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Habitat Selection by Crawfish Frogs (*Lithobates areolatus*) in a Large Mixed Grassland/Forest Habitat

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Abstract.—**Our objective was to examine breeding dispersal, burrow-use characteristics, and burrow habitat selection by Crawfish Frogs (*Lithobates areolatus*) in two distinct vegetation types (open grasslands and a mosaic of forest and transitioning grasslands) in southeastern Indiana, from March to August 2009 and 2010. We captured 14 frogs at their breeding ponds and tracked them to their burrows using radio telemetry. Once we identified their burrows, we compared habitat metrics at the burrows to random locations. We used an information-theoretic model selection approach to approximate the parsimony of logistic regression models comparing the habitat features of burrows to random, available sites. Frogs dispersed a straight-line average distance of 215 m and used an average of four burrows. They generally did not change burrows after June. Our top model included covariates for the number of burrows, canopy cover, and a site covariate. Our results suggested that habitat selection by Crawfish Frogs occurred hierarchically; in mixed grassland/forest habitats, they first selected areas with low canopy cover, and then selected areas with many available burrows. To manage habitat for Crawfish Frogs, we recommend preventing woody encroachment and reducing canopy cover in grassland areas occupied by Crawfish Frogs. Additionally, areas with a large number of burrows appear to provide the most suitable Crawfish Frog habitat.**

Crawfish Frogs (*Lithobates areolatus*) are solitary, secretive animals that use crayfish burrows as retreat sites (Thompson, 1915; Smith, 1950; Hoffman et al., 2010; Heemeyer et al., 2012). Their range includes portions of the Midwest, eastern Great Plains, and south–central United States (Parris and Redmer, 2005). Crawfish Frogs generally breed from March to April in ephemeral, temporary, and seasonal wetlands usually in open, damp grasslands but occasionally in wooded habitat (Busby and Brecheisen, 1997; Minton, 2001; Engbrecht, 2010). They have experienced substantial population declines (Hammerson and Parris, 2004; Parris and Redmer, 2005) and are listed as state endangered in Iowa (possibly extirpated from the state; Christiansen and Bailey, 1991) and Indiana (Minton, 2001). Reasons for their decline have been attributed to direct or indirect consequences from loss or alteration of their primary grassland habitat (Thompson, 1915; Wright and Wright, 1949; Busby and Brecheisen, 1997; Parris and Redmer, 2005). In places where remnant habitat patches exist, Crawfish Frogs appear to remain locally common (Busby and Brecheisen, 1997; Hammerson and Parris, 2004; Kinney, 2011; Williams et al., 2012). Crawfish Frog habitat is described as open, relatively flat, and grassy, including tall-grass prairie and degraded grasslands, with a large number of crayfish burrows (Thompson, 1915; Bragg, 1953; Johnson, 2000; Heemeyer et al., 2012). Additionally, the eastern extent of Crawfish Frog's range includes the prairie–forest transition zone with grasslands integrated with forests and breeding ponds sometimes located wholly or partly in forested areas (Minton, 2001).

Prior to 2009, no study had examined Crawfish Frog habitat selection using radio telemetry. From 2009 to 2011, two radiotelemetry studies were conducted: one in southwestern Indiana (Heemeyer et al., 2012), and this study. Heemeyer et al. (2012), working extensively in grasslands, documented Crawfish Frog migration patterns, burrow-use characteristics, and habitat selection. Heemeyer et al. (2012) found that frogs traveled up to 1,020 m from breeding wetlands to their primary burrows (primary burrows were defined as burrows used for most of the year). Additionally, frogs used up to 10 burrows during migration from breeding ponds or during ranging (i.e., localized movements), but they used only one burrow (i.e., their primary burrow) for a period >2 weeks (Heemeyer et al., 2012). Crawfish Frogs had a high degree of site fidelity between years; six of seven frogs tracked for consecutive seasons returned to the same primary burrow each year (Heemeyer et al., 2012). All burrows used by frogs were located in grasslands. Heemeyer et al. (2012) examined a suite of habitat characteristics (i.e., vegetation height, percent cover by forbes, percent cover by grass, percent bare ground, vegetation weight, and woody debris) at burrow sites and random sites. She found that frogs did not select burrows with significantly different characteristics from random sites.

