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*Crawfish frogs (*Lithobates areolatus*) base their nonbreeding activities in and around the entrances of crayfish burrows. This site preference allows individual crawfish frogs to be monitored using still and video imaging techniques. We used three camera types offering different continuities, scales, and resolutions of data to observe the frogs' activity patterns and nonbreeding behaviors. Together, these techniques allowed us to observe two behaviors in crawfish frogs previously unreported for amphibians: (1) circumdiel activity patterns, and (2) long periods (days) of surface activity. Although these behavioral findings are at this time specific to crawfish frogs, we suspect that they may not be unusual activity patterns for other frogs, as well. The use of imaging techniques that take advantage of these frogs' dependence on burrows and use of burrow entrances has allowed us to observe these patterns for the first time.*

Keywords: crawfish frogs, Lithobates areolatus, *activity patterns, circumdiel, video imaging*

The biology of crawfish frogs (*Lithobates areolatus*) and their two closest relatives, gopher frogs (*Lithobates capito*) and dusky gopher frogs (*Lithobates sevosus*), is noteworthy; adults of all three species inhabit upland burrows created by nonamphibian species (Jensen and Richter 2005, Parris and Redmer 2005, Richter and Jensen 2005). Whereas the two gopher frog species inhabit burrows created by gopher tortoises *(Gopherus polyphemus)*, crawfish frogs obligatorily rely on crayfish burrows for summer retreats and winter hibernation sites (figure 1). Unlike other burrow types found across the landscape, crayfish burrows extend deep into the soil (typically 1 to 1.5 meters; Thompson 1915, Smith 1934) to the water table, allowing crawfish frogs ready access to a nearby underground water source. Results from radiotelemetry studies from our two study sites (see below) have shown that adult crawfish frogs inhabit the same burrows, alone, for long periods of time. Further, crawfish frogs feed at or immediately outside their burrow entrances. Cameras can therefore be employed to study known individuals at burrows throughout the frogs' active season. Although the use of cameras to study animal behavior is certainly not novel (Pietz and Granfors 2000, Sanders and Maloney 2002, Stake and Cimprich 2003), cameras have not been used to study individual frogs, to the best of our knowledge. We used different camera types to capture crawfish frog behaviors at different scales, from low-resolution circadian activity patterns to high-resolution feeding bouts. Even though "no other species of *Rana* in the country exhibits such secretive habits" (Smith 1950, p. 99), once crawfish frogs have been located, they are relatively easy to film.

Field sites

Our field sites consisted of two large tracts of land managed as natural areas. Hillenbrand Fish and Wildlife Area West (HFWAW, 290 hectares [ha]) is a state-owned tract located in Greene County, in southwestern Indiana (see Lannoo et al. 2009 for a description of the human and natural history of this site). Big Oaks National Wildlife Refuge (BONWR) is a large (20,200 ha), federally owned tract located in Jennings, Jefferson, and Ripley counties in southeastern Indiana, about 200 kilometers southeast of HFWAW (see *www.fws.gov/refuges/profiles/index.cfm?id=31531*).

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Figure 1. Crawfish frog 270 in a typical feeding position at the mouth of its primary burrow. Photograph: Andrew S. Hoffman.

Imaging techniques

We used three types of cameras to observe adult crawfish frogs, two time-lapse cameras (one set at one-hour intervals, the other at one-twelfth-second intervals), and a continuously recording digital camcorder. Each camera captured a different type (continuity, scale, and resolution) of data. The data, overlapped and taken together, provide what is probably the most complete profile of the natural activity patterns of any species of amphibian ever observed.

