

RESEARCH ARTICLE

CRAWFISH FROG BEHAVIORAL DIFFERENCES IN POSTBURNED AND VEGETATED GRASSLANDS

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ABSTRACT

Amphibians are threatened globally and, with the increased emphasis on using prescribed fire as an important tool to manage ecosystems, it is essential to understand how amphibians respond when exposed to habitats managed by fire. Most studies have focused on survivorship and population-level effects; how survivors react to postburn landscapes has received less attention. Crawfish frogs (*Lithobates areolatus* Baird and Girard) are an obligate crayfish burrow-dwelling North American grassland species in steep decline. Individuals spend their nonbreeding season associated with a single crayfish-built burrow, which protects them from dangers, including fire. We compared activity patterns and behaviors of crawfish frogs occupying vegetated and postburned prairie grassland habitats. In total, 24581 images representing six weeks of observations on eight crawfish frogs (four each in vegetated and postburn habitats) were analyzed. While the number of individuals followed was small, our dataset demonstrated interesting differences in activity patterns and behaviors. In particular, while frogs occupying postburn and vegetated habitats exhibited similar nocturnal behaviors, diurnal behaviors were different. In daylight, crawfish frogs in vegetated habitats spent more time on their feeding platform away from their burrow entrance, while frogs in postburn areas spent most of their time at or in their burrow entrance. Further, frogs in postburn areas first emerged later in the day than frogs in vegetated areas. We conclude that while crawfish frog adults occupying a postburn landscape exhibit different behaviors compared to animals in vegetation, prescribed burns have little effect on adult crawfish frog survivorship and few indirect effects on fitness.

Keywords: activity pattern, crawfish frog, critical thermal maximum, fire effects, grassland, *Lithobates areolatus*, prescribed fire, prey availability, southwestern Indiana

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INTRODUCTION

Amphibians can flee neither far nor fast when threatened. With the increased emphasis in the United States on using prescribed fire as an essential tool to manage ecosystems as di-

verse as western forests, southeastern longleaf pine savannas, and midcontinental prairies, there has been an amplified effort to understand how amphibians respond when exposed to habitats managed by fire (Russell *et al.* 1999, 2002; Bury *et al.* 2002; Pilliod *et al.*

2003; Schurburn and Fauth 2003; Chelgren *et al.* 2011). Most of these studies have been conducted in forest ecosystems and have examined either population-level effects, including survivorship and recruitment (Mushinsky 1985, Papp and Papp 2000, Cummer and Painter 2007, Hossack and Corn 2007, Bagne and Purcell 2009), or community-level effects (Bennett *et al.* 1980, Ford *et al.* 1999, Cavitt 2000, Bury 2004, Perry *et al.* 2009). In addition to simply surviving fire, animals are known to alter their behavior in response to fire, which can have fitness consequences (Hossack *et al.* 2009). But, as Komarek (1969) has observed, the relationship between fire and animal behavior is “a much neglected scientific endeavor.”

Komarek (1969) goes on to describe the four possible behavioral responses of animals to fire: 1) an avoidance response to fire and smoke; 2) an attractive response to fire and smoke; 3) an attraction or repulsion to postfire blackened areas; and 4) an attraction to post-fire greening responses. While little work has been done on the reactions of individual amphibians to fire, most herpetologists would agree that from among the four described responses, amphibians are most likely to exhibit an avoidance of smoke and fire (response 1; Grafe *et al.* 2002, but see Stromberg 1997), a variable response to the thermal properties of postfire blackened areas (response 3; Hossack *et al.* [2009] demonstrated that boreal toads [*Bufo boreas*] are better able to meet their thermoregulatory needs in postburned areas than they are in naturally vegetated areas), and an attraction to postfire regrowth (response 4), due in part to invertebrates (prey) reacting to the presence of newly established vegetation.

Crawfish frogs (*Lithobates areolatus*) are obligate crayfish burrow-dwelling North American anurans taxonomically positioned within the *Nenirana* subgenus of Hillis and Wilcox (2005). They inhabit expansive grasslands and are in steep decline, especially east of the Mississippi River. Here, the historic

distribution of crawfish frogs once encompassed a collective 85 counties in Illinois, Indiana, Kentucky, Tennessee, and Mississippi; today they are thought to occur in only 34 counties (a 60% reduction; N.J. Engbrecht and M.J. Lannoo, Indiana State University, unpublished data). Further, there is evidence that numbers of populations within counties have also been reduced (Engbrecht and Lannoo 2010). Crawfish frog declines are out of proportion to syntopic wetland-breeding amphibian species and therefore are likely caused by unfavorable aspects of upland habitats (Parris and Redmer 2005, Engbrecht and Lannoo 2010, Heemeyer *et al.* 2012).