Heemeyer et al.'s (2012) study was located in relatively homogeneous habitat (i.e., mostly grasslands). Extensive grasslands are rare east of the Mississippi River and are considered a critically endangered ecosystem (Noss et al., 1995). A serious threat to grasslands is the increase and expansion of invasive woody vegetation (Bragg and Hulbert, 1976; Briggs et al., 2002, 2005; Heisler et al., 2003). Because of woody expansion, most former tall-grass prairies are characterized more accurately as either savanna grasslands or mixed shrub and woodland (Briggs et al., 2005). To date, no study has examined Crawfish Frog habitat selection in a large mixed grassland/forested habitat, and their habitat associations in transitioning grasslands are unknown. Thus, we examined Crawfish Frog habitat selection in two distinct vegetation types in southeastern Indiana. The first was grassland, and the second was a mosaic of transitional old fields and early successional forests and pole-sized deciduous forest (hereafter the successional site). Our main objectives were to (1) estimate post-breeding dispersal distance, (2) examine the temporal characteristics of burrow use, (3) compare frogs most-used (primary) burrows to other (secondary) burrows used during migration and ranging, and (4) estimate habitat variables at burrows used by frogs, when compared to habitat variables at other, available burrows and to

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examine whether these characteristics were different between the two vegetation types.

MATERIALS AND METHODS

Study Area.—We conducted our study at Big Oaks National Wildlife Refuge (BONWR; 208 km^2) located in Jefferson, Jennings, and Ripley Counties in southeastern Indiana. The easternmost known population of Crawfish Frogs is located at BONWR. The next closest confirmed population was located 90 km to the west (Monroe County, IN); however, this population is suspected to be extirpated (Engbrecht and Lannoo, 2010). BONWR has what is likely the largest assemblage of Crawfish Frog breeding sites of any contiguous managed area in Indiana (see Engbrecht and Lannoo, 2010) containing >26 confirmed breeding ponds. Prior to United States Fish and Wildlife Service (USFWS) assuming management of BONWR, it was the site of the United States Army (U.S. Army), Jefferson Proving Ground, which was used to test military ordnance from 1941 to 1995. Jefferson Proving Ground was subject to approximately 25 million rounds of ordnance, which resulted in bomb craters that created a mosaic of ephemeral, temporary, and seasonal wetlands many of which Crawfish Frogs use for breeding. During their tenure, the U.S. Army managed grasslands using prescribed fire, disking, mowing, and persistent herbicides (e.g., bromacil). Because of hazards associated with unexploded ordnance, the USFWS were unable to use mechanized management techniques (e.g., disking, mowing), which has resulted in the loss of grassland habitat attributable to woody vegetation encroachment.

We captured frogs from five different breeding ponds: three ponds at the north end of the refuge, and two at the south end. The north and south ends are approximately 18 km apart. We selected the five ponds from 26 confirmed Crawfish Frog breeding ponds at BONWR because they were in areas with relatively few unexploded ordnance. Four of these breeding ponds were in grassland areas, and one was in a heavily forested area that contained nearby patches of early successional forest (i.e., the successional site). The patches of early successional forests were formerly grasslands, but since the exclusion of mechanized management tools in 1995, they are becoming reforested. The grassland sites represent typical Crawfish Frog habitat (Bragg, 1953; Johnson, 2000; Minton, 2001; Heemeyer et al., 2012). The vegetation at the grassland sites is dominated by broom sedge (*Andropogon virginicus*) and steeplebush (*Spiraea tomentosa*) and to a lesser extent spike-rush (*Eleocharis tenuis*), early goldenrod (*Solidago juncea*), beardtongue (*Penstemon digitalis*), narrow-leaved mountain mint (*Pycnanthemum tenuifolium*), boneset (*Eupatorium perfoliatum*), and round-leaved boneset (*Eupatorium rotundifolium*). The successional site represents what we believe to be degraded habitat attributable to the exclusion of disturbances other than fire. The early successional patches within the successional site include some remnant grassland species similar to the grassland sites but is further characterized by woody encroachment of oak (*Quercus* spp.), black locust (*Robinia pseudoacacia*), sweet gum (*Liquidambar styraciflua*), winged sumac (*Rhus copallina*), persimmon (*Diospyros virginania*), and red maple (*Acer rubrum*). The forested area of the successional site is typical of eastern deciduous beech-maple forests (Braun, 1950). The climate at BONWR is warm, with humid summers and cold winters. Annual precipitation was 69.7 cm in 2009 and 98.9 cm in 2010. The soil types at both the grassland and successional sites are characterized as poorly drained clay.