Our coarsest data set came from six Cuddeback® (Non Typical, Inc.) wildlife cameras deployed at HFWAW. We fastened some cameras to treated deck spindles (nominal dimensions: 5 centimeters [cm] × 5 cm × 35 cm) buried in the ground for support, and suspended others above the burrow using a tripod of spindles. The cameras took daylight and nighttime photos; an infrared light source was used at night to avoid disturbing the frogs (figure 2). We first deployed the cameras on 18 May 2009 (two units were deployed early in the summer; we purchased additional units later, and a total of six were deployed by August). The data presented here were collected through the end of 2009, although with the onset of winter conditions,

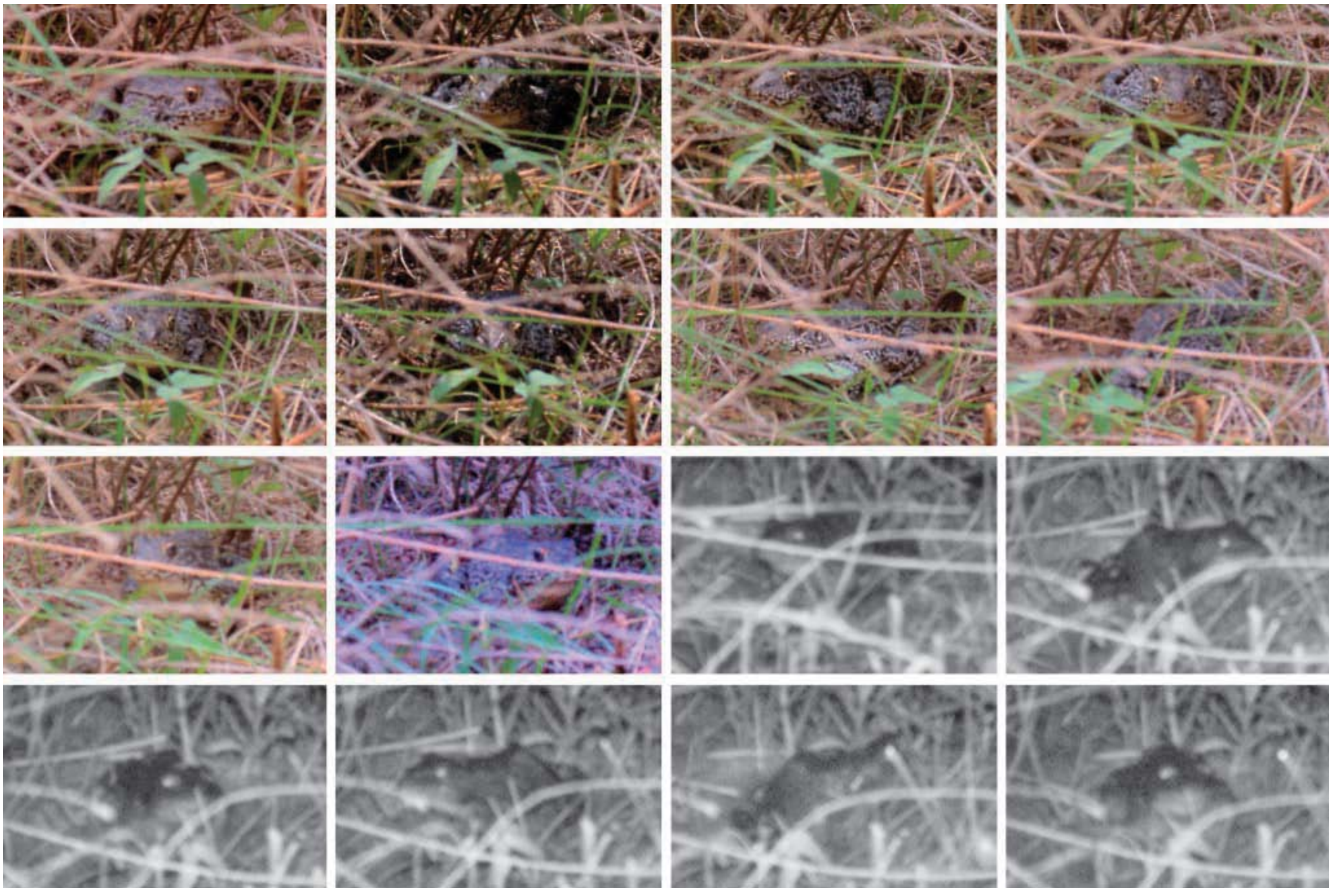

Figure 2. Sixteen photographs of crawfish frog 16 taken by a Cuddeback® wildlife camera at one-hour intervals from 1000 on 14 June 2009 to 0200 on 15 June 2009 at Hillenbrand Fish and Wildlife Area West. Images were taken at one-hour intervals with the exception of images taken at 1600 and 1800, which were excluded because of poor lighting and interference by vegetation. This sequence offers one example of the circumdiel activity pattern exhibited by crawfish frogs.

