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Habitat Relations

Obligate Crayfish Burrow Use and Core Habitat Requirements of Crawfish Frogs

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ABSTRACT Crawfish frogs (*Lithobates areolatus*) have experienced declines across large portions of their former range. These declines are out of proportion to syntopic wetland-breeding amphibian species, suggesting losses are resulting from unfavorable aspects of non-breeding upland habitat. Crawfish frogs get their common name from their affinity for crayfish burrows, although the strength of this relationship has never been formally assessed. We used radiotelemetry to address 4 questions related to upland burrow dwelling in crawfish frogs: 1) what burrow types are used and how do they function to affect crawfish frog survivorship; 2) what are the physical characteristics and habitat associations of crawfish frog burrows; 3) what are the home range sizes of crawfish frogs when burrow dwelling; and 4) where are crawfish frog burrows situated with respect to breeding wetlands? We tracked crawfish frogs to 34 burrows, discovered another 7 occupied burrows, and therefore report on 41 burrows. Crawfish frogs exclusively occupied crayfish burrows as primary burrows, which they inhabited for an average of 10.5 months of the year. With one exception, crawfish frogs also used crayfish burrows as secondary burrows—temporary retreats occupied while exhibiting breeding migrations or ranging forays. Burrows were exclusively located in grassland habitats, although crawfish frogs migrated through narrow woodlands and across gravel roads to reach distant grassland primary burrow sites. Home range estimates while inhabiting burrows were 0.05 m^2 (the area of the burrow entrance plus the associated feeding platform) or 0.01 m^3 (the estimated volume of their burrow). Crawfish frog burrows were located at distances up to 1,020 m from their breeding wetlands. To protect crawfish frog populations, we recommend a buffer (core habitat plus terrestrial buffer) of at least 1.2 km around each breeding wetland. Within this buffer, at least 3 critical habitat elements must be present: 1) extensive grasslands maintained by prescribed burning and/or logging, 2) an adequate number of upland crayfish burrows, and 3) no soil disturbance of the sort that would destroy crayfish burrow integrity.

KEY WORDS burrow philopatry, core habitat, crayfish, landscape connectivity, *Lithobates areolatus*, Nenirana, radiotelemetry.

Habitat can be generally defined as the area where an animal lives and the place where it can meet its needs, including finding food and water, avoiding temperature extremes, and finding protection from predators (Morrison et al. 2006). Among the habitats of most conservation concern are those where one species relies exclusively on another for its habitat or to create its habitat, and one of the best examples of such dependence involves burrow use. Although many species of amphibians, reptiles, mammals, and invertebrates, even some birds, use subterranean burrows as habitat, only a few of these species dig their own holes. Some non-burrowing species have come to obligately depend on the burrows of particular species for their habitat, and when dependent species become a focus of conservation concern, the relationship between these habitat specialists and their hosts must be fully understood.

Crawfish frogs (*Lithobates areolatus*) are members of the *Nenirana* subgenus (Hillis and Wilcox 2005), a clade of North America anurans containing species dependent upon burrows created by other animals for their upland habitat. Crawfish frogs have been associated with crayfish burrows (Thompson 1915, Hoffman et al. 2010), and derive their common name from this tendency. Crawfish frogs have also been reported to occupy mammal burrows, sewer pipes, manholes, sinkholes, and scrapes (Goin and Netting 1940, Wright and Wright 1949, Parris and Redmer 2005, Collins et al. 2010, Engbrecht et al. 2011).

Crawfish frogs have experienced dramatic declines and are of considerable conservation concern (Parris and Redmer 2005). They are a state endangered species in Indiana, where they continue to decline (Engbrecht and Lannoo 2010) and in Iowa, where they have not been seen since 1942

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(Christiansen and Bailey 1991). Crawfish frog declines have been out of proportion with syntopic pond-breeding amphibians such as southern leopard frogs (*L. sphenocephalus*), western chorus frogs (*Pseudacris triseriata*), and spring peepers (*P. crucifer*; Parris and Redmer 2005, Engbrecht and Lannoo 2010), and therefore discussions to petition crawfish frogs for federal listing have begun (Southeastern Partners in Amphibian and Reptile Conservation 2010). These declines have been attributed to a variety of factors including breeding wetland loss resulting from draining or the stocking of predatory fish (but see Palis 2009), as well as destruction of upland habitat resulting from development, agricultural and silvicultural practices, and fire suppression (Thompson 1915, Wright and Wright 1949, Busby and Brecheisen 1997, Parris and Redmer 2005). Attempts to understand the conservation status of this species have been hindered by the reclusive nature of crawfish frogs (Smith 1950), which spend most their lives associated with upland burrows (Hoffman et al. 2010, Heemeyer 2011).

Because of the dependence of crawfish frogs on upland burrows and their disproportionate decline compared with syntopic wetland breeding species, we felt to understand crawfish frog declines that we needed to explore the relationships between crawfish frogs and their burrow habitat. We therefore posed the following questions: 1) What burrow types are used and how do they function to influence crawfish frog survivorship; 2) What are the physical characteristics and habitat associations of crawfish frog burrows; 3) What are the home range sizes of crawfish frogs when burrow dwelling; and 4) Where are these burrows situated on the landscape with respect to breeding wetlands? We conclude by considering the conservation implications of these findings, and making management recommendations for core habitat designations.

STUDY AREA

Our study site was located on the 729 ha Hillenbrand Fish and Wildlife Area-West (HFWA-W), located approximately 5 km south of Jasonville, in Greene County, Indiana (39.120275°N, 87.222187°W). This area is the only portion of the larger Hillenbrand Fish and Wildlife complex that supports crawfish frogs. From 1976 to 1982, HFWA-W was surface mined for coal (Lannoo et al. 2009). Afterwards, the site was re-contoured and seeded to non-native vegetation. In 1988, the Indiana Department of Natural Resources (IDNR) purchased the land and began the process of converting the vegetation to native prairie species using seedings and regular controlled burns. The site was managed for hunting and fishing, and food plots were scattered through the property. To maintain the prairie ecosystem, IDNR periodically burned sections ranging from 2 to 45 ha. Two native species of large burrowing crayfish occured in this area—the painted-hand mudbug (*Cambarus* [*Tubericamberus*] *polychromatus*) and the digger crayfish (*Fallicambarus* [*Creaserinus*] *fodiens*; Thoma and Armitage 2008).