The primary burrowing crayfish species at BONWR are *Cambarus polychromatus* and *Cambarus diogenes*. These species are common across Indiana and appear to be habitat generalists that occupy any area where the water table is near the surface (Grow and Merchant, 1980; Pflieger, 1996; R. F. Thoma and B. J. Armitage, Burrowing Crayfish of Indiana, Final Report submitted to Indiana Department of Natural Resources, 2008), although little is known about their habitat preferences. The burrow structure for these species consists of a vertical channel that runs below groundwater and usually ends in a chamber at the bottom (Grow and Merchant, 1980, and references therein). The burrows generally have several openings at the surface, of which, a portion lacks water (Grow and Merchant, 1980; R. F. Thoma and B. J. Armitage, Burrowing Crayfish of Indiana, Final Report submitted to Indiana Department of Natural Resources, 2008).

We captured frogs at the five breeding ponds in March 2009 and 2010 using minnow traps and dip nets. After we captured them, we attached a VHF radio transmitter with an internal antenna (3.8 g, model PD-2T [expected battery life = 6 months], Holohil Systems Ltd., Carp, Ontario, Canada) using either a belt harness made of 2.5-mm plastic beads (model 2130–1008, Connecticut Laminating Company, New Haven, CT), or surgically implanting the radio into the intraperitoneal cavity of the frog. Surgical implantation followed the methods described by Heemeyer et al. (2012), and the references therein. Briefly, this consisted of first anesthetizing the frogs using tricaine methanesulfonate and then creating an incision in the abdominal skin and anterior abdominal wall muscles and inserting the transmitter. We sutured the frog's incision and let the frog recover overnight. We released frogs the following day at the ponds where we captured them. We tracked frogs by homing to their location using a three-element Yaggi antenna and an R-1000 handheld receiver (Communication Specialists Inc., Orange, CA). We tracked frogs daily from March to July and biweekly from July until the radio transmitters failed. Crawfish Frogs at our study area generally used multiple burrows. Heemeyer et al. (2012) categorized these as primary burrows (burrows that frogs occupied most of the year) and secondary burrows (burrows used during migration and ranging and for a period <2 weeks). Because burrow selection by individual frogs was not independent, and because some secondary burrows were used for only a brief period (e.g., 1 day), we only included the most used, primary burrow in our analysis of use versus availability. We examined habitat selection by comparing used resources (area around the primary burrows) to available (random) locations (sampling protocol A, Manly et al., 2002). To select our random locations, we calculated the maximum dispersal distance by Crawfish Frogs from their breeding ponds (447 m). We then used a geographical information system to create a circular buffer around each breeding pond with a radius equal to 447 m. We selected our available locations randomly within the circle for each breeding pond. Available locations had to have at least one burrow that a frog could potentially occupy for us to consider it in the analysis. Heemeyer et al. (2012) noted that Crawfish Frogs used burrows made by crayfish exclusively for their primary burrows, but they might use other types of burrows or habitat features for secondary burrows (see Thompson, 1915; Goin and Netting, 1940; Smith, 1950; Engbrecht et al., 2011). At our study area, variation of burrow structure made burrow classification

TABLE 1. Model selection results for models comparing Crawfish Frog (*Lithobates areolatus*) burrowing locations to random locations in southeastern Indiana, 2009–10, based on likelihood estimation ($N = 14$).

Model	Covariates	K[a]	AIC$_c$[b]	ΔAIC$_c$[c]	a priori $\omega^{d,e}$	a posteriori $\omega^{e,f}$
13[g]	Burrows + canopy cover × site	4	55.73	0.00	–	0.51
2	Burrows	2	56.66	0.93	0.66	0.32
3	Canopy cover	2	58.09	2.36	0.32	0.16
7	Site × burrows	3	66.01	10.28	0.01	0.00
5	Shrub cover	2	67.86	12.13	0.00	0.00
8	Site × canopy cover	3	68.61	12.88	0.00	0.00
1	Null	1	68.87	13.14	0.00	0.00
9	Site × vegetation mass	3	70.37	14.64	0.00	0.00
10	Site × shrub cover	3	70.55	14.82	0.00	0.00
6	Stem density	2	70.93	15.20	0.00	0.00
4	Vegetation mass	2	71.07	15.34	0.00	0.00
11	Site × stem density	3	71.13	15.40	0.00	0.00
12	Burrows + canopy cover + vegetation mass + shrub cover + stem density	6	71.69	15.96	0.00	0.00

[a] Number of parameters.
[b] Akaike's Information Criterion for small samples.
[c] Difference in AIC$_c$ between current model and best model.
[d] ω = AIC$_c$ weight; a priori ω was calculated before including model 13.
[e] Results of ω do not sum to 1 because of rounding error.
[f] A posteriori ω was calculated after including model 13.
[g] We developed model 13 during a posteriori analysis based on our a priori model results.

