ABSTRACT: The federally threatened flatwoods salamander (Ambystoma cingulatum Cope) inhabits fire-adapted longleaf pine (Pinus palustris Miller) flatwoods and savannas in the southeastern coastal plain. It breeds in ephemeral wetlands that typically dry during summer and refill in fall and winter. We collected data on burning trends of A. cingulatum habitat across the range of the species. Rangewide surveys indicate that prescribed fires typically are applied in winter and early spring. If prescribed fires are conducted primarily in winter, fires are unlikely to burn through water-filled wetlands, potentially affecting larval habitat. Based on what is known about the natural history of the species, the historical burning regime of the longleaf pine ecosystem, and the effects of fires on ephemeral wetlands, we suggest that land managers diversify their fire-management strategy to increase the likelihood of burning the breeding wetlands of flatwoods salamanders.

Index terms: Ambystoma cingulatum, amphibian, fire, longleaf, wetland

INTRODUCTION

The impacts of forest management activities on amphibian communities have received more attention in recent years. Most studies have focused on the negative effects of timber harvesting on amphibian populations (e.g., Petranka et al. 1994, Ash 1997, Grialou et al. 2000, Knapp et al. 2003). But other activities, such as ditching and bedding (often used in coastal plain silvicultural operations (Fechmann et al. 1989, Means et al. 1996) and fire suppression, may also affect amphibian diversity and abundance (deMaynadier and Hunter 1995, Russell et al. 1999, Pilliod et al. 2003). The federally threatened flatwoods salamander (Ambystomatidae: Ambystoma cingulatum Cope) has declined throughout its range. Major threats to the species include the degradation and loss of habitat from development, agriculture and silviculture, modification of breeding wetland hydrology, and fire suppression (Means et al. 1996, Palis 1996, U.S. Fish and Wildlife Service 1999).

Flatwoods salamanders inhabit fire-adapted longleaf pine (Pinus palustris Miller) flatwoods and savannas in the southeastern coastal plain. They breed in ephemeral wetlands (Means 1972, Anderson and Williamson 1976, Palis 1997a), which typically dry in summer and refill in fall and winter (Palis 1997b, Stevenson, unpubl. data). The historical fire regime of the longleaf pine included frequent summer fires from both lightning strikes and Native Americans (Ware et al. 1993, Battle and Golladay 2003). Winter fires are less likely to move through wetland basins than summer fires, except in drought years. Fire exclusion may impact vegetation composition, solar radiation, water temperature, water chemistry, hydrology, nutrient cycling, and productivity of wetlands (Kirkman 1995, Battle and Golladay 2003, Pilliod et al. 2003).

The purpose of this paper is to relate what is known about the natural history of flatwoods salamanders to the potential role of fire in structuring their breeding wetlands. We surveyed public lands containing known breeding populations of A. cingulatum and summarized burning patterns across the range of the species. Because data are limited on the effects of burning regime on flatwoods salamanders, we suggest fire-management decisions be based on what is known about the natural history of the species, the historical burning regime of the longleaf pine ecosystem, and the effects of fires on ephemeral wetlands.

METHODS

We collected fire histories from state and federal lands containing A. cingulatum breeding populations across the range of the species. Participants (Table 1) provided months and years of fires (Total N = 228) for an 11-year period (1 January 1992 to 31 December 2002). These data were used to evaluate the frequency of fires in surrounding uplands, not whether fires actually burned through wetlands, as these data were not available. However, because wetlands typically are burned in conjunction with surrounding uplands, these data can be used to assess the likelihood that fires would burn through wetland basins. We did not have sufficient data to separate wildfires from prescribed fires.
We calculated the average fire return interval (i.e., the average number of years between fires) by dividing the total number of years of fire history by the number of fires. For wetlands in compartments that never burned within the observed period, we set burn frequency for the next year. For example, if a compartment containing a wetland never burned in the observed 11-year period, we set burn frequency at a default value of 12 (i.e., the area burned an average of every 12 years). Thus, mean fire return interval may slightly overestimate the actual fire frequency. However, only nine of 154 wetlands were located in compartments that never burned in the observed period. All statistical analyses were conducted in SPSS 11.0.

RESULTS

Management areas containing historical breeding wetlands (Total N = 154) had an average fire return interval (± SD) of 4.4 ± 2.9 years (range: 1.2-12). Fires were more than three times as common in winter and early spring (December-April) as they were in summer (May-August) (Figure 1).

