gases (Spencer and Hauer, 1991). Although nutrient pulses can increase greatly immediately post-fire (Minshall et al., 1989; Spencer and Hauer, 1991; Rinne, 1996), the short-term consequences for aquatic organisms are unclear. For example, Spencer and Hauer (1991) reported phosphorus and nitrogen concentrations increased 5–60 fold over background levels for the first 2 days after a wildfire in Glacier National Park, Montana. In this stream, ammonium and nitrate levels peaked at 261 and 61 ug/l, respectively, levels an order of magnitude below lethal concentrations tested on tadpoles of several anurans (Hecnar, 1995; Xu and Oldham, 1997; Jofre and Karasov, 1999; Schuytema and Nebeker, 1999a,b). Some amphibian species have been shown to be sensitive to elevated levels of nitrite, nitrate, or other nitrogenous compounds (Marco et al., 1999; Schuytema and Nebeker, 1999a,b), but the frequency of such events in aquatic systems is poorly understood. Nutrient pulses in streams can occur for up to 5 years after a fire and are regulated by fire intensity, structure and composition of the riparian forest, spring runoff, and summer rains (Rieman and Clayton, 1997; Hauer and Spencer, 1998; Vose et al., 1999).

Nutrient loading can increase productivity of aquatic ecosystems (Minshall et al., 1997, 2001a,b). Increased algae production in streams and ponds may provide more food and, in turn, result in faster growth of herbivorous larvae of amphibians; ultimately body size at metamorphosis and survival could be affected. Increased productivity may also result in higher density and biomass of amphibians, especially those inhabiting low productivity streams (Kiffney and Richardson, 2001).

3.2.5. Duff and litter

Combustion and desiccation of downed wood, duff, and litter can create an inhospitable environment for frogs and salamanders that are associated with moist leaf litter, ground cover, and soil (McLeod and Gates, 1998; Ford et al., 1999; Hyde, 2000; Constible et al., 2001). We found significant reductions of leaf litter in wildfires in western Oregon and prescribed fires in western North Carolina (EJH, RBB, D. Major, unpublished data). Loss of cover in microhabitats can result in exposure to extremes in temperature and desiccation, and thereby, elevate predation risk or physiological stress. Loss of moist microhabitat availability may reduce dispersal and foraging capabilities of some species. Consumption of duff and litter by fire may also change species dynamics and community structure as individuals reform territories. Ford et al. (1999) reported no difference in amphibian abundance in burned and unburned upslope areas in the Appalachian Mountains, but they suggested that woodland salamanders could be negatively affected if fires burn leaf litter in riparian and mid-slope areas.

3.2.6. Woody debris

Woody debris provides important microhabitats for aquatic and, especially, terrestrial life stages of amphibians. Large pieces of coarse woody debris decompose slowly, and offer stable, moist terrestrial environments for many species of terrestrial salamanders. In old-growth Douglas fir forests in Oregon, salamander abundance is positively associated with greater amounts of down wood (Corn and Bury, 1991). Submerged woody debris and logjams in lakes and streams offer cover for amphibians from predators, and wood is a major structural component of stream ecosystems that influences sediment transport and pool formation (Triska et al., 1982; Harmon et al., 1986). In streams, larval salamanders are often associated with greater habitat complexity from wood and other aquatic cover (Hawkins et al., 1983; Parker, 1991); however, large amounts of instream woody debris appeared to decrease habitat quality for tailed frogs in coastal British Columbia (Dupuis and Steventon, 1999). Both prescribed and wildland fires result in altered woody debris dynamics in lakes, ponds, streams, and surrounding uplands (Harmon et al., 1986). Following a fire, landslides and flooding can result in initial inputs of large woody debris into streams, but increased peak flows, erosion, and decreased bank stability can remove large amounts of instream wood (Young, 1994; Minshall et al., 1997). Because snags decay slowly in arid regions, recruitment of large woody debris slowly increases over time, but depending on geography may not peak for as many as 80 years after a fire (Bragg et al., 2000).