TABLE 2. Generalized linear mixed-effects model-selection results for models comparing the primary (most used) burrow by Crawfish Frogs (*Lithobates areolatus*) to secondary burrows at Big Oaks National Wildlife Refuge, southeastern Indiana, 2009–10. The intercept was allowed to vary for each frog ($N = 33$, groups $= 14$).

Model	Covariates	AIC$_c$[a]	ΔAICc$_c$[b]	$\omega^{c,d}$
3	Canopy cover	44.89	0.00	0.50
8	Site × canopy cover	47.58	2.70	0.13
1	Null	48.20	3.31	0.10
4	Vegetation mass	49.61	4.73	0.05
7	Site × burrows	50.03	5.14	0.04
11	Site × stem density	50.20	5.31	0.04
5	Shrub cover	50.29	5.41	0.03
9	Site × vegetation mass	50.54	5.65	0.03
2	Burrows	50.60	5.71	0.03
6	Stem density	50.60	5.72	0.03
10	Site × shrub cover	50.62	5.74	0.03
12	Burrows + canopy cover + vegetation mass + shrub cover + stem density	58.28	13.40	0.00

[a] Akaike's Information Criterion for small samples.
[b] Difference in AIC$_c$ between current model and best model.
[c] ω = AIC$_c$ weight.
[d] Sum >1 because of rounding error.

difficult, and we were unable to correctly classify what animals created each burrow. Therefore, we considered burrows as potential Crawfish Frog burrows if the diameter was larger than 2.4 cm (the smallest burrow-entrance size in which we observed a Crawfish Frog) and was at least 10 cm deep (the average snout–vent length of Crawfish Frogs captured at BONWR).

At used sites and available sites, we collected information on habitat features we believed contributed to habitat selection. These were canopy cover, vegetation mass, woody stem density, burrow density, and shrub cover. We estimated canopy cover using a densiometer. We estimated shrub cover using an ocular estimate. We estimated vegetation mass using the methods described by Robel et al. (1970; vegetation mass = −6.2 + 117.2 × Robel height). Finally, we estimated woody-stem density and burrow density by counting the number of woody stems and burrows in a 5-m radius circle around the location. Because burrows were often difficult to detect, we assessed each observer's ability to detect burrows by having each observer count burrows in 20 plots of the same size and shape as our sample plots. At these plots, the number of burrows was known (through extensive surveys within 24 h after the trial period); therefore, we calculated a detection rate for each observer. We included our detection rate in our final estimates of the number of burrows in a plot.

We compared used sites to available sites to assess whether frogs selected certain resources disproportionately to what was available. We examined the correlation between our habitat metrics (i.e., canopy cover, vegetation weight, woody stem density, burrow density, shrub cover) and burrow selection using a model selection approach. We did this by developing a suite of models a priori to analysis. We included a no-effects (null) model (Table 1, model 1). We also included a model with the number of burrows in the 5-m radius plot as a covariate because we hypothesized that burrow selection was highly dependent on the availability of burrows for the frogs to occupy (model 2). We hypothesized that frogs would select areas with minimal canopy cover because Crawfish Frogs are considered a grassland species and do not occupy burrows in forested areas (model 3; Busby and Brecheisen, 1997; Minton, 2001; Heemeyer et al., 2012). We thought that areas with greater grass vegetation mass would be desirable to frogs because they provided more cover and, therefore, included a vegetation mass covariate (model 4). We hypothesized that frogs would avoid woody succession and select areas with little shrub cover and, therefore, included a model with a shrub covariate (model 5). Similarly, we thought woody stem density would be inversely correlated with burrow selection (model 6). Because of the drastic difference in vegetation at grassland sites and the successional site, we included models with the covariates in models 2 to 6 with a covariate for site (grassland sites = 1, successional site = 0; models 7–11). Finally, we included a global model that was a composite of all of our vegetation covariates (model 12).

We analyzed the model suite using generalized linear models with a binomial response variable using the STATS package in Program R (R Version 2.12.2, www.r-project.org, accessed 24 March 2011). We approximated the parsimony of each of our models using Akaike's Information Criterion for small samples (AIC$_c$). We considered the models with the lowest AIC$_c$ value as our most-parsimonious models. We evaluated each model's likelihood using model weights (ω, Table 1; Burnham and Anderson, 2002). If our a priori analysis suggested any additional model, we examined it a posteriori. We estimated the resource selection function (RSF) from our top model using the exponential function of the parameter estimates (i.e., RSF = $\exp(\beta_1 X_1 + \ldots \beta_p X_p)$. Finally, we assessed the goodness-of-fit of the final top model by calculating the area under the receiver operating characteristic (ROC) curve using the pROC package in Program R.