13 December was the last day that any frog was observed outside of its burrow. The Cuddeback® cameras took time-lapse images at one-hour intervals (the minimum permitted by the camera design), allowing us to determine summer activity patterns over long, continuous periods (weeks to months) for numerous individuals. Images were time-stamped and data were stored on 1- or 2-gigabyte (GB) memory cards and transferred to a desktop computer for analysis. Not all images could be interpreted because of poor lighting, lens fogging, or camera malfunction caused by either moisture inside the camera or other technical issues. Using this technique, we analyzed 6522 photos of a total of 14 crawfish frogs, representing 6508 hours of sampling, the equivalent in hours of nine months of observation.

One critique of the Cuddeback® camera observations is that animals could be employing activity patterns with a resolution finer than one hour. For example, it is possible that crawfish frogs use burrows on a one-hour cycle (e.g., frogs are on the surface at the top of the hour, then underground at half past), and the Cuddeback® might have captured only a subset of behaviors (just the surface activity or just the burrow habitation). To test whether this was true and to record finer-scale behaviors, we relied on a SCTLC300 Sony 24-hour monochrome time-lapse video recorder. This camera was employed during July and August 2009 at BONWR. The camera was powered by a 12-volt battery and set on a one-twelfth-second time interval for up to 36 hours at a time, allowing fine-scale resolution on a scale of hours to days. A Fieldcam 60 LED 940 nanometer infrared light (Fuhrman Inc., Seabrook, Texas) enabled continuous night recording without disturbing the frogs. We set the video recorder on a tripod and placed it outside of a known frog's burrow, and we draped a camouflage-patterned mesh over the top of the camera to decrease the likelihood of disturbing the frog. Three frogs were filmed; one for 247 hours (> 10.25 days), another for 61 hours (> 2.5 days), and the third for 23.75 hours.

The SCTLC300 Sony 24 time-lapse camera was not available at HFWAW; instead, we used a tripod-mounted Canon ZR 300 color digital video camcorder (Canon, Inc.) to record the summer daytime activity of crawfish frogs. This camera gave us high resolution, but at a cost of short film bouts (tens of minutes to a little less than one hour). Filming took place from 19 May to 26 September 2009; we obtained approximately 49 hours of video. Seven individual frogs were filmed for total times ranging from less than 23 minutes to nearly 20 hours. Data were stored on 2-GB memory cards that allowed for 45 to 50 minutes of continuous filming, after which the memory cards were replaced with fresh ones. We changed the camera batteries after every other memory card replacement (< 2 hours). Each filming event stored on a card constituted a bout; 82 bouts were recorded. On any given day, a single crawfish frog could be filmed for up to 4.5 hours. Replacing memory cards and batteries disturbed crawfish frogs and usually sent them into their burrows, although animals generally reemerged only a minute or two after the researcher retreated.

Evidence for prolonged, circumdiel activity patterns

Results from the Cuddeback® wildlife cameras provided the first clear evidence of circumdiel activity patterns in crawfish frogs (figure 2), and proof that these frogs can be aboveground for prolonged periods of time (figure 3).