3.2.7. Habitat succession and fire suppression

A legacy of fire suppression may increase the probability of catastrophic fire and associated changes in riparian forest structure and composition, and over time, terrestrial and aquatic habitats for wildlife may also be affected. To protect stream conditions and adjacent riparian habitats, current forestry practices usually recommend, or require, riparian buffers along headwater streams and streams with sensitive fish species (Hawkins et al., 1983; Sedell and Swanson, 1984; Beschta et al., 1987; Bury, 1994; deMaynadier and Hunter, 1995; Diller and Wallace, 1996). In the Oregon coast range, riparian buffer strips (typically 20 m or more) may reduce the effects of prescription burning on streams, ponds, and wetlands, and provide amphibian habitat, at least in the short-term (Cole et al., 1997). However, fire is a natural component of many riparian systems and may be necessary for maintaining ecosystem heterogeneity, open canopies, and natural riparian vegetation communities. For example, fire return intervals were 13–36 years in riparian zones and 10–20 years in upslope areas of dry, low-severity fire regime forests in the Blue Mountains of Oregon (Olson, 2000). In more mesic, moderate-severity fire regime forests on the western slopes of the southern Oregon Cascades, return intervals varied from 35–39 years in riparian forests and 27–36 years in upslope areas. Riparian forests surrounding coastal plain wetlands in the southeast experienced fires every 3–9 years in dryer forests and at intervals of 20 or more years in wetter forests that only burned during periods of drought (Wharton, 1978). Fire suppression in riparian areas for long periods will create fuel build-ups that may eventually lead to unnaturally severe fire in riparian zones, especially in the more productive, lower elevation forests (Olson, 2000). In moist temperate forests, such as in the Appalachians and coastal portions of the Pacific Northwest, fires and years of fire suppression may have less of an impact on amphibians because fires rarely burn through riparian vegetation (Pearson, 1994). For example, in the southern Appalachians, woodland salamanders were not affected by a prescription burn, apparently because they occurred primarily in riparian and midslope areas where understory vegetation and leaf litter burned only slightly (Ford et al., 1999).

In some areas, years of fire suppression have resulted in shrubs and trees becoming established in shallow wetlands and riparian areas where certain species of amphibians breed and forage. Succession of shallow wetlands (e.g. seepage bogs, sinkhole ponds, and forest pools) may have negative effects on those amphibians that prefer open, sunny areas or require sustained surface water for successful breeding. In New England, spring peepers (*Pseudacris crucifer*) are usually absent from ponds where forest canopies have grown over the pond basin, but wood frogs (*Rana sylvatica*) persist at these sites (Skelly et al., 2002). Using controlled experiments, Werner and Glennenmeier (1999) demonstrated that wood frogs grew and survived well in closed-canopy ponds, and northern leopard frogs (*Rana pipiens*) and

American toads did not, apparently due to lower oxygen levels and food resources. In the summer after a large wildland fire burned through an area containing several amphibian monitoring sites in Glacier National Park, western toads (*Bufo boreas*) were observed breeding in seven ponds that had not been used for breeding in the 2 years prior to the fire and three additional ponds that had been dry in previous years (PSC and B. Hossack, unpublished data).

Habitat changes associated with fire suppression could be another potential cause of regional amphibian declines. Resurveys of historic breeding sites in Michigan suggest that succession to closed-canopy conditions over a 30-year period and associated hydrological changes related to succession may be a primary factor contributing to local extirpations of amphibian populations (Skelly et al., 1999). In the southern Cascade Mountains, the cessation of cattle grazing and fire suppression have resulted in loss of open flooded-meadow habitat that may be one of several factors contributing to the disappearance of Cascades frogs (*Rana cascadae*) in northern California (Fellers and Drost, 1993). The loss of breeding habitat from encroachment of shrubs into seepage bogs in the southeastern US may be responsible for declines of the threatened Pine Barrens treefrog (Means and Moler, 1979). The flatwoods salamander (*Ambystoma cingulatum*) appears to have been negatively affected by fire suppression and subsequent hardwood succession in Florida (Palis, 1997). However, a 6-year study that examined the spatio-temporal dynamics of Florida gopher frog breeding and juvenile recruitment suggested that juvenile recruitment was significantly higher in ponds situated in savanna-like longleaf pine-wiregrass uplands compared to ponds located in fire-suppressed hardwood-invaded forests (Greenberg, 2001).