We also examined whether the primary burrow was different from secondary burrows that frogs used. We compared them using a generalized linear mixed-effects regression model with the LME4 package for Program R. To account for nonindependence in burrow selection by frogs, we considered frogs as a

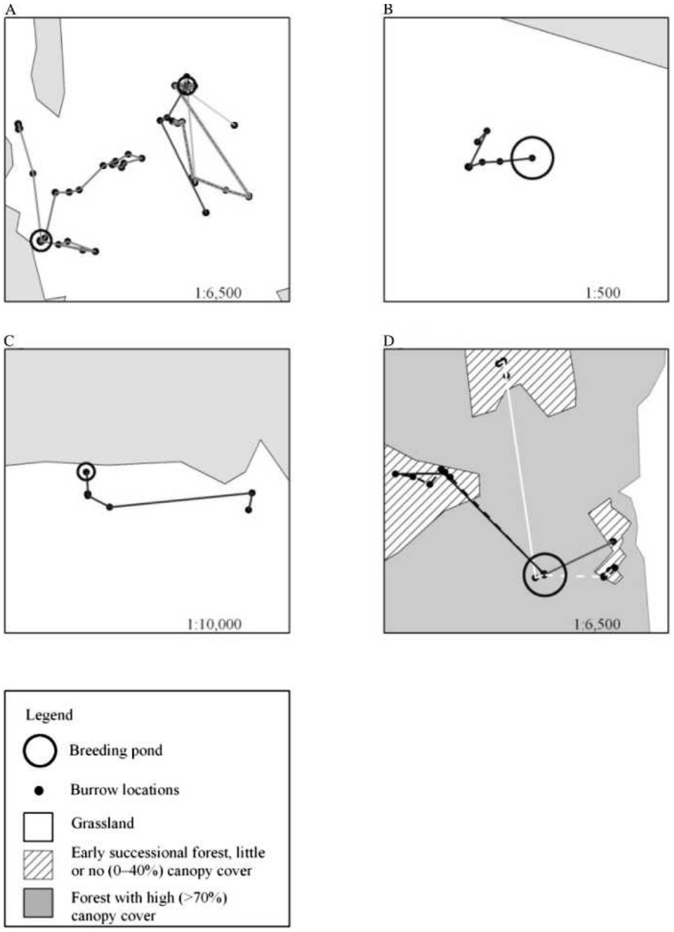

FIG. 1. Breeding pond locations, burrow locations, and straight-line paths between consecutively used burrows by Crawfish Frogs at Big Oaks National Wildlife Refuge in southeastern Indiana, from 2009–10. (A and B) are located at the north end of the refuge; seven frogs were captured from two breeding ponds in (A), and one frog was captured from one breeding pond in (B). (C and D) are at the south end of the refuge. One frog was captured from one breeding pond in (C). Three frogs were captured at the breeding pond in (D). Two of these frogs were monitored for two years ($N = 5$); the same frogs are indicated with the same color (black and white); the hashed lines indicate their second year of monitoring (i.e., 2010). Note that we used differing scales in (A–D) to improve detail.

random variable using a random-intercept model. We compared the same habitat covariates that we used for comparing used sites to available sites (canopy cover, vegetation weight, woody stem density, burrow density, and shrub cover; Table 2). We approximated the parsimony using AIC_c and examined model weights, ω.

RESULTS

We radio-marked five frogs in 2009 (3 M, 2F). Two were at grassland sites and three were at the successional site. We radio-marked seven new frogs in 2010 (3M, 4F), and two frogs that were also marked in 2009. The seven new frogs were at grassland sites, and the two frogs from 2009 were at the successional site. We treated the frogs monitored for two consecutive years at the successional site as separate samples between years. Therefore, our sample size was nine frogs at grassland sites and five frogs at the successional site (total $N = 14$). We collected 557 locations on our 14 samples (mean = 40, range = 17–67). The tracking period averaged 112 days (range = 27–292 days). Frogs dispersed a straight-line mean distance of 215 m and relocated to different burrows between 1 and 11 times (mean = 4). The dispersal direction appeared to be random, with the exception that frogs never entered forests if they bred in grasslands, even when forests were immediately adjacent to the breeding pond (Fig. 1). The five frogs at the successional site entered the forest to breed and then subsequently returned to areas with little (<40 %) canopy cover to occupy a burrow (Fig. 1D).