METHODS

Burrow Location

Telemetry.—We used radiotelemetry to track post-breeding crawfish frogs to upland burrows. We caught frogs at drift fences encircling 2 seasonal or semipermanent wetlands, Nate's Pond and Cattail Pond (Kinney 2011), or in minnow traps at a third semipermanent wetland, Big Pond. We used implanted or external radiotransmitters (3.8 g, PD-2T temperature-sensitive transmitters with internal helical antennae; Holohil, Ontario, Canada; see Heemeyer et al. 2010; IACUC number 3-24-2008 issued by Indiana State University). Nominal transmitter life was 6 months. We surgically implanted 68 transmitters into 49 frogs (we serially implanted transmitters into 15 frogs; at no time did any frog have more than 1 internal transmitter) and put external belts on 18 frogs. Transmitter insertion followed the methods outlined in Johnson (2006; for surgical details see Heemeyer et al. 2010). We used external transmitters when surgeries posed a threat to the frog (Heemeyer et al. 2010), or when we wanted to identify burrow locations by following frogs to their burrows but not track frogs through the non-breeding season. We attached external belt transmitters using metal beaded chains (Rathburn and Murphey 1996, Matthews and Pope 1999), similar to the plastic beaded chain that is currently being used successfully by J. Humphries (North Carolina Wildlife Resources Commission, personal communication) to track related gopher frogs. We tracked crawfish frogs using an R-1000 receiver and a Yagi unidirectional antenna (both manufactured by Communication Specialists, Orange, CA). We located frogs daily during the spring and summer of 2009 and 2010, every other day during the fall of both years, and once a week from late November to mid February (winter). Each time we located an individual, we measured weather variables at the site using a handheld Kestrel 4000® (Sylvan Lake, MI) weather meter. We recorded frog locations using a Garmin® GPSMAP 76CSx (Olathe, KS), and we plotted the location data using a Geographic Information System (GIS; ArcMap 9.3®). At each burrow, we noted changes or unusual features such as flooding or attempts to excavate the burrow, animals present or animal tracks, as well as activity at the burrow entrance since the last visit (we placed big bluestem stem sections in an "X" pattern across the entrance of each burrow during each visit and noted at the next visit whether they had moved). While tracking, we opportunistically recorded incidental observations of crawfish frog burrows. We also identified crawfish frog burrows by walking parallel transects over the ground left bare following prescribed burns, and by locating upland calling males.

Burrow Characteristics

Physical features.—To visualize crawfish frog burrow conditions without destroying burrows we used a VS72-10WD Digital Video Borescope® (Visual Optics, Wynnewood, OK). We examined every primary burrow inhabited by a radiotracked crawfish frog, but observations of burrow tunnels were often limited. Because of high water levels or bends along the course of many burrows (which caused dirt or mud to adhere to the leading lens of the scope and reduced or eliminated visibility), the deeper portions of many burrows could not be examined. On 10 September 2009, we fully scoped 4 occupied burrows; on 19 November 2010, we fully scoped 6 occupied burrows.

A HOBO® (Onset, Pocasset, MA) weather station located approximately 3.2 km from the field site at a secure location with similar grassland habitat characteristics recorded the air temperature data we used to compare with the frog temperatures provided by the internal transmitters.

Habitat characteristics.—In late July 2009, we took habitat measurements at 18 known crawfish frog burrows (the burrows containing radiotracked crawfish frogs at this time) and at 54 sites (3 times the number of known occupied crawfish frog burrows) throughout HFWA-W. Site locations were randomly generated using Microsoft Excel® v. 2003 (Microsoft Corporation, Redmond, WA). We excluded sites that were in heavily wooded areas, on roadways or railways, in lakes, or were plowed—places where crawfish frogs would not or could not occupy burrows. At each site, we measured maximum vegetation height using a tape measure, and vegetation weight using a Robel pole (Robel et al. 1970). We also estimated (to the nearest 5%) within a 1-m^2 quadrat the percent cover of forbs, living and dead woody vegetation, grass, and bare ground.

Home Range Estimates

To establish home range size, we measured (width $\times$ length) the surface areas of each burrow entrance and adjacent feeding platform. These must be regarded as approximations, because edges of feeding platforms grade into the surrounding vegetation and both burrow entrances and feeding platforms are irregular in shape. Additionally, because crawfish frogs spend most of their time in burrows, based on our measurements of inhabited burrows we used the formula for a cylinder ($\pi \times \text{radius}^2 \times \text{length}$), where the burrow diameter was 50 mm and length was 1 m, to estimate home range volume.

Burrow Distribution

To obtain information on the location, characteristics, and spatial distribution of all burrow types at HFWA-W, we surveyed areas burned in the fall of 2009 and in the spring of 2010. On 19 September 2009, IDNR land managers burned 2 sections (hereafter termed the north burn and the south burn) of HFWA-W, totaling 8.5 ha (1.9 ha in the north burn, 6.6 ha in the south burn). These fall burns eliminated most of the senesced overlying vegetation, exposing bare ground, and made burrow openings clearly visible. We used this opportunity to systematically survey for all burrows, and from among these burrows to identify candidate crawfish frog burrows (medium-to-large-bore holes associated with a small area of compacted soil characterizing feeding platforms). We censused and recorded the location of every burrow in 5.6 ha of the total 8.5 ha (all the north burn and the grassland portion of the south burn) using a Garmin® GPSMAP 76CSx. We also measured the diameter of every burrow, and, when crayfish chimneys were present, measured their height. The 2010 spring burn covered approximately 40.5 ha and was much less complete (because of wetter combustible material and higher relative humidity) than the 2009 fall burns, and thus we could not search it completely.