Amphibian response to fire can depend on the composition of upland forests. For example, marine toads (*Bufo marinus*), an introduced species in Australia, were captured more frequently in areas of native forests that had been burned every 3–5 years compared to unburned areas, but in managed exotic pine plantations they were captured more frequently in unburned areas compared to areas that had been burned every 2–7 years (Hannah and Smith, 1995). In the southern US, the succession of pine forests to hardwoods following years of fire suppression appears to have changed species composition and altered upland habitat-use patterns of remaining amphibian species (Means and Campbell, 1981). Pearson (1994) suggested that possibly the most important effect of fire on wetlands may be the change in frequency and spatial configuration of habitats in the surrounding landscape.

3.2.8. Community responses

Changes in invertebrate populations and habitats due to fire may alter prey resources, food webs, and competition and predation in amphibian communities. For example, shortly after a California wildfire, increased prey availability resulted in reduced cannibalism among California newts (Kerby and Kats, 1998). Fires may locally extirpate some insect groups (e.g. grasshoppers) (Komarek, 1969; Folk and Bales, 1982), and the immediate loss of this important prey for amphibians could affect amphibian growth and survival. However, Bamford (1992) found no differences in invertebrate prey populations in unburned Australian forests compared to recently burned areas. Insects probably invade burned areas quickly and the lack of cover may increase accessibility to prey for amphibians that can tolerate these environmental conditions (e.g. toads). For example, 1 year after a 9 ha prescribed burn in south-central Pennsylvania, more amphibians, and particularly American toads, were found in recently burned oak woodlands compared to adjacent unburned stands (Kirkland et al., 1996). Russell et al. (1999) point out that fire suppression could have indirect negative effects on gopher frogs and other fossorial species that use burrows if gopher tortoises decline as a result of shrub and hardwood succession in the southeastern coastal plain.

4. Potential effects of management activities associated with fire and fuel reduction

The National Fire Plan has increased efforts of federal agencies and cooperators to reduce the amount of vegetative fuels using primarily prescription burning and mechanical fuel reduction (USDA and USDI, 2001). In 2001, the US Forest Service and Department of Interior agencies performed hazardous fuel treatments on over 900,000 ha of federal lands (USDA and USDI, 2002). To accomplish specific resource

management objectives, an additional 81,000 ha of lightning-ignited wildland fires were allowed to burn. All of these fuel management activities have the potential to directly and indirectly (via habitat alteration) affect amphibians, but the magnitude, duration, and direction (positive or negative) of effects are mostly unknown. Ironically, 'no action' alternatives may also have consequences for amphibians. Without fuel reduction, habitats may become overgrown or undergo vegetative succession, thus changing the quality of amphibian habitats. Fire suppression may also result in riparian forests becoming increasingly prone to higher severity fires. Timely scientific research that can provide information regarding the effects of fire, fire suppression, and fuel-reducing activities on federal lands is critically needed.

4.1. Prescription burning

Prescription burning is the primary method of fuel reduction in the United States, but the effects of controlled burns on fauna are poorly understood. In 2001, nearly 650,000 ha of federal lands were burned with prescribed fires (USDA and USDI, 2002). In a recent review, Russell et al. (1999) suggested that prescribed fire would likely benefit herpetofauna in the southeastern coastal plain and other fire-maintained ecosystems by restoring historical mosaics of successional stages, habitat structures, and vegetative species compositions. Returning fire to riparian forests may also benefit amphibians by reducing forest canopy cover and creating breeding habitat, particularly if hydroperiods are extended due to reduced evapotranspiration. Stream amphibians may be negatively affected by prescription burning if surface erosion results in sedimentation and thus subsequent loss of breeding, feeding, and cover habitats. Megahan et al. (1995) report that surface erosion rates on burned areas in granitic watersheds can be 66 times greater than on undisturbed slopes, and annual sediment yields can be elevated for 10 years or more.

Russell et al. (1999) argue that any fire-induced mortality or decrease in herpetofaunal diversity in a particular patch will be outweighed by increased habitat heterogeneity and maintenance of preferred or required habitat resources. Although positive relationships between amphibian abundance and prescribed burning have been reported for a few amphibian species in North America, we caution against making management decisions based on relationships that result from studies with small sample sizes and limited geographic area (Russell et al., 1999). Furthermore, Russell et al. (1999) recommend that future prescribed fire studies should have more rigorous experimental designs, including larger sample sizes, pre-fire baseline data, more carefully selected controls, and better replication.