Temporal use of burrows varied among frogs. Three frogs did not switch burrows after they occupied their first burrow, 10 frogs used many burrows ($\bar{x} = 4$) before 31 June but did not move after that time, and one frog changed burrows as late as 30 October 2009 during unseasonably warm temperatures (26°C). This frog stayed at its new burrow from 30 October 2009 until 2 March 2010, before returning to its original (pre–30 October 2009) burrow, two weeks before it migrated to its breeding pond. The average time at each burrow was 11 days until 31 June. After 31 June, frogs appeared to remain in the same burrow for a much longer period ($\bar{x} = 42$ days). However our sample size after 31 June was limited ($N = 5$) because of radio failures. Further, our estimates of the length of time a frog used a burrow after June was likely biased toward shorter occupancy periods because four of five transmitters failed while the frogs were still at their burrows. The most-used burrows for seven frogs were burrows that they occupied early in the year, vacated, and then returned there.

BONWR staff burned the successional site on 21 March 2010. After the burn, the two frogs we monitored for both years of the study migrated from their burrows toward their breeding pond. They were at the breeding pond for four and six days. When they left the breeding pond, one frog went in a different direction when compared to its movement in 2009 (north in 2009, east in 2010; Fig. 1D, white lines), and one frog went in the same direction as its 2009 dispersal but stopped short of its previous burrow; both frogs stopped within 15 cm of the burned area. Neither frog entered the burned area until 29 April 2010.

We collected data on our habitat metrics at 14 frog burrows (one for each frog) and 49 random locations. Based on our a priori analysis, burrow selection was most correlated with the number of burrows available (Table 1, model 2, $N=14$). The top model was 1.43 AIC_c units better than the next top model and had 66% of the a priori Akaike weight (ω, Table 1). Thus, the number of burrows appeared to be highly correlated with burrow use. There was an average of 3.2 burrows per m^2 (range = 1–7 burrows per m^2) at used sites, and 1.6 burrows per m^2 (range = 1–5 burrows per m^2) at available sites (combined mean = 2.3 burrows per m^2). Areas with high canopy cover contained fewer burrows than grasslands, on average (1.6 burrows per m^2, 2.2 burrows per m^2, respectively). The model that contained canopy cover was also a competitive model (i.e., <2 $\Delta\mathrm{AIC}_c$ units from the top model; model 3). Because the number of burrows and canopy cover were competing models, and because of the difference in canopy cover at grassland and successional sites, we examined an additional model containing a covariate for the number of burrows, and a canopy cover × site interaction, a posteriori (Table 1, model 13). We approximated the parsimony of this model using the same methods described for our a priori model suite. We recalculated the AIC_c weights (ω) after we included this model (Table 1). Our a posteriori model had the lowest AIC_c value, indicating it was the most parsimonious