Based on the burrow descriptions of Hurter (1911), Thompson (1915), and Stevenson and Dyer (2002) as well as personal observations, we identified possible crawfish frog burrows as those that: 1) did not have a crayfish chimney; 2) were between 40 and 150 mm in diameter; 3) had an oval opening; and 4) had a cleared, compacted feeding platform outside the burrow entrance. We classified all other burrows by the type of animal that made them. Mammal burrows were in complexes with multiple openings and tunnels, had burrows that were shallow and leveled out into horizontal passages, and were associated with lighter (drier) soils, because of the aeration provided by the underlying burrows. Turtle forms were large in diameter but shallow. Crayfish burrows were variably sized, deep, often had chimneys, and had circular openings. We identified potential crawfish frog burrows using the criteria noted above. To determine whether crawfish frogs inhabited these burrows we flushed them using the method of Heemeyer and Lannoo (2010). Captured crawfish frogs were weighed, measured (snout-vent length; SVL), and scanned for a passive integrated transponder (PIT) tag number (Christy 1996). If frogs lacked a PIT tag (i.e., if we had not previously encountered the animal at a breeding wetland and implanted one; Kinney 2011), we inserted a PIT tag and released the frog back into its burrow. We implanted a radio transmitter in 1 frog from the south burn.

We examined crayfish burrow distribution in both the 2009 north and south burn areas using independent minimum enclosing rectangles that included all crayfish burrows measured in each respective site. After recording burrow position, we used average nearest neighbor (ANN) distance and multi-distance spatial cluster analysis (Ripley's K-function) tools within the spatial statistics toolbox of ArcMap 9.3® (Ripley 1981, Venables and Ripley 2002) to determine whether burrows were distributed randomly or clustered (Fortin and Dale 2005, Rittenhouse and Semlitsch 2007). Average nearest neighbor is an average of the distances from each point to the next-nearest point within the area denoted by an enclosing rectangle. This measured average is then compared to a random hypothetical ANN value. If the measured ANN is greater than the hypothetical ANN, the measured points are considered dispersed; if the measured ANN is less than the hypothetical ANN, points are considered clustered. We also analyzed the spatial distribution of the 6 known crawfish frog burrows in the area.

Core Habitat

To determine core habitat, we used GIS to measure the straight-line distance of each crawfish frog burrow to the centroid of the occupant's breeding wetland. We did not observe differences in straight-line distance measurements between years ($P = 0.14$); therefore, we pooled data to estimate core habitat and buffer. Based on these distances, we calculated core habitat and buffer radii around each breeding wetland.

Analyses

We performed all statistical analyses using Program R® (R Version 2.10.1, www.r-project.org, accessed 27 Feb 2011). We used a Kruskal–Wallis test to compare numbers of burrows used by males and females within and between years. We used Wilcoxon rank-sum tests with continuity correction to test for differences in the straight-line distance of burrows from wetlands per year. We used a Spearman rank correlation matrix to estimate relationships between number of burrows used and straight-line distance, SVL of each frog, mass of each frog, and number of movements each frog made, as well as to estimate correlation of habitat variables to each other and the number of burrows used. Because the grass and forbs variables were highly correlated (Rho = −0.97; see Results section) we removed forbs from the model analysis. We fit a set of generalized linear models (GLMs), with a binomially distributed response variable, to the burrow selection data (Table 1). We then approximated the parsimony of these models using Akaike's Information Criterion for small samples (AIC_c). The model with the lowest AIC_c score was our top model. We examined the relative support for each model by estimating the Akaike weight (ω) based on the ΔAIC_c (Anderson et al. 2000), and we performed a 10-fold cross-validation for regression with a binary response (Efron and Tibshirani 1993).

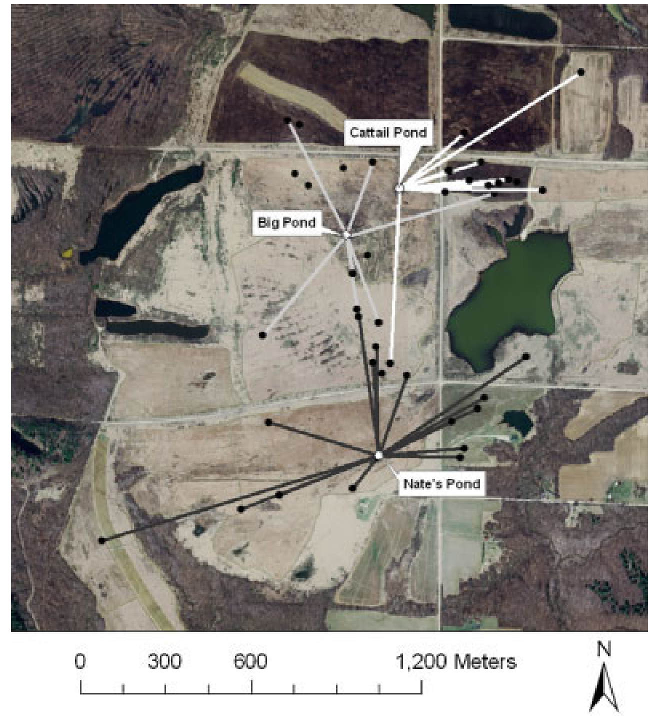

Figure 1. The straight-line distance from respective breeding wetlands to the upland crayfish burrows (black dots) used by crawfish frogs at Hillenbrand Fish and Wildlife Area-West in Indiana from May 2009 to November 2010. Black dots not associated with a line represent frogs whose breeding wetland was unconfirmed.

RESULTS

Burrow Location

Using radiotelemetry, we tracked 34 frogs from their breeding wetlands to their upland burrows (7 at Big Pond, 12 at Cattail Pond, 15 at Nate's Pond; Fig. 1). We tracked an additional 22 animals away from breeding wetlands but they could not be followed to burrows because of lost signals (cause unknown: 8 animals), death (e.g., predation or chytridiomycosis: 8 animals; Kinney et al. 2011), or transmitter removal (6 animals; Heemeyer et al. 2010). During the course of our fieldwork, we discovered an additional 7 frogs occupying upland burrows: 3 were found during post-burn surveys, 3 were found while tracking other frogs, and 1 male was located when heard calling from its upland burrow. In total, we located 41 crawfish frog burrows (representing between a quarter and a third of the adults in this population based on a multi-year drift fence study at breeding wetlands; Kinney 2011).