4.2. Mechanical fuel reduction, thinning, and logging

There is public concern about allowing prescribed burning near urban areas, and the use of mechanical fuel reduction (e.g. removal of brush and thinning of trees) has increased in popularity. In 2001, 160,000 ha of federal forests were thinned to reduce hazardous fuels (USDA and USDI, 2002), and this amount may increase with passage of the Healthy Forests Initiative of 2002. To our knowledge, no studies have directly examined the effects of thinning understory brush or removing coarse woody debris on amphibians, although the effects of logging on amphibians are fairly well documented (Bury and Corn, 1988; Corn and Bury, 1989; Welsh, 1990; Dupuis and Steventon, 1999; Naughton et al., 2000). If thinning understory "ladder" fuels results in increased air temperatures, decreased soil moisture, and lower habitat complexity, amphibian populations could decline in thinned forests (Dupuis and Steventon, 1999). We need more research on what habitats are suitable for amphibians in undisturbed forests versus forests where understory has been removed.

The use of timber harvest to simulate fire has been proposed under the framework of ecosystem management, and some land managers are attempting to simulate natural fire mosaics using selective harvesting practices. Constible et al. (2001) tested this concept by comparing amphibian populations in undisturbed, harvested, and naturally burned landscapes in the mixed conifer boreal forests of northeastern Alberta. In an attempt to simulate fire mosaics, harvested areas were cut in varying shapes and sizes (5–60 ha) and had at least one clump of mixed age trees per hectare with unmerchantable timber, snags, understory, downed logs and slash piles. In both terrestrial and lake margin habitats, researchers could not detect consistent

differences between burned or logged areas, but suggested that wood frogs and boreal chorus frogs (*Pseudacris maculata*) require extensive ground cover and moist soil conditions, both of which can be reduced after burning or logging (Constible et al., 2001). To our knowledge, there is no other information on harvesting as a surrogate for fire as related to amphibians.

Salvage logging (removal of trees after a wildfire) is a complex issue. Land managers are faced with difficult decisions regarding burned forests: should the standing snags and charred trees be left in place to provide habitat for wildlife (e.g. snags, and coarse woody debris for stream health) or should the dead trees be removed to provide usable timber. One might expect some similarities between the effects of logging and salvage logging, although salvage logging operations may result in higher rates of soil disturbance, sedimentation, and the magnitude and frequency of severe spate events resulting in channel scour. In the longleaf pine sandhills of Florida, capture rates of amphibians in spring-burned and felling plots were similar to frequently burned reference stands (Litt et al., 2001). More information on the effects of salvage logging on amphibians is critically needed.

4.3. Fire roads and firebreaks

There are 644,000 km of unpaved roads on federal lands in the United States, that can lead to direct mortality of amphibians and degradation of amphibian habitats (Forman and Alexander, 1998; Trombulak and Frissell, 2000). Roads that are near wetlands and bisect amphibian dispersal or migration routes can kill considerable numbers of animals, even with low traffic levels of 10 vehicles per hour (Van Gelder, 1973). Most forest roads have low volumes of traffic, especially at night when most amphibians migrate, and therefore concern about significant population-level effects of road mortality on amphibians may be unwarranted (deMaynadier and Hunter, 1995). However, unpaved roads can act as a barrier to migration and dispersal and thus potentially influence population dynamics across a landscape (deMaynadier and Hunter, 2000). Sedimentation is the most likely detrimental effect of forest roads on amphibians (deMaynadier and Hunter, 1995; Welsh and Ollivier, 1998). Roads are responsible for greater increases in sediment mobility and erosion than logging or fire (Swanson and Dyrness, 1975; Reid and Dunne, 1984; Rieman and Clayton, 1997).

Firebreaks constructed by firefighters and bulldozers can be extensive and could result in similar habitat changes and biotic responses as those associated with roads and road construction. In a 57,000 ha wildfire in northern California in 1999, over 240 km of fire line were constructed, ranging in size from 1 to 10 m across (Ingalsbee and Ambrose, 2002). Firebreak restoration features, such as water bars and revegetation, may mitigate erosion rates and "road 'effects'". In the southeast, fire breaks are plowed around isolated wetlands to "protect" their rich biodiversity, but this action may be harmful to species that do poorly in ponds where hardwood succession and canopy closure has occurred as a result of years of fire suppression (Russell et al., 1999). Allowing fire to burn into riparian forests surrounding wetlands may benefit many wetland species and will likely be less disruptive than fire suppression efforts.