Burrows are essential to crawfish frog survival (Heemeyer *et al.* 2010). An individual crawfish frog typically spends the 10 to 11 months during its nonbreeding season associated with a single crayfish-built burrow (Hoffman *et al.* 2010, Heemeyer *et al.* 2012). Burrows can be located >1 km from breeding wetlands. Following breeding, crawfish frogs will home to these burrows. Some frogs will use the same burrow for at least three consecutive years, and it is likely that many frogs use the same burrows their entire lives (>5 yr; Heemeyer *et al.* 2012). Burrows provide thermal relief, especially during summer and winter temperature extremes; an opportunity to rehydrate; and protection from dangers such as predators and fire (Heemeyer *et al.* 2012). While survivorship among larval and juvenile crawfish frogs is unusually low, survivorship among adults is unusually high—a characteristic that has been attributed to burrow dwelling (Kinney 2011, Heemeyer *et al.* 2012). At their burrows, crawfish frogs are one of the few vertebrate species that exhibit no demonstrable circadian rhythm. They can be active around the clock for periods of time ranging from days to weeks (Hoffman *et al.* 2010). Because crawfish frogs inhabit a single burrow, which they rarely leave, they offer herpetologists a nearly unprecedented opportunity to examine the behavior of individual animals under natu-

ral conditions for long periods of time, even across years (Hoffman *et al.* 2010). But, because crawfish frogs are sensitive to human disturbance, remote sensing techniques are required to observe them (Hoffman *et al.* 2010).

In 2009, after a mid-September prescribed burn eliminated the vegetation covering the burrow of a frog that we had been tracking, we took the opportunity to examine this particular animal's postburn behavior. Prior to the fire, this frog was active around the clock; after the burn, it appeared to become nocturnal. Our observations were limited not only to this one frog but also to portions of a few days, and were therefore suggestive. A 2011 mid-August prescribed burn allowed us to revisit this question. Here we tested the null hypotheses that there will be no differences in either activity patterns or behaviors between crawfish frogs occupying vegetated and postburned prairie grassland habitats.

METHODS

On 16 August 2011, Indiana Department of Natural Resources land managers burned a 45 ha section of our Greene County, Indiana, study site (Figure 1). We carefully surveyed the burned area and observed no crawfish frog mortality. We then took advantage of this opportunity to collect comparative data on activity patterns and other potential behavioral differences between crawfish frogs occupying burned and vegetated grassland habitats. At the time of the burn, we were monitoring four crawfish frogs occupying burrows in areas that were not burned. To find frogs for study in the burn, we first located burrows ($n = 5904$), no matter their origin. From among these burrows we identified candidate crawfish frog burrows (characterized by an oval, 40 cm to 60 cm opening adjacent to a similarly sized feeding platform cleared of vegetation; $n = 12$). Using wildlife cameras (Hoffman *et al.* 2010), we determined that, from among these 12 candidate burrows, three were unoccupied, five



Figure 1. Map of Indiana indicating our study site (Greene County highlighted) and satellite image (GoogleEarth™) of our site locating the eight crawfish frog burrows monitored during this study. Burrows in the postburn habitat are indicated by black dots; burrows in the vegetated habitats by white dots. Light strips in the postburn habitat are areas disked to promote the growth of annual plants as a component of a larger game bird management strategy.

were occupied by crayfish, and four were inhabited by crawfish frogs, which were those that we chose to observe. Thus, our comparison consisted of four crawfish frogs in vegetated grassland and four in recently burned grassland (Figure 1).

Observations of Crawfish Frogs

To observe crawfish frogs, we used Bushnell model 119456C Trophy Cam® trail cameras equipped with both daytime (color) and nighttime (infrared; black and white) capacity set to record at 5 min intervals. Six cameras were deployed, three in each habitat type. Cameras were rotated on a weekly basis among the four occupied burrows in each habitat (i.e., at any one time, we were monitoring three of

the four occupied burrows in each habitat type). Lifelike, painted polyacrylic crawfish frog models with iButton® thermochron dataloggers (Maxim, Sunnyvale, California, USA) inserted into their ventral surfaces were placed 5 m north and 5 m south of each crawfish frog burrow; the dataloggers were programmed to record every 30 min. As the study proceeded, nocturnal mammals (coyotes were recorded by our cameras) relocated frog models and overturned others; as well, they displaced two cameras (one of which was never recovered). We discarded all compromised data, which included overexposed or underexposed photographic images that precluded visualizing frogs, and temperature records from models that had been displaced.