Table 1. Model selection results for correlates of habitat selection by crawfish frogs. The response variable (y) was burrow sites or random sites and the covariates were: vegetation height (VH), vegetation weight (VW), percent cover of woody (W), grass (G), bare (B), and percent dead woody debris (DW). The 10 models with the lowest Akaike's Information Criterion (AIC_c) values are shown with the number of parameters (K), AIC_c differences (ΔAIC_c), and Akaike weights (ω). We collected data (n = 72) at Hillenbrand Fish and Wildlife Area-West in Greene County, Indiana, USA during 2009.

No.	Model	K	AIC_c	ΔAIC_c	ω
1	y = VW × B × VH + VW × B + VW × DW + B × DW + VW × G + B × G + VW × VH + B × VH + G × VH	15	76.20	0.00	0.581
2	y = VW × B + B × G + B × VH	8	79.20	3.00	0.130
3	y = VW × B + VW × G + B × G + B × VH	9	79.41	3.21	0.117
4	y = VW × B + DW + B × G + B × VH	9	81.76	5.56	0.036
5	y = VW × B + DW + VW × G + B × G + B × VH	10	81.91	5.71	0.033
6	y = VW × B × VH + VW × B + VW × DW + B × DW + VW × G + B × G + VW × VH + B × VH + G × VH + VW × W	17	82.03	5.82	0.032
7	NULL	0	82.98	6.77	0.020
8	y = VW × B + VW × DW + VW × G + B × G + VW × VH + B × VH + G × VH	13	83.09	6.89	0.019
9	y = VW × B + DW + B × G + B × VH + W	10	83.60	7.39	0.014
10	y = VW × B + DW + VW × G + B × G + B × VH + W	11	83.81	7.60	0.013
11	y = VW × B + VW × DW + VW × G + B × G + VW × VH + B × VH + G × VH + W	14	85.23	9.03	0.006

Burrow use.—We distinguished 2 types of burrows: primary burrows—the single burrow where an individual frog spent most of its time, typically the entire non-breeding season (from Apr or May through late-Feb or Mar); and secondary burrows—the series of burrows that were used by an individual while migrating to and from the breeding wetland or while ranging from the primary burrow. Ranging is the term used by Dingle (1996) and Wells (2007) to define movements outside of an established home range to explore new resource patches; also termed forays (Conradt et al. 2003). Primary burrows were used for between 260 and 334 days; secondary burrows were usually used for periods of only a few days, never more than 2 weeks. Therefore, we regarded crawfish frogs as inhabiting primary burrows if they did not change burrows for at least 2 weeks, although in practice crawfish frogs typically inhabited these burrows for the entire non-breeding season. Crawfish frog primary and secondary burrows are similar to the long-term and temporary burrows of giant bullfrogs (*Pyxicephalus adspersus*), described by Yetman and Ferguson (2011). However, giant bullfrogs excavate their own burrows and will exhibit torpor while in them, whereas crawfish frogs do neither.

The 34 frogs that we tracked to their individual primary burrows used a range of 1–11 burrows per post-breeding migration ($\bar{x} = 3.5$, SD $= 2.6$), including the primary burrow. We did not find differences in the number of burrows used by males and females ($P = 0.11$). All burrows used by crawfish frogs were in grassland habitats. Further, all burrows used by crawfish frogs were dug by crayfish with the exception of a secondary burrow consisting of a single shallow scrape dug in loose soil by frog 33 in 2010 (Engbrecht et al. 2011). Both within and across years, frogs often re-used the same secondary burrows during pre- and post-breeding migrations and after ranging forays from burrows. They also used the same primary burrows across years; of the 34 frogs tracked to primary burrows, we tracked 8 during consecutive 2009 and 2010 post-breeding migrations. In 2010, all 8 frogs returned to the vicinity of their 2009 primary burrows: 6 to their original primary burrows, 1 to a nearby burrow (within a few meters), and 1 that was approaching its former burrow when it was taken by a predator.

Burrow Characteristics

Physical features.—All occupied burrows (both primary and secondary), with the exception of the shallow scrape dug by frog 33, were crayfish burrows. These burrows ranged from 40 to 140 mm in diameter and could best be distinguished from burrows not supporting crawfish frogs by the presence of a feeding platform approximately 50–75 mm in diameter situated at the entrance of the burrow. Feeding platforms were reformed every summer and in 1 instance (frog 8) formed on the opposite side of the burrow from the previous year.

Using the burrow scope, we observed that the shape of individual burrows varied. For example, some maintained a constant diameter and others opened up into a larger tunnel; some burrows had sharp turns and others were straight. We did not observe any side chambers or evidence of multiple tunnels. Slopes of burrows were generally steeper than 45°. Within burrows, we often saw insect remains (especially beetle elytra) embedded into the walls. We occasionally saw live invertebrates (e.g., millipedes, isopods, and spiders). In 1 active crawfish frog burrow, we identified a rodent nest (confirmed by Cuddeback® [Green Bay, WI] photographs of a vole [*Microtus* sp.] as well as by the presence of small mammal tunnels through the snow in the winter [Murie and Elbroch 2005]). Three burrows were <1 m in depth (79, 89, and 92 cm). In other burrows, the scope traveled as far as 122 cm and did not reach bottom. Burrow walls were smooth, often punctuated with cracks or protruding roots and rocks. We observed 3 frogs in burrows. In 2009, we observed 1 female sitting in the water pooled at the bottom of a straight burrow. In 2010, burrows were dry and we saw 1 female sitting at the end of her burrow facing the entrance. We observed a male at the bottom of his burrow, where it was flat and wide enough for him to sit horizontally.