In some circumstances, ruts and ditches created by road building and firebreaks may actually create small temporary wetlands that attract amphibians (Adam and Lacki, 1993; Cromer, 1999). Although rut ponds and ditches are possibly a beneficial consequence of road building for adult and juvenile amphibians, they may act as population sinks if amphibians attempt to breed in these ephemeral wetlands that are subject to rapid drying, high reproductive failure, and increased road mortality.

4.4. Chemical applications

During suppression activities associated with large wildland fires, hundreds of tons of ammonia-based fire retardants and surfactant-based fire suppressant foams are dropped from air tankers and sprayed from fire engines. Some of these fire-fighting chemicals are toxic, or hazardous, to aquatic organisms (Gaikowski et al., 1996a,b; McDonald et al., 1996, 1997; Buhl and Hamilton, 1998, 2000). Although fire fighters attempt to avoid riparian areas during chemical releases, accidental contamination of streams, lakes, and ponds has occurred, especially from aerial applications (e.g. Minshall and Brock, 1991). When dropped directly into water, fire retardant chemicals often form ammonium compounds that are slightly to moderately toxic to algae and invertebrates (McDonald et al., 1996,

1997), and moderately to highly toxic to fish (Gaikowski et al., 1996a,b; Buhl and Hamilton, 1998, 2000). In 2001, an accidental retardant drop in a Washington stream resulted in a large fish kill. Immediately after the fish kill was observed, ammonia levels reached a maximum of 58.8 mg/l and were still as high as 3.67 mg/l 8 days later (J. Fisher, Entrix Inc., personal communication).

Despite the evidence that fire retardants and suppressants can be toxic to aquatic organisms, there is little evidence that toxicity from fire retardants is a common occurrence in the wild and poses a threat to amphibians. Further, amphibians may be less sensitive to ammonia toxicity than fish. Prolonged exposure to elevated levels of ammonium compounds have been shown to have minimal to moderate effects on the survival and development of amphibian embryos and larvae (Hecnar, 1995; Xu and Oldham, 1997; Jofre and Karasov, 1999; Schuytema and Nebeker, 1999a,b) and therefore may only be of concern in smaller lentic water bodies.

Possibly more important than ammonia toxicity is the release of yellow prussiate of soda (also known as sodium ferrocyanide), an ingredient of fire retardants and suppressants used as a corrosion inhibitor to minimize damage to equipment during storage and transport. This substance has been shown to be highly toxic to fish and amphibians at very dilute concentrations, especially upon exposure to sunlight (Burdick and Lipschuetz, 1950; Little and Calfee, 2000). Little and Calfee (2000) reported that fire retardants and foam suppressants with sodium ferrocyanide were highly toxic to southern leopard frogs and boreal toads under natural light conditions when compared to treatments using the same chemical formulations without sodium ferrocyanide or without exposure to sunlight. Sodium ferrocyanide is oxidized in the presence of solar ultraviolet radiation, releasing higher concentrations of free cyanide.

Fire retardant chemicals also have potential to impact amphibians through bioaccumulation. In controlled experiments, trace amounts of brominated diphenyl ether, a byproduct from fire retardant foams, have been detected in toads consuming crickets that were housed on a substrate treated with fire retardant (Hale et al., 2002). Similarly, cyanide may accumulate in the tissue of herbivorous tadpoles feeding on tainted algae or in predaceous amphibians feeding on invertebrates that feed on tainted algae.

Some fuel reduction practices also involve the application of herbicides to forests prior to prescription burning to improve combustion of fuels. In the Oregon Coast Range, the herbicide glyphosate was applied 1 year prior to prescription burning but did not have any noticeable effects on six amphibian species (Cole et al., 1997). However, several of the species were migratory forms and may have been simply passing through the sampled stands. In Oklahoma, amphibians were most abundant in plots that were either untreated (no burn or herbicide application) or treated with the herbicide tebuthiuron and not burned, relative to those plots that were burned after treatment with tebuthiuron (Jones et al., 2000). In Florida, application of the herbicide hexazinone prior to prescribed burning resulted in only slight differences in herpetofaunal assemblages compared to areas without herbicide application (Litt et al., 2001). Herbicides are also being applied to forests after wildland fires to combat noxious weeds. Investigations on the effects of such applications on terrestrial life stages of amphibians and the movement of these chemicals into streams and ponds from surface runoff are urgently needed.