DISCUSSION

Adult flatwoods salamanders move to breeding wetlands from October-January on rainy nights associated with cold fronts and decreasing atmospheric pressure (Means 1972, Anderson and Williamson 1976, Palis 1997a, Safer 2001). They typically breed in open-canopy wetlands (Anderson and Williamson 1976, Palis 1997b). Larvae can be captured December-April (Means 1972, Palis 1996) by dipnetting herbaceous vegetation (Palis 1996; Sekerak et al. 1996, pers. observations), which typically is more abundant in open-canopy wetlands and in open sections within a wetland (Bishop, unpubl. data). It is unknown why larvae choose areas with high understory coverage and open canopies within a wetland, but they potentially offer greater protection from predators, higher water temperatures, higher dissolved oxygen (DO) concentrations, and possibly more prey items. All of these factors likely increase growth rates and the chances of surviving to metamorphosis.

The potential for fire exclusion to affect flatwoods salamanders negatively has been suggested (Means et al. 1996, Palis 1997b, Safer 2001). However, because no long-term monitoring datasets exist and capturing adequate numbers of individuals for research is difficult, there is limited direct evidence that suppression of wetland fires is harmful to *Ambystoma cingulatum*. Populations occasionally persist in fire-suppressed areas, but casual observations suggest that breeding areas that are fire-suppressed produce fewer larvae than those that are

<table>
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<th>Location</th>
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<th>Breeding Wetlands</th>
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<tr>
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<td>1992-2002</td>
</tr>
<tr>
<td>Eglin Air Force Base</td>
<td>FL</td>
<td>18</td>
<td>1992-2002</td>
</tr>
<tr>
<td>Fort Stewart (Army)</td>
<td>GA</td>
<td>18</td>
<td>1992-2002</td>
</tr>
<tr>
<td>Francis Marion National Forest</td>
<td>SC</td>
<td>5</td>
<td>1992-2002</td>
</tr>
<tr>
<td>Holley Field (Navy)</td>
<td>FL</td>
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<td>1992-2002</td>
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<td>FL</td>
<td>13</td>
<td>1992-2002</td>
</tr>
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<td>J. W. Jones Research Center (Univ. Georgia)</td>
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<td>4</td>
<td>1992-2002</td>
</tr>
<tr>
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<td>1</td>
<td>1992-2002</td>
</tr>
<tr>
<td>Pine Log State Forest</td>
<td>FL</td>
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<td>1992-2002</td>
</tr>
<tr>
<td>St. Mark’s National Wildlife Refuge</td>
<td>FL</td>
<td>41</td>
<td>1992-2002</td>
</tr>
</tbody>
</table>

Table 1. Locations that contributed fire histories. The number of breeding wetlands (N = 154) indicates the number of *Ambystoma cingulatum* breeding wetlands for which we were given data.

Figure 1. Percentage of fires (Total N = 228) by month over an 11-year period in locations containing flatwoods salamander breeding wetlands.
burned frequently (D. Printiss, Apalachicola National Forest, pers. comm.). In the absence of direct evidence, we must rely on indirect evidence to determine appropriate management strategies and, whenever possible, mimic the natural processes that shaped the evolutionary history of the species.

Ephemeral depression wetlands in the southeastern coastal plain are structured by two primary factors – hydrology and fire frequency (Kirkman et al. 2000). Fire frequency declines as hydroperiod increases; however, fire frequency also may affect hydrology. Fire exclusion allows woody vegetation to increase, possibly altering evapotranspiration rates. In flatwoods communities, removal of woody vegetation can alter the hydrology of uplands and wetlands (Sun et al. 2000, Bliss and Comerford 2002). Cypress domes, limesink ponds, Carolina bays, and other southeastern ephemeral wetlands naturally burn when dry (Ewel and Mitsch 1978, Sutter and Kral 1994, Ewel 1995), but managers have been reluctant to incorporate burning wetlands in fire-management plans. As a result, many depression wetlands in the southeast likely are overgrown after years of fire suppression (Huffman and Blanchard 1991).