Crayfish burrows occupied by crawfish frogs had water at their base during times of average or above-average rainfall, but during prolonged droughts, their bases were dry, though still moist and humid. We observed crawfish frogs sitting at the base of burrows in water when conditions were dry. Unlike other ranids (southern leopard frogs, green frogs [*L. clamitans*], and bullfrogs [*L. catesbeiana*]), crawfish frogs will drown if submerged for a prolonged period (Heemeyer and Lannoo 2011). During heavy rains, burrows often flooded. When this occurred, crawfish frogs appeared to remain close to the burrow entrance, presumably so they could breathe. Intentionally flooding burrows typically causes crawfish frogs to surface to breathe every 30–45 minutes (Heemeyer and Lannoo 2010), although we have observed frogs will stay submerged longer at colder temperatures.

Mean daily crawfish frog temperatures varied seasonally between approximately 7° C in winter to 30° C during the late summer (Fig. 2A). Crawfish frog temperatures correlated with air temperatures, however, the correlation varied by season. Through the summer as well as during warmer portions of the spring and fall, when weather conditions allowed crawfish frogs to move freely in and out of their burrows, crawfish frog temperatures were similar to air temperatures (Fig. 2B). During the winter (1 Nov 2009–24 Feb 2010), when crawfish frogs generally remained deep in their burrows (although we have observed crawfish frogs out of their burrows every month of the year during favorable weather), frog temperatures were on average 5.4° C warmer and were as much as 15° C warmer than air temperatures (Fig. 2B).

Habitat characteristics.—We created and compared 23 GLMs using AIC_c. The model that had the lowest AIC_c score, and thus was estimated to be the most parsimonious model, was a complex model that included vegetation weight, vegetation height, percent bare ground, percent dead woody debris, percent grass, and interactions between these variables (model 1; Table 1). Based on our 10-fold cross validation, we expect our model to be accurate 75% of the

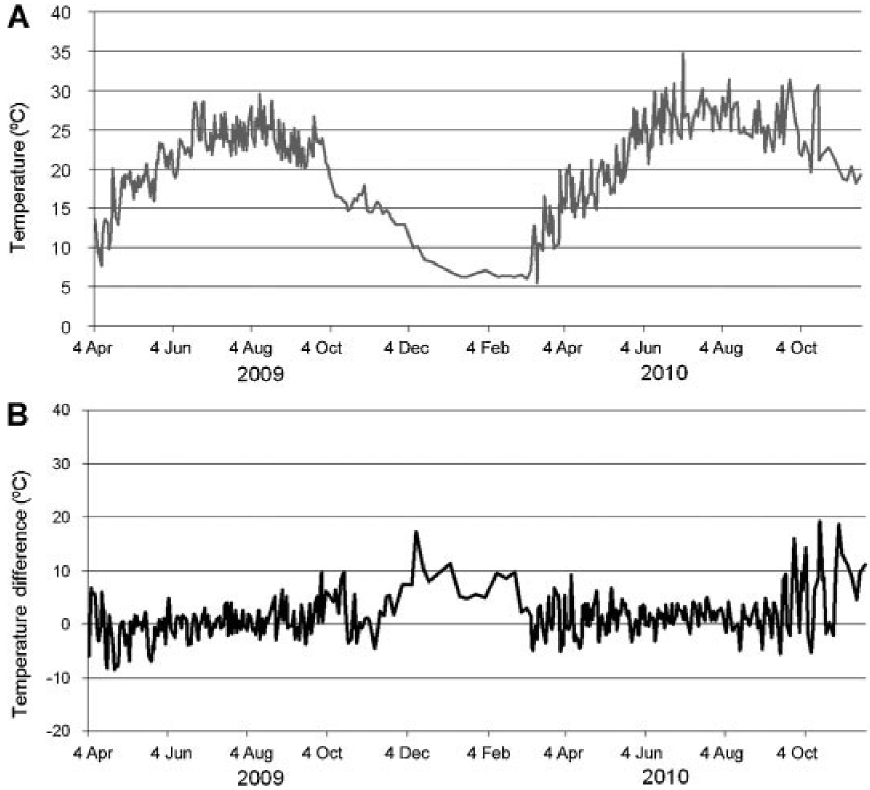

Figure 2. A plot of air temperatures (A) and the daily average difference of crawfish frog temperatures subtracted from air temperatures from 4 April 2009 to 30 November 2010 (a period of 20 months; B) at Hillenbrand Fish and Wildlife Area-West in Indiana. Note that throughout the summer, temperature difference oscillates around zero, indicating little difference between frog temperature and air temperature. During the winter, however, frog temperatures were consistently, and often substantially (>15° C), warmer than air temperatures.

time. This model suggests that burrow site selection was influenced by complicated habitat interactions.

Home Range Estimates

From measurements of surface areas of feeding platforms and burrow entrances, we calculated crawfish frog home range size (area) to be about 0.05 m^2. We estimated the average home range size (volume) of their burrow to be about 0.01 m^3 (assuming an average burrow diameter of 50 mm and depth of 1 m).

Burrow Distribution

Within the 2 areas burned in September 2009, we identified and measured 432 burrows, as follows: 381 crayfish burrows, 47 mammal burrows, and 4 turtle forms (Fig. 3). The spatial distribution of crayfish burrows within both burned areas was non-random; in particular, crayfish burrows were more clustered than predicted by a random spatial distribution ($P \leq 0.01$). Crayfish burrows tended to occur along stream beds and around seasonal and semipermanent wetlands.