5. Summary and recommendations

Although the potential effects of fire on amphibians are far-reaching, we found few empirical data to support recommendations. Generalizations are confounded by great taxonomic and ecological diversity among amphibians; as well as complex life histories that including fully aquatic forms, aquatic breeders with terrestrial adults, and fully terrestrial forms. Furthermore, each life-history stage could be affected by fire differently. Fire-related reproductive failure might not be detected for several years for species primarily detected as adults or when larvae fail to survive to adulthood. Most of the available information is associated with studies on the coastal plain of the southeast US, a fire-prone ecosystem (e.g. short fire return interval) where the lack of fire has had detrimental effects on amphibian communities because dense canopies have overgrown ponds, and forest succession has shifted to hardwoods. In contrast, amphibians in regions with long fire regime intervals (e.g. coastal forests of North America) may be less resistant and resilient to frequent

fuel-reducing activities (e.g. periodic prescription burning) or catastrophic wildland fires following years of fire suppression. The effects of fire may be greatest for amphibians that are habitat specialists compared to species that occupy different types of habitat and tolerate a range of environmental conditions.

Further complicating generalizations about the effects of fire on amphibians is the dynamic nature of fire across a landscape and the simplified approach (burned or not burned) used in most studies to date. Fire severity and scale is influenced by habitat structure and composition, climate, weather, prior fire history and management activities, and physical properties such as elevation and aspect. Fire usually creates a mosaic of burn severities from unburned to stand-replacing all in the same watershed. Therefore, interpretation of amphibian responses to fire is greatly complicated by burn severity across a landscape. We encourage future studies to examine fire effects across the range of burn severities encountered after a prescribed or wildland fire. To fill additional information gaps, we suggest research emphasizing the following topics.

5.1. Responses of populations of amphibians to fire

Population-level studies are particularly needed in fire-adapted forests where large, catastrophic fires have recently occurred or in forests where fuel reduction is being implemented. We encourage studies that consider landscape or synthetic analyses, because modifications of upland or upstream communities (e.g. prior logging history) may greatly influence receiving aquatic communities. Specific research topics include: effects of fire suppression on amphibians in fire-adapted ecosystems; population-level effects of direct mortality from fire; changes in water temperature associated with canopy loss; lethal and sublethal effects of increased temperature on eggs and larvae of aquatic life stages of amphibians; effects of fire on water chemistry and productivity of lakes and ponds; effects of sedimentation in streams and ponds on amphibian reproduction and recruitment; and effects of fire and post-fire conditions on terrestrial movement patterns of amphibians.

5.2. Predictive models

Empirical data cannot be gathered in every situation. Therefore, there is a need to develop and test models for predicting the range of responses that might be expected from different amphibian species to short-, mid- and long-term habitat changes associated with fire suppression, wildland fires, and fuel reduction practices, especially mechanical fuel reduction and prescription burning. Much of the data required to develop realistic models does not yet exist but could be derived from the research described above.

5.3. Relevance to management

Cooperative research must provide information useful to land managers. Requirements for analysis of impacts under the National Environmental Policy Act (NEPA) would be facilitated by supplying the results of research on rare, sensitive, or threatened species in a timely manner. Many management-related questions remain unanswered. For example, in watersheds where prescription burning is used to reduce fuels, how do amphibian populations respond when riparian forests are allowed to burn compared to responses in forests when riparian buffers are not burned? Are amphibian responses to prescription burning similar to responses after wildland fires burn through a watershed? How much sedimentation results from erosion of fire lines and how effective are current restoration efforts? How readily do fire retardant chemicals and forest management herbicides enter streams and ponds, and what are the effects on aquatic productivity, food webs, and amphibians? Managers, researchers, and, most importantly, amphibians and their habitats will all benefit from a more comprehensive understanding of how non-game aquatic species respond to fire and related management activities.

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