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Wildlife Cameras Reveal High Resolution Activity Patterns in Threatened Crawfish Frogs (*Lithobates areolatus*)

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***Abstract*.—Crawfish Frogs (*Lithobates areolatus*) are obligate crayfish burrow dwellers with small home ranges (0.05 m^2) and strong philopatry. Using wildlife cameras, we monitored the behavior of adults and juveniles at a high-resolution time scale (down to 5-min intervals) around-the-clock and across years, from 2009–2013 at Hillenbrand Fish and Wildlife Area-West in Greene County, Indiana, USA. We found that Crawfish Frogs demonstrated a consistent pattern of seasonal activity. Peaks of highest activity occurred in May and September when frogs were active around-the-clock (circumdiel). Early spring and late fall lulls were due to frogs being predominately diurnal; the summer plateau was due to frogs being predominately nocturnal. Individual frogs were strictly diurnal or strictly nocturnal depending on the season. We assessed the activity of these frogs in relation to environmental variables, including ambient temperature, vapor pressure gradient between the atmosphere and frog skin (a measure of evaporative water loss in frogs), and precipitation. Activity was best explained by daily temperature and vapor pressure gradient. Our results suggest that Crawfish Frogs will alter their activity patterns in response to changing environmental conditions, such as temperature and vapor pressure gradient. Although we examined changes across seasons, this behavioral plasticity may also provide them with resilience to changes associated with climate change.**

*Key Words.—*circumdiel; Crawfish Frogs; diurnal; *Lithobates areolatus*; nocturnal

Introduction

Crawfish Frogs (*Lithobates areolatus*) are obligate crayfish burrow dwellers whose historic range included the grasslands and savannas of the southeastern Great Plains and Mississippi Delta regions, USA (Parris and Redmer 2005). In many regions where Crawfish Frogs were once common, habitat loss and disease have caused declines (Engbrecht et al. 2013). As a result, Crawfish Frogs are a species of conservation concern in every state where they are found. Crawfish Frogs are listed as Endangered in Indiana and Iowa, and as a Species with Greatest Conservation Need in Illinois, Missouri, Kansas, Texas, Arkansas, Mississippi, Kentucky, Tennessee, and Oklahoma (Engbrecht and Lannoo 2010; Association of Fish and Wildlife Agencies. 2014. State Wildlife Action Plans: A Strategic Approach to Conservation. Available from http://www.fishwildlife.org/index.php?section=teaming_with_wildlife [Accessed 10 February 2017]). Crawfish Frogs have not been observed in Iowa since 1942 (Christiansen and Bailey 1991), and until recently were thought to have been extirpated from Louisiana. Recent records suggest that Crawfish Frogs now occupy only 34 of 85 counties where they historically occurred east of the Mississippi River, a region where experts estimate only 3,500 breeding adults remain (Engbrecht and Lannoo 2012). Discussions to petition Crawfish Frogs for federal listing as threatened or endangered have begun (Williams et al. 2013). Over the past eight years, we have been a part of a collaborative team (including other researchers from Indiana State University, Terre Haute, Indiana, Hanover College, Hanover, Indiana, the Indiana Department of Natural Resources [IDNR], Indianapolis, Indiana, and the United States Fish and Wildlife Service, Big Oaks National Wildlife Refuge, Madison, Indiana) that has been investigating the life-history and natural-history features of this species to determine effective management practices.

Crawfish Frogs are both rare and difficult to locate, and as a result sample sizes tend to be small. The risks of drawing conclusions from small sample sizes include a larger sampling error in the estimate of sample means, greater likelihood of failing to reject a false null

(Type II error), and a lower chance of discerning small effects (Whitlock and Schluter 2009). Crawfish Frogs obligately occupy abandoned burrows dug by upland crayfish, including species in the genera *Cambarus* and *Fallicambarus* (Heemeyer and Lannoo 2012; Heemeyer et al. 2012). Adults are typically found either in or at their burrow entrance on a bare spot of soil, termed a feeding platform (Hoffman et al. 2010; Engbrecht and Lannoo 2012). Heemeyer et al. (2012) estimated their upland (non-breeding) home range was 0.05 m^2, which simplifies studying this species because a miniscule home range allows individual frogs to be monitored using wildlife cameras. Using wildlife cameras to study Crawfish Frogs also has the advantage of not encumbering the animal with a radio-transmitter, and unlike telemetry, provides a visual record of what the animal is doing at the time of each activity assessment.

We previously detailed the value of digital photography in elucidating the activity patterns of Crawfish Frogs, which have small home ranges and high, multiyear, upland site fidelity (Heemeyer and Lannoo 2012; Heemeyer et al. 2012). Using this technique, we demonstrated these frogs exhibit around-the-clock (circumdiel) activity patterns, and that they do not sleep or exhibit winter torpor (Hoffman et al. 2010). Here, we use modifications of this photography technique to observe fine-scale activity patterns of a relatively larger number of free-ranging Crawfish Frogs. For example, we followed the behavior of individual frogs at 5-min intervals from the time they emerged from winter senescence in the spring until they began winter senescence late the following fall. We then compared activity to abiotic environmental variables, including temperature, vapor pressure gradient (defined below), and precipitation. We hypothesized that frog activity is tied to the environmental variables of temperature, vapor pressure gradient between the atmosphere and frog skin, and precipitation. We predicted activity would increase with increasing temperature, vapor pressure gradient, and precipitation, but were unsure how interactions among these factors might affect frog activity patterns.