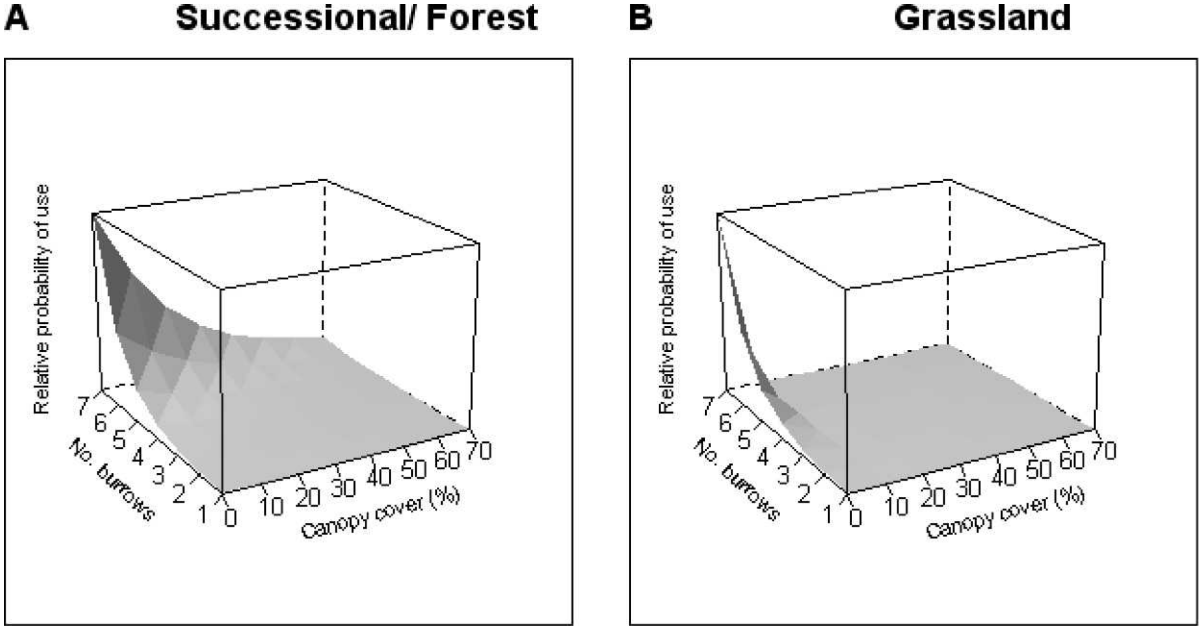

FIG. 2. Graphical display of the resource selection function (RSF) estimates of the relative probability of use by Crawfish Frogs in relation to canopy cover and the number of burrows available at Big Oaks National Wildlife Refuge in southeastern Indiana, 2009–10. We estimated the resource selection function (RSF) using exponentiation of the parameter estimates of the most parsimonious model for our data (RSF = exp($\beta_1$successional canopy cover + $\beta_2$grassland canopy cover + $\beta_3$burrows)). (A) is the estimated RSF for a predominately forested site with patches of early successional vegetation, and (B) is the estimated RSF for grassland sites.

(Table 1). It had 51% of the a posteriori AIC_c weight (Table 1). Thus, we retained this model as our top model to make inferences. Based on these results, Crawfish Frogs in our study area appeared to select habitat based on canopy cover, and the number of burrows, with the effect of canopy cover differing by whether it was at the successional site or not. The parameter estimates for this top model were number of burrows = 0.87 (SE = 0.30), canopy cover (successional site) = −0.043 (SE = 0.024), and canopy cover (grassland site) = −1.49 (SE = 2.29). Thus, the relative probability that a frog used a location increased with the number of burrows available and decreased with canopy cover, especially in grassland habitat (Fig. 2). Our top model fit the data well; the area under the ROC curve was 0.89.

The top model explaining the differences between primary burrows and secondary burrows was the one that included the canopy cover covariate (Table 2, model 3). The primary burrows had less canopy cover ($\bar{x}$ = 2.5%, SE = 1.6%) than secondary burrows ($\bar{x}$ = 8.5%, SE = 3.9%). This model had 50% of the AIC_c weight, and there were no competing models. Therefore, we retained this model to make inference.

DISCUSSION

The temporal characteristics of burrow use varied among frogs. On average, they switched burrows every 11 days early in the summer but were more sedentary later in the year (only one frog moved after June). Why frogs changed burrows was unclear but could be a result of food availability, the amount of canopy cover, access to the water table or variation in the water table, other co-inhabitants of the burrow (e.g., crayfish, snakes; Hoffman et al., 2010; Heemeyer et al., 2012), or fidelity to another burrow (Heemeyer et al., 2012). Our results (frogs used between 1 and 11 burrows) were the same as results for Crawfish Frogs in southwestern Indiana (Heemeyer et al., 2012). At both our study area and in southwestern Indiana, the rate of relocation was higher between March and June than from July to winter. On average, secondary burrows contained more canopy cover than primary burrows. This suggested that frogs preferred primary burrows in areas with less canopy cover.

Heemeyer et al. (2012) monitored the breeding movements of seven individual Crawfish Frogs for two consecutive years. She found that they had a high degree of site fidelity (six of seven frogs returned to their burrows from the previous year) and hypothesized that frogs generally had one primary burrow they return to each year but used up to 10 other secondary burrows, each for a period less than two weeks. Our results are consistent with the hypothesis of a primary burrow but also show that frogs can switch burrows late in the year; one frog switched on 30 October. Additionally, one frog we monitored for two years went in different directions each year after breeding and used different primary burrows. Thus, it is possible for adult Crawfish Frogs to colonize new areas after they establish their initial burrows, although it is likely a small proportion of the population (only one of the combined nine samples monitored for two years from this study and Heemeyer et al. [2012] exhibited this behavior).

At our study area, six frogs occupied more than one burrow for longer than two weeks; four frogs occupied two different burrows for ≥2 weeks; and two frogs occupied three different burrows for ≥2 weeks. Two weeks was the maximum time frogs used secondary burrows at Heemeyer et al.'s (2012) study area. Thus, although frogs in our study area did appear to have a most-used primary burrow, they also used secondary burrows more extensively than in Heemeyer et al. (2012). Reasons for differences in secondary burrow use between Heemeyer et al. (2012) and this study may be attributable to weather, other co-inhabitants of the burrows, or differences in habitat including vegetation or burrow availability. Burrow availability at our study area (2.3 burrows per m^2) was 38 times larger than at the Heemeyer site (2011; 0.06 burrows per m^2), and the large number of burrows might provide more suitable secondary burrows.