Our observational units were individual crawfish frogs. We realize that a sample size of 4 frogs per treatment is low, but crawfish frogs are rare, and even when relatively abundant are seldom seen outside of the breeding season (Thompson 1915). They have been called “the most secretive *Rana* in North America” (Smith 1950), and prior to this research program only one paper published nearly a century ago systematically addressed questions regarding their upland ecology (Thompson 1915). To compensate for the relatively low number of frogs, we attempted to collect a large number of observations on each frog.

This study lasted 6 weeks, from 26 September to 4 November 2011. At this time of year, crawfish frogs are either in their burrow, at their burrow entrance, or on their feeding platform, where they feed and thermoregulate. In late November, as temperatures cool, frogs retreat to the depths of their burrow (below the frost line) to overwinter (Heemeyer 2011). Cameras monitoring these behaviors were generally deployed during the week from Monday ~0800 hours to Friday ~0800 hours to minimize the potential of theft. Our study site is a public fish and wildlife area that gets heavy use during fall weekends and throughout the

week during the bobwhite quail (*Colinus virginianus* L.) hunting season (which began on 4 November 2011).

Temperatures

Weather conditions during this study were generally conducive to observing crawfish frogs, with clear skies and daytime high temperatures ranging from 7°C to 35°C (\bar{x} = 25.5°C, SD = 7.0) and nighttime lows ranging from 2°C to 15°C (\bar{x} = 7.1°C, SD = 3.3). However, during the fourth week of this study, the weather was cool (lows in the single digits, highs <12°C) and rainy (total precipitation 63.7 mm), and frogs were inactive. Because they offered no resolution between crawfish frog behaviors in vegetated and postburned areas, data were discarded on days that there was inclement weather (18 to 20 and 27 October), severe disturbance (i.e., attempted predation by eastern gartersnake [*Thamnophis sirtalis* L.]), or camera malfunction.

Vegetation

We noted vegetation characteristics, including species composition and height, in the prairie grasslands. In the postburn areas we noted burn patterns and, as the study proceeded, vegetative recovery and senescence.

Prey Availability

To explore prey availability in vegetated and postburn habitats, we vertically suspended 6 Catchmaster™ Scented Bug and Fly Catcher Strips (Atlantic Paste and Glue Company, Brooklyn, New York, USA) from 61 cm insulation supports. These heavy wires were inserted into the ground at 50 m intervals arranged along a 250 m transect. This transect was centered on and perpendicular to a fire lane that separated the vegetated and burned areas. We did not place fly strips near crawfish frog burrows because these strips are conspic-

uous, especially in the open postburn landscape, and we did not want to draw attention to the locations of crawfish frog burrows (or to our cameras). Crawfish frogs feed on both aerial and terrestrial prey (Parris and Redmer 2005, Hoffman *et al.* 2010). The vertical placement of our fly strips likely underrepresented terrestrial invertebrates in our samples. We did not lay fly strips on the ground because they quickly become covered with soil, ash, and plant material, which makes them lose their stickiness. The fly strips themselves also likely underrepresented larger prey, such as grasshoppers (Orthoptera), which can generate enough force to escape. Strips were left out for a full week, from 24 August to 4 September, then placed in individual plastic containers and stored frozen until analyzed. For each strip, invertebrates were sorted into diagnostic taxonomic groups and counted.

Statistics

To examine crawfish frog activity patterns (i.e., diurnal, nocturnal, crepuscular), we noted for each animal the average time of day when first seen (emerged from burrow) and the time when last seen (descended into burrow). To explore behavioral differences, images were sorted into day or night and scored for whether crawfish frogs were on their feeding platforms, at the burrow entrances (visible to the camera), or in their burrows. Because of the low number of frogs observed and the percentage values used to describe the amounts of time that the animals spent at various locations (feeding platform, burrow entrance, and in the burrow), we used nonparametric Wilcoxon Rank Tests for our analyses. Statistics were performed using SPSS® statistical software (SPSS 17; IBM®, Chicago, Illinois, USA).

The iButton temperature data were analyzed in two ways. First, we recorded temperatures associated with individual crawfish frogs each day at the times when they first emerged from and last descended into their burrows. Secondly, average temperatures

across vegetated frog habitat were plotted with average temperatures across postburn frog habitat, then the vegetation temperatures were subtracted from postburn temperatures to give mean temperature differences between habitat types for each (30 min) recording time.