Materials and Methods

Study site.—Our study site was located on the 729-ha Hillenbrand Fish and Wildlife Area-West (HFWA-W), approximately 5 km south of Jasonville in Greene County, Indiana, USA. Historically, this region was covered with Eastern Deciduous Forest with scattered Pocket Prairies (Transeau 1935), later converted to agriculture prior to being surface mined for coal. Our study site was mined from 1976−1982; post-mining, the soil was re-contoured and seeded to herbaceous vegetation. The state purchased the land in 1988, and the site is currently managed as prairie by the Division of Fish and Wildlife of IDNR (Lannoo et al. 2009). Within these Pocket Prairies, two species of large crayfish, the Paintedhand Mudbug (*Cambarus polychromatus*) and the Devil Crayfish (*C. diogenes*), excavate upland burrows used by Crawfish Frogs (Thoma and Armitage 2008; Heemeyer et al. 2012).

Photography.—We used digital images from wildlife cameras to record the activity of adult and juvenile Crawfish Frogs from 2009−2013. We defined juveniles as individuals less than approximately 70 mm snout-vent length, which we estimated visually and was much smaller than the average adult size (about 95–100 mm). Initially (2009–2011), we deployed Cuddeback® (Non Typical, Inc., De Pere, Wisconsin, USA) wildlife cameras, which photographed adult frogs at 1-h intervals (the minimum permitted by the camera design). In 2012, we began deploying Bushnell Trophy Cam® (model 119456C; Bushnell Outdoor Products, Overland Park, Kansas, USA) trail cameras, set to photograph at 5-min intervals. We fastened cameras to treated deck spindles (5 × 5 × 35 cm) or wooden stakes (2 × 2 × 50 cm) that we drove into the soil approximately 75 cm from occupied burrows. We trimmed vegetation between the camera and burrow entrance to allow unobstructed viewing of frogs. Cameras recorded around-the-clock. We classified images by photoperiod: daytime photographs were taken between sunrise and sunset, and nighttime photographs were between sunset and sunrise (determined for Jasonville, Indiana by United States Naval Observatory. 2013. Data Services. Available from http://aa.usno.navy.mil/index.php [Accessed 1 February 2013]). We conducted scheduled camera maintenance weekly and as necessary after thunderstorms to ensure that no data were lost due to memory cards filling, batteries dying, or cameras shifting position in wet, windy weather. Because Crawfish Frogs exhibit reduced activity following disturbance (Hoffman et al. 2010), we discarded images recorded 5 min after camera maintenance. We transferred the time-stamped images to a desktop computer for subsequent analysis. Not all images could be analyzed for a variety of technical and weather-related reasons, including malfunctioning cameras, shifting cameras, poor lighting conditions, lens fogging, or animals being obstructed by fast-growing vegetation.

We surveyed all burrows and determined those most likely to host Crawfish Frogs (i.e., about 50 mm in diameter adjacent to a larger sized bare spot of soil) with wildlife cameras to assess occupancy. We then monitored the Crawfish Frog-occupied burrows (sensu Engbrecht and Lannoo 2012; Heemeyer et al. 2012). We were able to follow juveniles only in 2012 (Table 1). These frogs had metamorphosed in 2011 and were at least one year away from breeding (Kinney 2011).

Table 1. Number of Crawfish Frogs (*Lithobates areolatus*) monitored and photographs analyzed from 2009–2013 (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana, USA). Frog totals are the total number of individuals, not the marginal totals for each row. The total numbers of adult frogs were monitored for multiple years: nine for 2 y, four for 3 y, and one for 4 y.

	2009	2010	2011	2012	2013	Total
Frogs						
Adults	1	2	6	10	3	11
Juveniles	0	0	0	6	0	6
Total	1	2	6	16	3	17
Photographs						
Adults	2,642	5,245	43,636	375,337	120,880	547,740
Juveniles	0	0	0	155,576	0	155,576
Total	2,642	5,245	43,636	522,383	120,880	694,786

Overall, we monitored both adult and juvenile frogs at their burrows from late February (minus the time adults were breeding and therefore absent from their burrows) through the third week in October (Figs. 1 and 2), when we had to remove our cameras to accommodate quail hunting season in Indiana. We continued to track one adult on private property until December when cold temperatures restricted it to the depths of its burrow.