Of the 381 identified crayfish burrows, 96 were at least 40 mm in diameter (57 in the south burn, 39 in the north burn)—large enough to accommodate an adult crawfish frog. We flooded (Heemeyer and Lannoo 2010) the subset ($n = 12$) of these burrows that appeared to have feeding platforms and found 3 crawfish frogs: a female in the north burn, 1 frog of undetermined sex in the south burn, and a male in the south burn. The undetermined frog left its burrow (after a no-till drill collapsed the burrow entrance) before we could capture it. In addition, 1 frog (frog 29) had her burrow burned over during the fall of 2009, but was unharmed. Similarly, during the spring burn of 2010, 2 frogs (frogs 3 and 7) had their burrows burned over but were not harmed. These prescribed grassland burns tend to burn hot but fast, and a crawfish frog in its burrow (crawfish frogs in burrows face the burrow entrance) seeking refuge from the

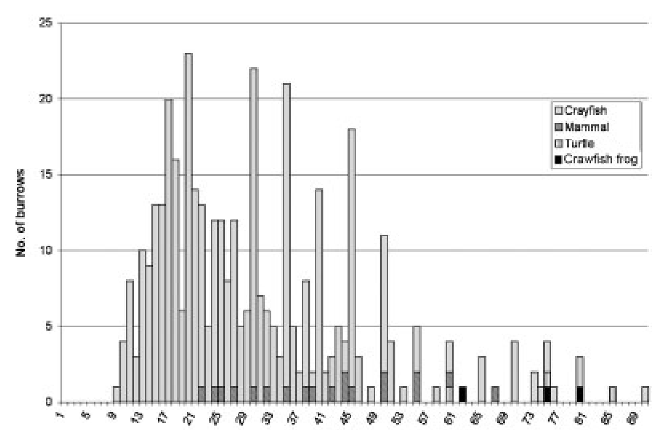

Figure 3. Histogram of entrance diameters of burrows measured following a prescribed burn on 19 September 2009 at Hillenbrand Fish and Wildlife Area-West in Indiana. We classified burrows either by who made them (crayfish, small mammals, and turtles) or who inhabited them (crawfish frogs). Crawfish frog burrows constituted a subset of the largest crayfish burrows.

heat of a fire likely backs down deeper into the burrow until it feels less discomfort. In extreme heat, frogs have the option of sitting in the water at the base of the burrow until the flame front passes.

Because of the small sample size ($n = 6$), we could not perform a meaningful spatial analysis on crawfish frog burrows similar to the analysis we performed on crayfish burrows. However, we noted that crawfish frogs did not occupy crayfish burrows in areas where burrows could be inundated, such as the middle of stream beds and the centers of seasonal or semipermanent wetlands.

Core Habitat

We calculated core habitat based on the straight-line distances from each primary burrow to the centroid of the respective breeding wetland. From these data, we calculated that a radius of 350 m from each wetland would encompass 53% of the total known crawfish frog burrows; a radius of 500 m would encompass 79% of known burrows; a radius of 750 m would encompass 94% of known burrows; and a radius of 1,020 m would encompass 100% of known burrows (Fig. 4).

DISCUSSION

We identified crawfish frog burrows by radiotracking post-breeding adults to burrows (34 animals; 7 other burrows were identified during the course of our fieldwork); an additional 22 animals were tracked but because of several factors (transmitters were removed, signals were lost, or animals were preyed upon) not all animals could be tracked to primary burrows. Lost signals are a common problem in telemetry studies (Madison et al. 2010) and might be due to transmitter failure or from predation by a mobile predator such as a hawk, owl, or coyote, which could easily grab a frog and carry it out of signal range. From among our total of 56 animals tracked, only 8 (14%) were lost due to signal failure. We made every attempt (multiple people with receivers) to find frogs whose signals went missing, and we do not generally feel that lost frogs with an active transmitter evaded us. During post-breeding migration periods we tracked frogs once a day and often more frequently during warm, wet conditions when frogs were most likely to move (Heemeyer 2011). Further, we quickly found that we could find lost frogs (signals) by moving away from the wetland on the same vector the frog had been previously using. The longer a frog migrated (i.e., the farther its burrow was from the breeding wetland), the more it was exposed to predators, and as time passed, the more likely it was to experience transmitter failure. This may have biased our results towards frogs using burrows closer to wetlands. If so, this bias must be put into context: we identified the primary burrows of 67% of our telemetered frogs and we drew our conclusions from this dataset.

Burrow Use

With one exception, a shallow scrape dug by a female on her way to a breeding pond, crawfish frogs in our study only occupied burrows in grassland habitats constructed by crayfish. Crayfish burrows have at least 2 advantages for crawfish frogs: they extend to the water table during years with normal rainfall amounts, and they extend below the frost line (Thompson 1915). All primary burrows were crayfish burrows. On average, crawfish frogs spent approximately 10.5 months of each year in primary burrows—throughout the summer, fall, and overwinter (from Apr or May through late-Feb or Mar)—the remaining time was spent breeding or migrating to and from breeding wetlands, when they often used secondary burrows.

The type of burrows inhabited by crawfish frogs has been equivocal. Thompson (1915:6; see also Wright and Wright 1949) writes: "Professor LaRue found the frogs in the mammal burrows along the shores of the ponds, as well as in crayfish holes, but it is probable that they were only temporarily occupying the former during the spawning season for we were unable to discover any mammal burrows, either nearby ponds or elsewhere, inhabited by frogs." If burrow types other than crayfish burrows are used, they are likely secondary burrows, when crawfish frogs are either migrating to and from breeding sites or exhibiting ranging forays (Heemeyer 2011). Although we have never observed crawfish frogs using mammal burrows as secondary burrows, on 1 occasion mentioned above, a frog dug a shallow scrape in an open area near a breeding wetland. We thought this unusual because crawfish frogs possess no morphological specializations for digging (Engbrecht et al. 2011). Observations of use of other burrow types (e.g., Goin and Netting 1940, Dundee and Rossman 1989, Parris and Redmer 2005, Collins et al. 2010) may have occurred during breeding migrations, when only temporary retreats were required and crawfish frogs had less access to crayfish burrows. Alternatively, our study site is