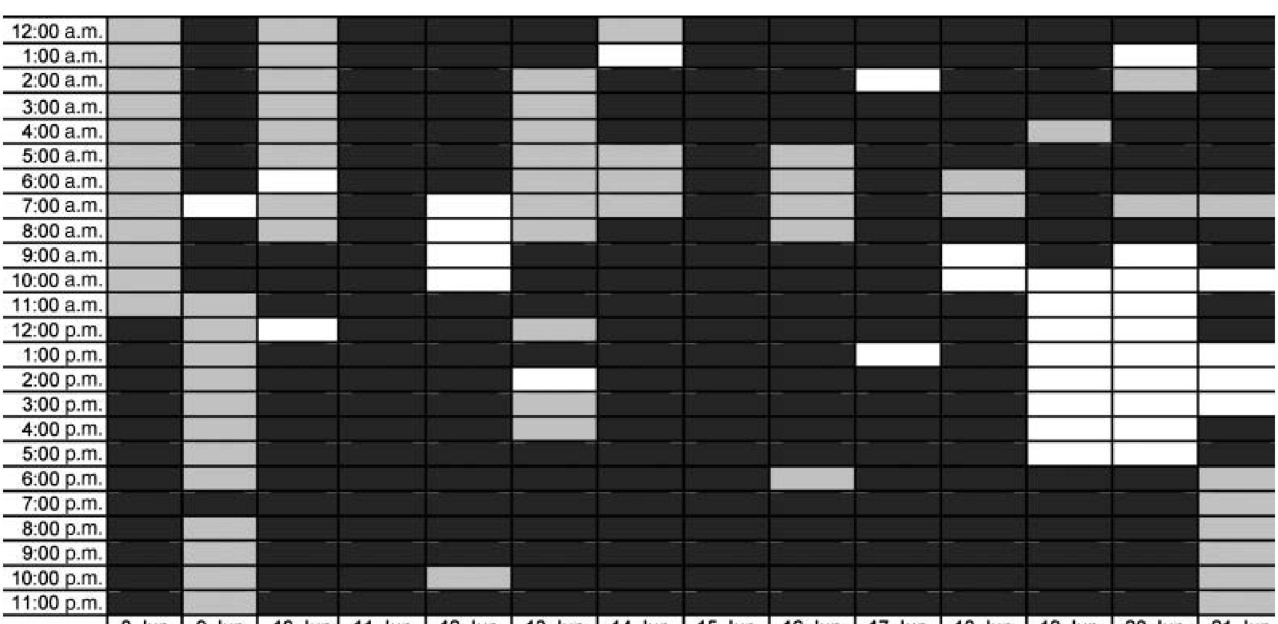

Figure 3. Pattern of crawfish frog 16 between noon on 8 June and 21 June 2009 as determined by a Cuddeback® wildlife camera taking time-lapse photographs at one-hour intervals. Days are indicated on the x-axis, time of day on the y-axis. Black cells indicate frog activity aboveground, white cells indicate frog in burrow, and gray cells indicate camera malfunction or no data collected for that period.

Between noon (1200) on 8 June and 1700 on 21 June (a total of just under 13 days), frog 16 was observed out of its burrow for 237 total hours (87% of observations) and in its burrow only 36 hours (13% of observations). In this time period there were 318 possible hours of observation—45 hours were lost to poor lighting or the technical issues mentioned above (figure 3). During this frog's longest period of continuously observed activity—between 0900 on 10 June and 0600 on 12 June—it was outside its burrow for 45 hours (98% of the time) and in its burrow only 1 hour (figure 3). Similar long bouts of activity were observed in frog 33, which was outside of its burrow 85% (108 out of 127) of observable hours from 1800 on 21 June to 1700 on 27 June. Frog 3 was active 91% (126 out of 139) of observable hours from 1100 on 20 September to 1700 on 26 September. Frog 6 was active for long periods of time on two different occasions: (1) from 1800 on 27 August to 2100 on 31 August it was active 90% (77 out of 86) of observable hours, and (2) from 0700 on 20 September to 0000 (midnight) on 27 September it was active 98% (108 out of 110) of observable hours. Some frogs exhibited long periods of inactivity, which they spent in their burrows (frog location was verified using radiotelemetry). For example, frog 6 was in its burrow from 2000 on 16 August to 1800 on 24 August (91% of the time; 162 out of 179 observable hours). This period of inactivity preceded a long period of activity (see above).