In other aquatic ecosystems, canopy overgrowth has lead to local population extinctions (Skelly et al. 1999) and loss of diversity (Werner and Glennemeier 1999) of amphibians. Closed canopies diminish growth and developmental survivorship rates in some species, presumably because shading decreases the amount of understory vegetation, lowers DO concentration, limits prey base, and decreases water temperature (Werner and Glennemeier 1999, Skelly et al. 2002, Halverson et al. 2003). Larval amphibians are highly sensitive, both behaviorally and physiologically, to changes in DO and water temperature in the field and lab (Costa 1967, Nolans and Ultsch 1981, Nie et al. 1999). Fires also affect nutrient and pH levels in depression wetlands in longleaf pine ecosystems (Battle and Golladay 2003), factors that may alter habitat composition and developmental rates of larvae. Amphibian species that breed in ephemeral habitats must complete metamorphosis before dry-down; hence, growth and survivorship rates need to be maximized. Slow-growing individuals often metamorphose at smaller sizes, a factor that may affect adult fitness in Ambystoma (Semlitsch et al. 1988, Taylor and Scott 1997).

Land managers recognize that fire is a critical component in maintaining the longleaf ecosystem, but there is considerable debate on the importance of seasonality of fires. Some suggest that growing-season fires are better than winter fires at maintaining the longleaf vegetation community (e.g., Brockway and Lewis 1997), but others believe that fire frequency is the most important characteristic, rather than season (e.g., Hiers et al. 2000). Too often, the number of acres burned, the frequency of fires, or the seasonality, rather than the ecological effects, evaluates the success of a prescribed burning program.

In the Southeast, prescribed fires typically are applied in winter and early spring, principally because winter weather conditions often are more favorable for controlling burns than summer fires (Wade and Lunsford 1989). Winter and early spring fires, however, are unlikely to burn through water-filled wetlands, except in drought years (Battle and Golladay 2003, pers. observations). Land managers in many locations make an effort to apply growing-season fires, although months that are considered part of the growing season do not necessarily correspond to the peak lightning season (May-August, Robbins and Myers 1992). Fire personnel may be reluctant to burn wetlands because of the misconception they are protecting them or their desire to avoid ‘muck’ fires, so firebreaks are plowed around the perimeters of wetlands. Water-filled wetlands often are used intentionally as natural firebreaks in prescribed burns.

Besides excluding fires, we have other concerns about firebreaks surrounding wetlands. First, they may alter hydrology. Second, adult flatwoods salamanders deposit eggs terrestrially prior to inundation (Anderson and Williamson 1976). The environmental cues that a female uses to decide where to deposit her eggs are unknown. If females search for a depression area in the general vicinity of the wetland, a plow line may be sufficient to trigger oviposition. Lastly, firebreaks are potential death traps to larval amphibians. When a wetland is filled completely, a firebreak may be submerged within the boundaries of the wetland. As the wetland dries, the plow line becomes an isolated moat, typically drying before the interior of the wetland and leaving any trapped amphibians with less time to complete metamorphosis. In January 2002, we counted more than 500 dead leopard frog (Rana sphenocephala utricularia) tadpoles in a recently dried plow line surrounding one A. cingulatum breeding wetland.

The accumulation of organic material in fire-suppressed wetlands concerns fire personnel wishing to avoid lingering fires and resulting smoke (Miller et al. 1998). An increase in organic material may contribute to successional change within the wetland (Russell et al. 1999) and alter DO concentration (Werner and Glennemeier 1999). This is not a concern in many A. cingulatum breeding wetlands because of frequent dry periods (e.g., Battle and Golladay 2001); however, some have substantial organic layers. Continuing to exclude fires, however, is not a solution and only allows organic matter to continue to accumulate, possibly leading to catastrophic fires in the future in addition to potentially modifying the habitat of larval flatwoods salamanders. Even if fires only burn through the outer edge of wetlands, larval salamanders likely will benefit from greater understory growth, higher water temperatures, and higher dissolved oxygen levels. Larvae often are captured in the inundated wiregrass ecotone (pers. observations), which flowers after growing-season fires (Seamon et al. 1989).

It is difficult to know the appropriate amount of canopy and understory coverage in ephemeral depression wetlands, if such a range exists. Likewise, we do not know what the natural fire frequency in wetland basins should be. The preferred fire frequency may vary among different amphibian species (e.g., Schurbon and Fauth 2003). If the longleaf pine ecosystem historically burned every 1-4 years
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