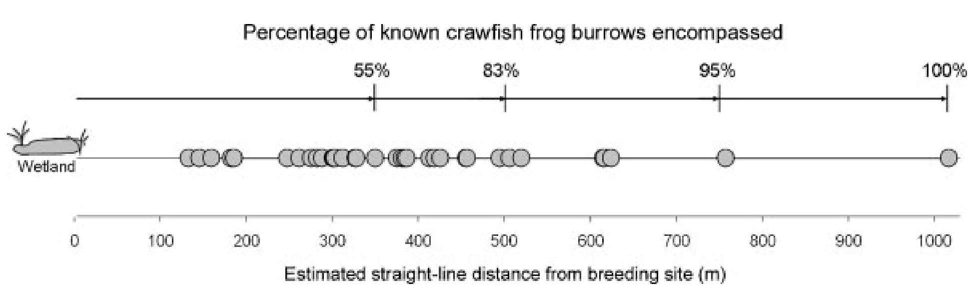

Figure 4. Distance from breeding wetland of all known crawfish frog primary burrows (gray circles) at Hillenbrand Fish and Wildlife Area-West in Indiana. A radius of 350 m from each wetland encompassed 55% of the known crawfish frog burrows, 500 m encompassed 83%, 750 m encompassed 95%, and 1,020 m encompassed all known burrows.

near the northern extreme of the current distribution of this species. Crawfish frogs in southern populations, where the frost line is negligible and the relative humidity is high, may not need the same protection from freezing and desiccation that northern populations require, and therefore might regularly use other burrow types as upland retreat sites.

Burrow Function and Crawfish Frog Survivorship

To avoid temperature extremes and dehydration, many terrestrial amphibians seek refuge during the day, and burrows offer excellent refugia (Cohen and Alford 1996, Schwarzkopf and Alford 1996, Seebacher and Alford 1999, 2002). Burrows provide access to a cool, moist environment and prevent excessive water loss from summer exposure (Schwarzkopf and Alford 1996, Rothermel and Luhring 2005, Rittenhouse et al. 2008). We saw crawfish frogs at their burrow entrance hourly through the hottest portion of the hottest days of the year (Hoffman et al. 2010), a behavior that might also allow them to clear infection (Kinney et al. 2011); the microclimate and proximity of their burrow allows them to escape the heat and hydrate as needed. Amphibians also commonly use refugia to avoid freezing temperatures (Costranzo and Lee 1994). Crayfish burrows buffered crawfish frogs from cold winter temperatures; frogs were an average of 5.4° C warmer than the air temperature (Fig. 2B).

Crayfish burrows also provide protection from predators. Crawfish frog burrows are oval shaped in cross section—similar to crawfish frogs—and they are only slightly larger bore than the frogs themselves. In their burrows, crawfish frogs face the burrow entrance (Hoffman et al. 2010). When frightened, crawfish frogs will lower their heads and inflate their bodies, much like toads (Smith 1961, Altig 1972). Inflating and lowering their heads while in a burrow allows crawfish frogs to wedge themselves against the burrow walls (Smith 1961, Heemeyer and Lannoo 2010) making them nearly impossible for us, or potential predators (snakes, raccoons, etc.), to pry out (Engbrecht and Heemeyer 2010). Crawfish frogs in crayfish burrows were 12 times less likely to be preyed upon than when migrating or ranging (Heemeyer 2011). At HFWA-W, over the 20 months of this study, we know of only 2 frogs that died while inhabiting burrows; 1 was eaten by a hog-nosed snake (Engbrecht and Heemeyer 2010), the other was winterkilled (Heemeyer and Lannoo 2011).

Crayfish burrows also provide crawfish frogs with protection from the direct effects of prairie fires. Three burrows inhabited by frogs implanted with transmitters were burned over, 1 in the fall of 2009 (frog 29), 2 in the spring of 2010 (frogs 3 and 7). These frogs survived without injury. However, reduced vegetative cover and increased exposure may have created indirect effects of burns. About 6 weeks after the 2009 fall burn, when the ground was still bare, coyotes attempted to dig frog 29 out of its burrow; the same night they tried to dig out an untelemetered crawfish frog in a nearby (60 m) burrow. We saw no other excavations in the burned areas—only crawfish frog burrows appeared targeted, and neither frog was harmed. However, frog 29 later died while migrating to her breeding wetland through the burned area. Despite these observations, the crawfish frogs in our study area did not appear to alter migration routes or burrow selection to avoid burned areas. Four frogs that migrated through burned areas in 2010 used the same routes and burrows that they used in 2009, when these routes were heavily vegetated (Heemeyer 2011).

Plowing of burrows, on the other hand, compromises crawfish frog survivorship. One crawfish frog in the 2009 south burn disappeared immediately after its burrow was destroyed by a no-till drill. Thompson (1915:7) writes: "... since more of the land is being cultivated and ... [crawfish] frogs are killed in comparatively large numbers each year by the plow." Crawfish frogs that are uninjured likely are able to extract themselves. Thompson (1915:5) writes: "Apparently when alarmed the frogs do not descend far into burrows, for they are plowed out in numbers and the ground in that region is only plowed to a depth of about 3 inches [7.5 cm]." Although we have not directly observed this (at the time of this study we brokered a no-new-plow policy with the land manager), Thompson's (1915) paper clearly shows that plowing either kills or displaces crawfish frogs. Although displacement would seem to be benign, almost a nuisance, adult crawfish frogs at our study site show fidelity to individual burrows—frogs we tracked throughout the study inhabited the same burrows for 3 consecutive seasons. Displacing these animals exposes them to environmental extremes and makes them vulnerable to predators, both factors can be expected to reduce their probability of survival.

Home Range Estimates

Millspaugh and Marzluff (2001:130) point out that home range is a concept, not an entity, and that an appropriate definition of home range is the "extent of area with a defined probability of occurrence of an animal during a specified time period." Based on the biology of crawfish frogs, one definition of home range includes the feeding platform and burrow entrance of the primary burrows that crawfish frogs inhabit for 8–11 months of the year. A second definition of home range could include ranging behaviors after crawfish frogs have established their primary burrows, although not all frogs exhibited ranging movements (Heemeyer 2011). A third definition for home range could include all frog movements, including time at their burrow, the distance to (and from; crawfish frogs primarily migrate in a straight line between the breeding wetland and the burrow) breeding wetlands, and breeding wetlands. Given the unusual biology of crawfish frogs, we feel that the 0.05 m^2 area of the primary burrow and feeding platform that an animal occupies most of the year is the best approximation of upland home range size.