RESULTS

A total of 24581 images representing six weeks of observations on eight crawfish frogs were used for our analyses. We used 13321 images from the four frogs in vegetated areas, and 11260 images from the four frogs in postburned areas. Individual frog samples ranged from six to 17 days observed, and from 1639 to 4431 images analyzed. There were no significant differences between frogs in the vegetated and postburn treatments in either number of days observed ($Z = -1.16$, $n = 8$, $P = 0.24$) or images analyzed ($Z = -1.16$, $n = 8$, $P = 0.24$).

Daily Activity Patterns

There were differences in the activity patterns of crawfish frogs between vegetated and postburn grasslands. In the vegetated areas, crawfish frogs emerged from their burrows on average at 1101 hours (SD = 1 h 0 min) during daylight, and stayed at or near the soil surface for an average of 9 hours 40 minutes (SD = 2 h 11 min) until 2041 hours (SD = 1 h 16 min), after nightfall.

In the postburn areas, crawfish frogs emerged later ($Z = -2.02$, $n = 8$, $P = 0.04$) but did not stay out longer ($Z = -0.57$, $n = 8$, $P = 0.56$) than frogs in vegetation. Frogs in postburn areas first emerged on average at 1213 hours (SD = 0 h 8 min), 72 minutes later than frogs in vegetated areas. They stayed out an average of 10 hours 46 minutes (SD = 2 h 17 min), 66 minutes longer than frogs in vegetated areas. They descended into their burrows on average at 2254 hours (SD = 1 h 30 min), about three hours after sunset.

Burrow-Dwelling Behaviors

The pattern of behavior between crawfish frogs occupying vegetated and postburn areas was not different at night. Crawfish frogs spent a nighttime average of 16.5% (SD = 5.9%) on their feeding platforms in vegetated areas and 13.4% (SD = 8.7%) of their time on their feeding platforms in postburn areas ($Z = -0.29$, $n = 8$, $P = 0.77$; Figure 2). Crawfish frogs spent a nighttime average of 4.3% (SD = 6.2%) at their burrow entrances in vegetated areas, and 4.9% (SD = 2.6%) at their burrow entrances in postburn areas ($Z = -0.58$, $n = 8$, $P = 0.56$). Crawfish frogs spent a nighttime average of 79.2% of their nighttime in their burrows in vegetated areas, and 81.6% in their burrows in postburn areas ($Z = -1.16$, $n = 8$, $P = 0.25$; Figure 2). In sum, at night there were no differences between vegetated and postburn areas in the time that crawfish frogs spent on their feeding platforms, at their burrow entrances, or in their burrows.

In contrast, the pattern of behavior between crawfish frogs occupying vegetated and

postburn areas was significantly different during the day. Crawfish frogs spent a daytime average of 59.9% (SD = 21.9%) of their time on their feeding platforms in vegetated areas, but only 14.0% (SD = 8.6%) of their time on their feeding platforms in postburn areas ($Z = -2.31$, $n = 8$, $P = 0.02$). Further, while crawfish frogs spent a daytime average of only 9.8% (SD = 6.5%) of their time at their burrow entrances in vegetated areas, they spent 35.9% (SD = 14.6%) of their time at their burrow entrances in postburn areas ($Z = -2.02$, $n = 8$, $P = 0.04$). Finally, while crawfish frogs spent a daytime average of 30.3% (SD = 15.5%) of their time in their burrows in vegetated areas, they spent 50.4% (SD = 7.9%) of their time in their burrows in postburn areas ($Z = -1.44$, $n = 8$, $P = 0.15$; Figure 2). In sum, there were significant differences between vegetated and postburn areas in the time crawfish frogs spent on their feeding platforms and at their burrow entrances, but not in their burrows, during the day. The most notable behavioral difference was the daytime tendency for frogs in vegetation to be on their feeding