Frogs in our study appeared to avoid recently burned areas when returning to their burrows. They selected burrows within 15 cm of a burn line. After 54 days, on average, frogs then entered burned areas. This movement coincided with regrowth of vegetation at the burned sites. However, our sample size in burned areas was low, and we cannot conclude whether frogs avoided burned areas or did not enter them for other reasons (e.g., areas that burned were not conducive to frog use because they were dry). Heemeyer et al. (2012) noted that four Crawfish Frogs traveled through burned areas when traveling to their burrows.

Johnson (1980:66) defined resource selection as “the process in which an animal actually chooses [a] component” of the environment. We examined two habitat types at BONWR. Four of five sites were in grasslands with few trees and little canopy cover, which was typical of the habitat occupied by Crawfish Frogs across their range. By comparison, the fifth site was atypical of what is generally characterized as Crawfish Frog habitat; the breeding pond was located in a heavily forested area, with small pockets of early successional forest distributed around it and likely represented degraded habitat. Although the heterogeneous habitat at our successional site was not optimal, it provided a framework to examine habitat selection. The frogs in our study selected similar habitat features between the two vegetation types: areas with low canopy and areas that had a large numbers of burrows. The grassland sites offered more of this habitat, both more burrows and more area with no canopy. In addition, although frogs bred in the heavily forested area of the successional site, they avoided areas with high canopy cover for burrow use, but selected areas with low canopy cover instead.

Our results were consistent with hierarchical habitat selection theory (Johnson, 1980). That is, frogs appeared to select areas within the study area that had low canopy cover and then, at a finer scale (third-order selection, Johnson, 1980), selected their burrows based on the habitat characteristics of the site (i.e., burrow availability). Third-order selection was most closely associated with the number of burrows available. It was not strongly associated with other vegetation characteristics, except canopy cover, which occurs at a larger scale. Thus, third-order selection might have been simply a result of a frog finding a suitable burrow, given it was in an area with low canopy cover. Although burrows at our site and other Crawfish Frog sites (see Heemeyer et al., 2012) probably were not limiting, more burrows likely increased the probability that a frog found a suitable burrow and, thus, used a site.

Roznik and Johnson (2009) found similar habitat-selection results for the closely related Gopher Frog (*Lithobates capito*). In their study, juvenile Gopher Frogs dispersed in random directions but ultimately selected areas characterized as fire-maintained, with open canopy cover, and few hardwood trees (Roznik and Johnson, 2009). Roznik et al. (2009) found similar habitat associations for adult Gopher Frogs. Heemeyer (2011) noted that Crawfish Frogs never inhabited burrows in thick forest. Why Crawfish Frogs and Gopher Frogs select areas with little canopy cover is unknown. Possible explanations include differing amounts of critical resources such as burrows (as was the case at our study area), prey availability, sun exposure, or stability of the water table.

Prior to 1995, the early successional forests that frogs used at the successional site were grasslands. Despite efforts to prevent woody encroachment using prescribed fire, the area has changed rapidly, likely because of the exclusion of other disturbances (e.g., mowing or disking). At this site, one of our radio-marked frogs was ≥7 years old (i.e., we captured him breeding in 2004 and recaptured him in 2010). Given their potentially long lives, and the fast rate of growth of some early successional tree species, it is possible that the habitat changed during the lifespan of the frogs (i.e., when the frogs selected the area it was a grassland but has since changed to early successional forest). The change in habitat at this site has corresponded with a perceived (albeit, anecdotal) population decline of Crawfish Frogs based on uneven survey effort across years (13 were captured in 2003, and only two were captured in 2010). If Crawfish Frogs rely on grassland with little canopy cover, then the vegetation at the south site is becoming less suitable as the remaining pockets with low canopy cover continues to mature. This may be affecting Crawfish Frog adult survival or recruitment. Although we did not investigate population declines and their association with grassland loss, Crawfish Frog selection of areas with limited canopy cover suggests that preventing woody encroachment in grasslands would be beneficial to Crawfish Frog conservation. This study suggests that the current widespread loss of grasslands to woody plant encroachment may be having a negative effect on Crawfish Frog populations because it limits the presence of preferred habitat features.

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