In general, during mid- to late summer (June through mid-September), periods of inactivity tended to be shorter than periods of activity. Later in the season, all monitored frogs (frogs 3, 9, 26, 33, 16, and 6 at HFWAW; frogs 270, 319, and 341 at BONWR) began restricting their activity to the warmest part of the day (afternoons), although some morning and late-evening activity persisted. We observed frog 16 outside of its burrow on 13 December at 2100, after the first snow of the year had accumulated and then melted.

We saw no evidence that camera presence attracted frog predators to the burrow sites. Some cameras were displaced or chewed, most likely by mammals, but no frogs with cameras at their burrows were preyed upon. The single confirmed act of predation on a burrowed crawfish frog was by an eastern hog-nosed snake (*Heterodon platyrhinos*; Engbrecht and Heemeyer 2010), and this individual was never filmed.

Results from the Sony time-lapse video recorder confirmed the activity patterns suggested by the Cuddeback®. For example, the three frogs followed at BONWR were active both during the day and at night (figure 4). They spent 60% of their time out of their burrows (30% during the day [average = 465.5 minutes, standard deviation (SD) = 161.3], 30% at night [average = 460.8 minutes, SD = 198.9]). They spent an additional 24% of their time at the entrances to their burrows, facing out (15% during the day [average = 227.6 minutes, SD = 170.7], 9% at night [average = 131.1 minutes, SD = 267]). The remainder of their time (16% total: 11% during the day [average = 170.2 min, SD = 127.5], 5% at night [average = 80.2 min, SD = 169.3]) was spent in their burrows.

Before this study crawfish frogs were described as emerging "only early in the morning" (Smith 1950), being nocturnal (Conant and Collins 1998, Minton 2001, Parris and Redmer 2005), being nocturnal following rains (Johnson 2000), or being crepuscular (Thompson 1915). These authors were not wrong; they were just incompletely correct. By virtue of being close to burrows and by typically diving into them at the first hint of threat, crawfish frogs are extraordinarily difficult to observe during daylight. At HFWAW, daily checks without seeing particular frogs (especially frog 16) over the course of weeks led to concern about their health (transmitter signals emitting from burrows did not distinguish live from dead frogs). In every case during the 2009 field season, Cuddeback® camera images showed active frogs, up and out of their burrows a majority of the time.

Burrow use

Both of our high-resolution cameras (Sony time-lapse and Canon camcorder) recorded daily activities such as burrow exiting, feeding attempts (both successful and unsuccessful), and burrow entering (headfirst quickly to avoid threats, headfirst slowly when simply seeking shelter, backward when subduing or swallowing prey). There were large variations in these behaviors. For example, when emerging from burrows, crawfish frogs usually appeared at the burrow surface and then stopped, moved farther out (head emergence), stopped,

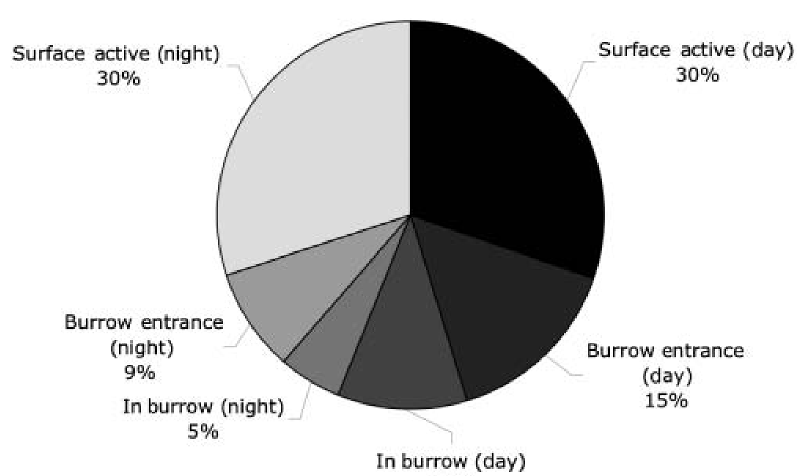

Figure 4. Pie chart showing the average amount of time three frogs from Big Oaks National Wildlife Refuge spent in their burrows during the more than 332 hours they were recorded in August 2009. Note the high proportion of time spent outside the burrow (60% summed day and night values) and at the burrow entrance (24%), the low proportion of time spent in the burrow (16%), and the overall similarity between day and night values.