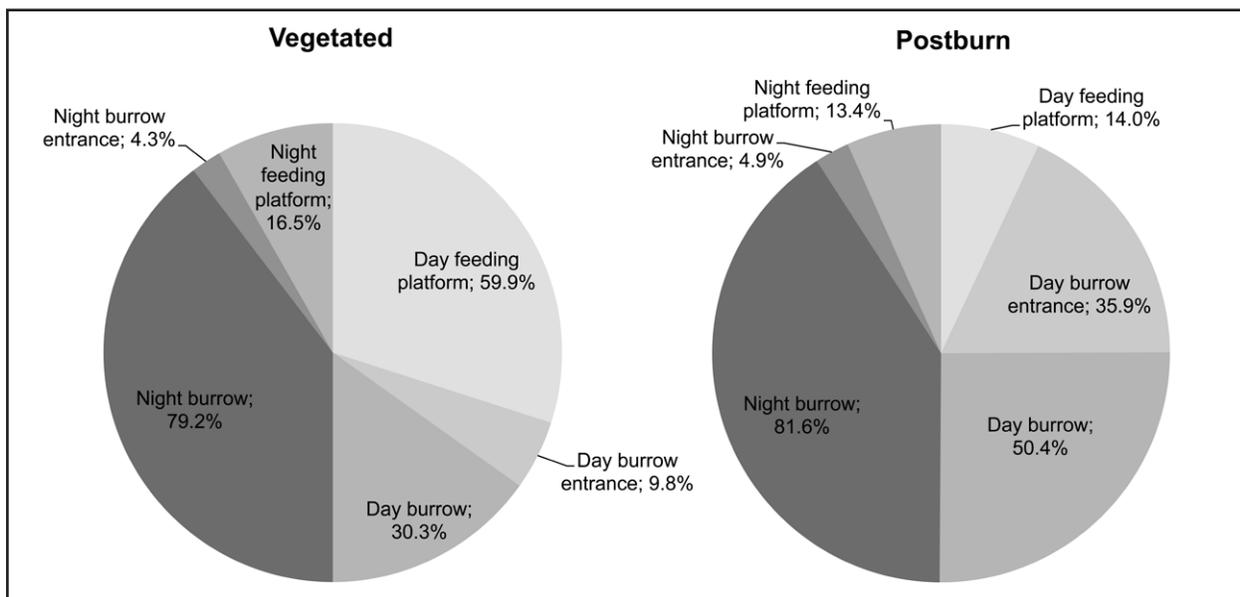


Figure 2. Percentage of time that crawfish frogs spent on feeding platforms, at their burrow entrances, and in their burrows, day and night, in vegetated and postburn habitats. Note how nighttime percentages do not differ between vegetated and postburn areas, while, during the day, frogs in postburn areas spent more time at burrow entrances and in burrows.

platforms, while frogs in postburned areas remained at their burrow entrances.

Temperatures

On average, crawfish frogs emerged from their burrows when temperatures were 16.5°C (SD = 3.8). The coolest temperature at which we observed a frog emerge was 12°C, and the warmest was 20.3°C. At night, crawfish frogs descended into their burrows at an average temperature of 13.2°C (SD = 3.1). The coolest temperature at which we observed a frog descend was 9.7°C, and the warmest was 16.2°C.

Temperatures between vegetated and postburn areas tended to be similar during evenings, nighttime, and mornings, but divergent during the middle of the day (Figure 3A). During the day, postburn temperatures were as much as 12.5°C higher than temperatures in vegetated habitats (Figure 3B). On average, temperatures in postburn habitats were 4.0°C (SD = 3.7°C) warmer than temperatures in vegetated areas. Average high temperatures were 5.2°C warmer in postburn areas ($Z = -4.46, n = 26, P < 0.01$); average low temperatures were 0.4°C cooler in postburn areas ($Z = -2.35, n = 26, P = 0.02$).

Vegetation

The composition of grassland vegetation varied among the four crawfish frogs observed here. Frog V-1 inhabited a grassland area consisting primarily of native big bluestem (*Andropogon gerardii* Vitman) with scattered non-native smooth brome (*Bromus inermis* Leyss). Frog V-2 inhabited an area of big bluestem, although a plowed firebreak was within 1 m of the burrow. Frog V-3 was on private land adjacent to the state-owned land and inhabited an area consisting exclusively of smooth brome. Frog V-4 inhabited a dense prairie consisting of big bluestem as well as scattered Indian grass (*Sorghastrum nutans* L.), compass plant (*Silphium laciniatum* L.), and blazing star (*Li-*