We have considered that the most accurate, albeit unconventional, way to describe home range in crawfish frogs is to use burrow volume, and if so, our estimate of home range size is 0.01 m^3. When occupying burrows, crawfish frogs, and perhaps their sister species, gopher frogs (*L. capito*) and dusky gopher frogs (*L. sevosus*), which inhabit a variety of burrow types (Carr 1940, Richter et al. 2001, Jensen and Richter

2005, Richter and Jensen 2005, Blihovde 2006, Roznik et al. 2009) may be the only ranid frogs that move more in a vertical direction through soil layers than they do horizontally across the soil surface. Either way, using an area or a volume estimate, crawfish frog upland home ranges are minuscule, especially when compared to the unusually long distances these frogs will migrate to breed (Heemeyer 2011).

Burrow Distribution

Crawfish frogs are obligate crayfish burrow dwellers, and therefore crawfish frog burrow distribution is, by necessity, a subset of crayfish burrow distribution. In short, crayfish dig burrows and crawfish frogs inhabit a small subset of these. On our study site, crayfish burrows tended to be clustered in wetter areas (along wetland margins and temporary stream beds). We have evidence that crawfish frogs actively select from among available burrows. For example, we have never observed crawfish frogs inhabiting burrows in the lowest lying (wettest) crayfish burrows. We also know that a poor choice of burrows has consequences for survivorship. Winter burrow flooding followed by a hard freeze and thick ice formation will kill crawfish frogs (Heemeyer and Lannoo 2011).

When habitats for a species are created by the actions of another, we must determine if the rarity of the host is contributing to the rarity of the dependent species. We cannot definitively answer whether crayfish burrows limit population sizes in crawfish frogs with the information we have, but our data suggest that numbers of crayfish burrows per se are not limiting at HWFA-W. During the 2009 post-burn burrow survey, we assessed the occupancy of 12 burrows that appeared to be actively inhabited by crawfish frogs (exhibited large-bores, oval entrances, smooth sides, and what seemed to be a feeding platform) and we found only 3 frogs. The remaining burrows were uninhabited, suggesting that not all potentially suitable burrows were occupied. In fact, the landscape at HFWA-W appears to support a high density of crayfish burrows. We counted 381 crayfish burrows per 5.6 ha, (i.e., 1 crayfish burrow every 15 m^2). Of these crayfish burrows, 96 were at least 40 mm in diameter, large enough to accommodate an adult crawfish frog. Assuming the same burrow density (96 burrows/5.6 ha), we estimate HFWA-W (729 ha) has 12,393 potential crawfish frog burrows. Only 4 (of 96) burrows in the burned areas were inhabited by crawfish frogs. Assuming that this occupancy rate (4%) holds across our study site, crayfish burrows at HFWA-W offer capacity for 516 crawfish frogs. Both number of potential burrows (12,393) and number of potential burrows $\times$ occupancy rate (516) are several times greater than the 2 current crawfish frog population estimates at HFWA-W (164 confirmed adult frogs at HFWA-W, Kinney 2011; a range of 100–200, Engbrecht 2010). Although burrows may not be limiting, they may contribute to which site is used; increasing the number of burrows in an area might increase the probability that a frog would find a suitable burrow to occupy (Williams et al. 2012).

Core Habitat

The amount of time crawfish frogs spend in upland burrows, the survival advantages that burrows offer, and the fact that crawfish frogs will return to the same burrows across years, confirm that burrow habitat is a key ecological feature for this species. However, until recently, amphibian habitat use outside of breeding has not been emphasized (for exceptions see Semlitsch and Jensen 2001, Rittenhouse and Semlitsch 2007, Rittenhouse et al. 2009). From the perspective of breeding amphibians, wetlands cannot be considered in isolation from their surrounding habitat; when considering conservation of aquatic-breeding species the terrestrial habitat that surrounds them must be taken into account (e.g., Semlitsch 1998, Semlitsch 2006, Welsh 2011). Semlitsch and Bodie (2003) proposed a stratified wetland buffer system to protect the surrounding terrestrial habitat. This system of buffer classification involves levels of zones around the core wetland with the aquatic buffer being part of the core habitat that is the most protected, and the outside terrestrial buffer being the most available to human use (Semlitsch and Jensen 2001, Semlitsch and Bodie 2003). This method takes into account all species of amphibians that might use a wetland and allows for protection of the terrestrial habitat surrounding the wetland as well as space to prevent edge effects.

A buffer of 1,000 m, representing the core habitat, was recommended for the protection of dusky gopher frogs (Richter et al. 2001; although this has recently been interpreted as 350 m, United States Fish and Wildlife Service 2010). For crawfish frogs in the present study, the average straight-line distance of upland burrows from breeding wetlands was 370 m, with the longest straight-line distance being 1,020 m. Our data, therefore, suggest at least a 1.1-km radius of core habitat around each breeding crawfish frog wetland. In addition, we propose adding an additional 100 m, which would act as the outer terrestrial buffer, preventing edges from affecting the most distant burrows, making the total buffer 1,200 m.

MANAGEMENT IMPLICATIONS

These data show that crawfish frogs inhabit a pinpoint spot (0.05 m^2; 0.01 m^3) on the landscape—composed of a crayfish burrow and a feeding platform—for most of the year. With one exception, crawfish frogs at our study site were obligate crayfish burrow dwellers, and are therefore the only North American amphibian that relies exclusively on another species group for its upland habitat. Crayfish burrows provide hydration, thermal buffering, protection from predators, and access to food. Following breeding, crawfish frogs return to burrows, and to do so will undertake migrations of >1 km. Our data suggest establishing a total buffer with a 1.2-km radius of core habitat around each crawfish frog breeding wetland. This core area must provide at least 3 critical habitat elements: 1) extensive grasslands maintained by prescribed burning and/or logging; 2) an adequate number of large upland crayfish burrows; and 3) no soil disturbance of the sort that would destroy crayfish burrow entrances.

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