moved farther out (half-body emergence), stopped, and then fully emerged onto their "feeding platform." Most frogs averaged three to five exit movements before they emerged; frog 5, however, usually exhibited only one (16 of 22 times, 73%). We found that after either exiting or entering burrows, crawfish frogs almost immediately turned around to face the burrow entrance. When outside the burrow, this orientation offered a quick escape (with little to no time spent turning to face the burrow before jumping in); when inside the burrow this posture offered opportunities to feed, but also allowed frogs the ability to resist predators (our videography recorded an eastern racer [*Coluber constrictor*] and a common garter snake [*Thamnophis sirtalis*] entering occupied crawfish frog burrows). In the one confirmed act of predation on crawfish frogs by snakes in 2009 (see above), the frog—known to be occupying a burrow—was taken headfirst and the carcass showed signs that the frog had resisted (Engbrecht and Heemeyer 2010).

Feeding rates

We calculated feeding rates from the videos. At BONWR, the highest recorded feeding rate was eight prey taken in approximately 31 hours (roughly one prey taken every 3.9 hours). At HFWAW, the highest feeding rate observed (daytime) was two prey taken in approximately 0.5 hour (one prey every 15 minutes, by frog 5). Also at HFWAW, frog 6 took two prey in about 0.7 hour; frog 26 took two prey in approximately 0.9 hour. Prey included moths, ants, spiders, large grasshoppers, and small beetles. Bees were snapped at but missed.

Do activity patterns reflect activity?

The use of various overlapping imaging techniques allowed us to observe circumdiel activity patterns and long periods of surface activity in crawfish frogs. Throughout this article, we have assumed that being aboveground equates with being active, and that being underground in burrows equates with inactivity. The data presented here provide substantial evidence that the first assumption is correct. Both daytime and nighttime images of crawfish frogs out of their burrows show them moving—changing positions and orientations in response to potential prey and perhaps to thermo- or osmoregulate (figure 2). We never saw behaviors—such as closed eyes or limbs tucked in toward the body—that indicate sleep in amphibians. In fact, unlike tree frogs (Hylidae; Hobson et al. 1968) and true toads (Bufonidae; Huntley et al. 1978), classic sleep behavior is undocumented in true frogs (Ranidae), a group that includes crawfish frogs, although bullfrogs *(Lithobates catesbeianus)* are quiescent at night (Hobson 1967).

We have no visual evidence to support the belief that frogs in burrows are inactive. We know crawfish frogs overwinter in burrows, where we suspect they are inactive, at least when surface temperatures are below freezing. And we assume, as with bullfrogs, that during the summer crawfish frogs have periods of quiescence. If this is the case, however, inactivity must take place in burrows, because we did not observe inactivity aboveground. But we do not know for sure whether crawfish frogs in burrows are always inactive. It may be that crawfish frogs in burrows behave similarly to Hobson's (1967) description of quiescent bullfrogs: "They rest without loss of vigilance."

How atypical are these activity patterns?

As unusual as circumdiel activity patterns and long periods of surface activity may appear, it strikes us that they might not be uncommon behaviors for frogs, especially for true frogs (Hobson 1967). The dependence of crawfish frogs on crayfish burrows and their use of burrow entrances has simply allowed us to observe these patterns for the first time. Clearly, frogs that feed during the day but breed at night (a typical, if not *the* typical, pattern; Wells 2008) have the sensory and neural capacity to operate both in the presence and absence of daylight (Gordon and Hood 1976). Instead, it may be that extended circumdiel activity patterns have not been previously observed in frogs because of the difficulty in monitoring individual, free-ranging frogs over long periods of time.

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"He obsesses over his carbon footprint."