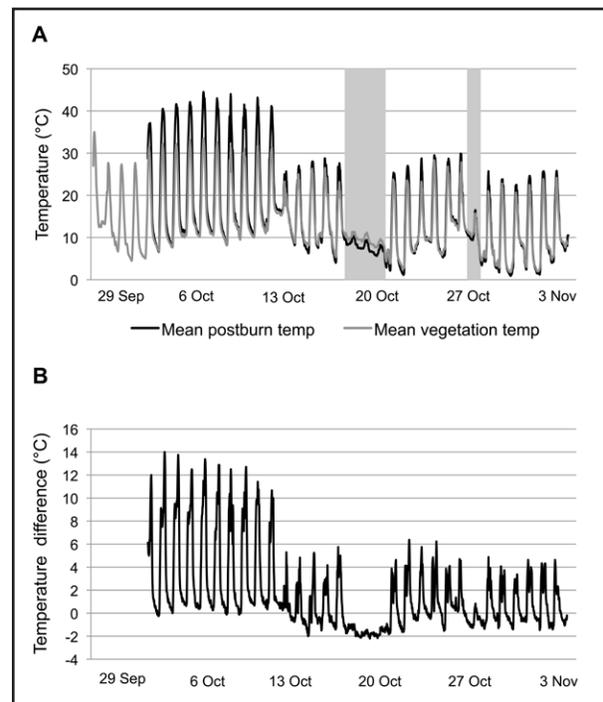


Figure 3. A) A summary of average temperatures at 30 min intervals recorded by iButtons inserted into the ventral surface of painted polyacrylic crawfish frog models placed in association with crawfish frog burrows in vegetated and postburn habitats. On 4 days (18 through 20 and 27 October) temperatures were low, frogs did not emerge, and data were discarded (shaded areas). B) Temperature differences calculated by subtracting average temperatures in vegetated areas from corresponding average temperatures in postburn areas. Note that daytime highs in the postburn areas were as much as 14°C warmer than highs in postburn areas, and during cold conditions, postburn habitats were cooler. On average, postburn areas were 4°C warmer than vegetated areas.

atrus sp. L.). Grassland height varied from about 40 cm in smooth brome areas to >175 cm for big bluestem areas, although the leaves of big bluestem provided dense cover up to about 60 cm. The scattered compass plants and blazing stars did not provide continuous, dense cover. Heemeyer *et al.* (2012) have shown that while crawfish frogs exclusively inhabit burrows in grassland habitats, there are no demonstrable differences in the behaviors of crawfish frogs based on the species composition of these grasslands.

All crawfish frogs in the burn area had their vegetative cover completely incinerated, although the blackened stems of Chinese bush clover (*Lespedeza cuneata* [Dum. Cours.] G. Don) remained. Three of these frogs (B-1, B-2, B-3) were in burrows in Chinese bush clover habitat on south-facing slopes. Frog B-4 was in a big bluestem area on a north-facing slope.

As this study progressed, grassland vegetation began to senesce by dehydrating, browning up, and slumping. In contrast, in the burn area, vegetation became more pronounced: forbs and cool season grasses sprouted from seeds or regrew from roots, while warm season grasses and wild onions (*Allium* sp.) regrew quickly. However, none of this postburn vegetation grew substantially (heights were ≤ 30 cm by the end of the study); bunched warm season grasses were infrequent and scattered, and neither they nor the wild onions contributed substantial shading to the crawfish frog feeding platforms and burrows.

Prey Availability

According to the data obtained by the vertically hung bug and fly strips, there were sig-

nificant differences in the numbers of types of insects and spiders available to crawfish frogs in the postburned and vegetated areas (Table 1). While dipterans, especially flies, were most commonly trapped in both areas, over three quarters of the insects and spiders captured were flies on the postburned landscape, while in the vegetation, flies accounted for only about a quarter of the captures. There were more hymenopterans ($Z = -1.96$; $n = 6$, $P = 0.05$) and arachnids ($Z = -2.02$, $n = 6$, $P = 0.04$) captured in the grassland than in the postburned areas. While dipterans, coleopterans, and arachnids were easily identified, some small individuals of groups lacking hard exoskeletons or clearly diagnostic features (e.g., compound eyes) were too decomposed or incomplete to identify.

DISCUSSION

Our data, while limited to eight animals, demonstrate that crawfish frog activity patterns differ between vegetated areas and areas where prescribed burns have completely removed the overlying vegetation. In particular, crawfish frogs in postburn areas emerge from their burrows about one hour later during the day; frogs

Table 1. Numbers of invertebrates captured on vertically hung bug and fly strips. Invertebrates are sorted taxonomically; means represent average numbers taken from the three strips in each habitat; percentages reflect taxonomic representation in each habitat.

Taxon	Vegetated habitat			Postburn habitat		
	\bar{x}	SD	%	\bar{x}	SD	%
Diptera	21.0	16.6	26.2	74.0	42.3	79.6
Homoptera	16.0	8.5	20.0	11.3	5.5	12.2
Hymenoptera	12.3	2.5	15.4	2.0	1.0	2.2
Arachnida	9.3	1.2	11.7	1.3	0.6	1.4
Hemiptera	3.0	2.6	3.8	0.3	0.6	0.4
Orthoptera	2.7	2.1	3.3	0.7	0.6	1.0
Coleoptera	2.3	2.5	2.9	3.3	2.1	3.6
Lepidoptera	3.0	2.6	3.8	0.0	0.0	0.0
Trichoptera	5.7	5.0	7.1	0.0	0.0	0.0
Unknown	4.7	5.7	5.8	0.0	0.0	0.0
Total	80.0		100.0	92.9		100.4 ^a

^aGreater than 100% due to rounding.

in both areas remained active after nightfall (Figure 2). Thus, these data confirm the observations of Hoffman *et al.* (2010) that crawfish frogs have no well-defined diurnal period of activity tied positively or negatively to sunlight; that is, their activity patterns cannot be considered diurnal, nocturnal, or crepuscular. While the crawfish frogs monitored here exhibited stronger synchronized activity than noted by Hoffman *et al.* (2010), the observations of Hoffman and colleagues were made during the middle of the summer, while the observations reported here were from late summer and fall, when nighttime temperatures were cooler and frogs tended to be less active.

The pattern of crawfish frog activity at their burrow entrances differed diurnally between vegetated and postburn areas. While there were no differences in nighttime activity between animals in vegetated and postburn areas, there were significant differences in daytime activity patterns (Figure 2). During the day, crawfish frogs in vegetated areas spent the majority of their time outside their burrows on their feeding platforms, while frogs in postburn areas spent the majority of their time outside their burrows at the burrow entrances. Frogs in postburn areas also spent more time during the day in their burrows. Based on these observations, we rejected our null hypothesis.

Postburn crawfish frog activity patterns in 2011 differed from that exhibited by the single frog observed in 2009. The frog observed in 2009 appeared to shift its activity pattern from circumdiel to nocturnal following the burn; however, our observations were limited. One observation was consistent across years: crawfish frogs in postburn areas exhibited an aversion to leaving the proximity of their burrow entrances during daylight conditions.

Differences in Behavior between Vegetated and Postburn Areas during Daylight

There are at least three possibilities for why crawfish frogs in exposed, postburn habitats exhibit behavioral differences: predator

avoidance, thermal preference, and prey availability. We consider each, as follows.

Predator avoidance. Amphibians and reptiles that are active during the day in devegetated, postburn areas are highly visible, and therefore face increased predation pressure (Lawrence 1966; Wilgers and Horne 2006, 2007). Crawfish frogs are no exception to this generalization, which may be the reason that we noted a nocturnal activity pattern in the frog observed in 2009. Known predators of crawfish frogs include snakes (Engbrecht and Heemeyer 2010, Heemeyer 2011) and raccoons (Heemeyer *et al.* 2010). Further, we suspect from examining carcasses and tracks that other mammals, such as minks, and birds of prey will take crawfish frogs (Heemeyer 2011). Heemeyer (2011) has shown that crawfish frogs in burrows are 12 times less likely to be preyed upon than animals exhibiting migrating and ranging behaviors (crawfish frogs in burrows inflate their bodies and lower their heads in response to threats [Altig 1972, Engbrecht and Heemeyer 2010]). There can be no doubt that crawfish frogs at their burrow entrances both reduce their visibility and minimize their distance to the safety of their burrows.

On both 10 and 12 October, a garter snake entered Frog B-1's burrow and was visible for 2 (10 October) and 4 (12 October) frames, suggesting that the snake was present from as little as 7 min on 10 October to as many as 23 min on 12 October. In both cases, this frog remained in its burrow for the remainder of the day, then emerged and became active for most of the night. Adult garter snakes will prey on adult crawfish frogs (Heemeyer 2011). We suspect that the avoidance of further daytime activity following these encounters was an attempt to avoid that particular potential predator, and that this danger disappeared at sunset, when garter snakes become less active (Rossman *et al.* 1996).

From among the known or suspected crawfish frog predators at our study site, hawks, crows, most other bird species, and snakes are

diurnal, while mammals and owls are nocturnal. One potential advantage of not being tied to a specific diurnal activity pattern is that crawfish frogs can shift from diel to nocturnal activity in the presence of daytime predators. We perceived such a shift in 2009. In 2011, we noted a significant tendency for frogs in postburn areas to emerge from their burrows later in the day, and a weaker (nonsignificant) tendency for frogs to remain active later into the night (until about 3 hr after sunset).

Thermal preferences. To our knowledge, only one study has examined the costs and benefits to amphibians living in postburn habitats. Hossack *et al.* (2009), working in the Rocky Mountains of Montana, USA, found that burned forests were warmer than unburned forests across all microhabitats, and noted that there were fitness-linked benefits such as increased growth, fertility, and perhaps disease resistance to boreal toads (*Anaxyrus boreas*) in burned habitats. They also found that areas that burned with high intensity remained warmer than unburned areas three years after the fire. Our data agreed with Hossack *et al.* (2009) that postburn habitats are warmer than corresponding natural habitats. Measurements taken by our iButton-equipped models showed that daytime temperatures of postburn sites were as high as 44°C, which was 12.5°C warmer than temperatures in nearby vegetated sites. In contrast, nighttime, morning, and evening temperatures did not differ between vegetated and postburn areas. While Hossack *et al.* (2009) found several potential fitness benefits to boreal toads using postburn habitats, for crawfish frogs, the lack of daytime thermal buffering may be disadvantageous during warm weather when a frog's critical thermal maximum can be exceeded (Brattstrom 1963, Hutchison and Dupré 1992, Rome *et al.* 1992, Angilletta 2009). During cooler fall weather, the heat generated by the lack of burrow shading and darker soil surface may offer thermal (and therefore fitness) advantages, although

during our study, by the time cooler temperatures arrived, the black ash had washed away and vegetation had started to regrow.

Hossack *et al.* (2009) were able to measure thermal differences in forested habitats 3 yr postburn. It is unlikely, however, that effects of late summer or fall grassland burns extend past mid-summer of the following year, when postburn grasslands resemble unburned grasslands. There is potential, however, for postburn overwinter effects to affect survivorship. Overlying senescent vegetation insulates soil from winter freezing temperatures and can reduce the depth of the frost line. Absent this insulating layer, and absent a snowpack, severe cold temperatures can penetrate deep into the soil, especially with a burrow acting as a conduit for airflow. Crawfish frogs have no freeze tolerance and can be winterkilled (Heemeyer and Lannoo 2010).

Prey Availability. While the overall numbers of prey were similar between burned and unburned grasslands, dipterans (flies) predominated in the burned areas (Table 1). Flies are both attracted to and produced by unscavenged vertebrate carcasses, especially eastern box turtles (*Terrepenne carolina*), which are vulnerable to fall burns at this site (M.J. Lannoo, unpublished data). The fact that our bug and fly strips were scented and hung vertically likely biased our results, which affected the number and type of insects captured on each strip, but probably not the number or type of insects captured between strips in the postburned and vegetated areas.

Prey availability could potentially affect crawfish frog activity patterns. Crawfish frogs are generalist feeders (Hoffman *et al.* 2010), and we assume that individuals will shift food habits based on available prey. Given this, it is also conceivable that crawfish frogs, which have the option of being active during the day or at night, will shift activity patterns to correspond with the activity of their primary prey at the time. In contrast, prey availability will

likely not influence the differences in position of crawfish frogs relative to their burrow entrances in the vegetated and postburn areas, which we observed. Crawfish frogs almost certainly have access to the same prey base whether they are on their feeding platforms or a short (two frog lengths) distance away at their burrow entrances.

Do Prescribed Burns Affect Crawfish Frog Population Viability?

Prescribed burns are an essential tool when managing ecosystems as diverse as North American western forests, southeastern coastal plain forest, and midcontinental grasslands (Wright and Bailey 1982). Studies examining the impacts of either prescribed burns or wild-fire on amphibian populations demonstrate variable population-level effects ranging from positive effects (Means and Campbell 1981, Kirkland *et al.* 1996, Langford *et al.* 2007, Hossack *et al.* 2009), through no measured ef-

fects (Moseley *et al.* 2003, Keyser *et al.* 2004, Lemckert *et al.* 2004, Renken 2006, Greenberg and Waldrop 2008), to negative effects (Miller *et al.* 2001, Halstead 2007, Perry *et al.* 2009, Rochester *et al.* 2010, Hossack and Pilliod 2011). As Pilliod *et al.* (2003) summarized, amphibian responses to fire vary widely by species, geography, and both the timing and the nature of the fire. Because of the dependence of crawfish frogs on grassland habitats, and the dependence of grassland habitats on prescribed burning, it is likely that without prescribed burns, there would be little upland grassland habitat for crawfish frogs. While we showed that the behaviors of adult crawfish frogs differ following fall burns, the burns themselves produced no direct mortality on adult animals in burrows. Because the persistence of these populations depends on adult survivorship (Kinney 2011), prescribed burns done in the fall likely have few fitness consequences for breeding animals to compromise these populations (Kinney 2011).

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