We analyzed 694,786 digital photos, representing 65,129 h of sampling (Table 1). We classified individuals in each photograph as either active (i.e., frog was visible either out of its burrow or at the burrow entrance) or inactive (i.e., frog was in its burrow; sensu Engbrecht and Lannoo 2012; Heemeyer and Lannoo 2012; Heemeyer et al. 2012). Crawfish Frogs can be active aboveground for long periods of time, and Hoffman et al. (2010) did not observe inactivity when frogs were on the surface. Therefore, we considered frogs active even if they did not move between consecutive photos. We measured activity as the percentage of images in which a frog was observed aboveground on a given day. To analyze photoperiod, we split activity into the percent of photos with an active frog during daytime hours (sunrise-sunset) and during nighttime hours (sunset-sunrise). To assess compatibility of photos taken at 1-h (2009–2011) and 5-min (2012–2013) intervals, we randomly selected 30 d with 5-min data and reanalyzed at 1-h intervals. A preliminary paired *t*-test analysis in program R version 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria) suggested these intervals were statistically compatible (t = 1.22, df = 29, P = 0.232); therefore, we used both intervals in our analysis.

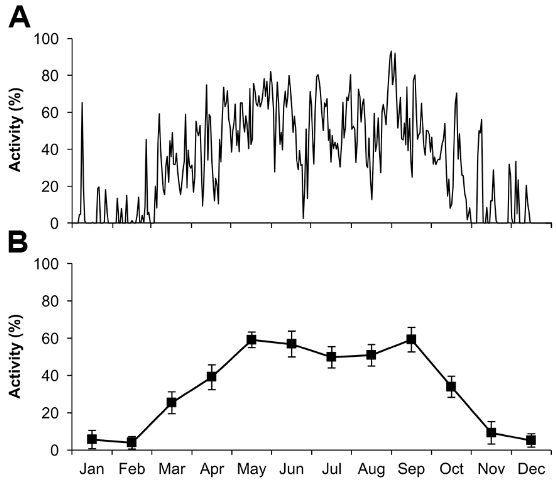

Figure 1. Activity of Crawfish Frogs (*Lithobates areolatus*; n = 17) at Hillenbrand Fish and Wildlife Area-West (Greene County, Indiana, USA), 2009–2013, averaged for each day (A) and then each month (B). We measured activity as the percent of photos during which a frog was active (and photographed by a wildlife camera) on a given day. Note the overall increase in activity from the spring (beginning in March and April) through the fall (October), with a summer plateau centered in July. Error bars represent 95% Confidence Intervals.

Weather data.—We recorded weather data corresponding to our observations of activity. We measured air temperature, relative humidity, and precipitation at 1-h intervals using a HOBO® (Onset, Pocasset, Massachusetts, USA) weather station positioned at a secure locality with similar grassland-habitat characteristics, approximately 3 km from HFWA-W. We filled in data gaps with weather data recorded every hour from a station 20 km away operated by Southwest Purdue Agricultural Center-Vincennes (SPAC-V), Knox County, Indiana, USA. The percentage of weather data from SPAC-V included the following for each year: 2009, 100%; 2010, 31%; 2011, 74%; 2012, 84%; and 2013, 69%.

For evaporative water loss, we calculated the water vapor pressure gradient, defined as the difference between the vapor pressure of frog skin (assumed for ranids to be equivalent to that of an open water surface) and the atmospheric vapor pressure (Spotila and Berman 1976; Shoemaker and Nagy 1977; Hillman et al. 2009). A larger pressure gradient indicates drier air or more desiccating conditions, while a gradient equal to zero represents 100% relative humidity or highly saturated air (Feder and Londos 1984). We calculated open

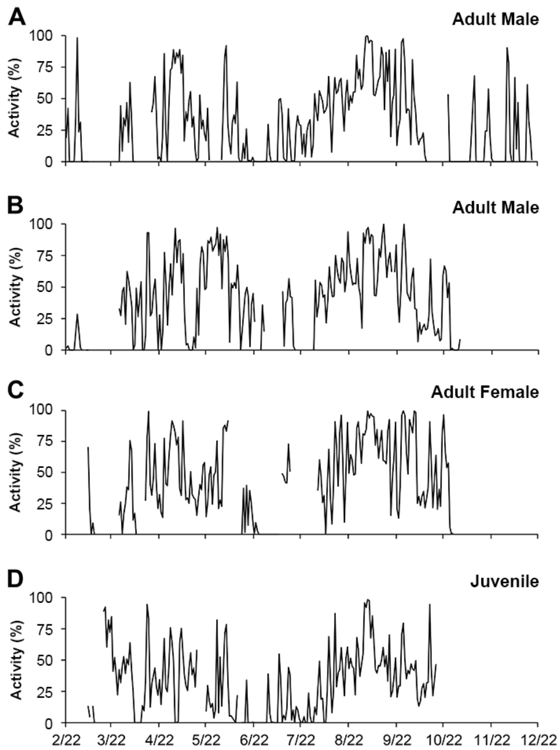

Figure 2. Daily activity of the four longest monitored Crawfish Frogs (*Lithobates areolatus*) at Hillenbrand Fish and Wildlife Area-West (Greene County, Indiana, USA) in 2012. (A) and (B) adult males (Frogs 44 and 26, respectively); (C) an adult female (Frog 53); and (D) a juvenile. We measured activity as the percent of photos during which a frog was active (and photographed by a wildlife camera) on a given day. Notice the similarity in activity patterns across sexes and life stages.

water surface vapor pressure from ambient temperature (using an approximation for the temperature range -20 to 50° C, max error = 0.083%), and atmospheric vapor pressure from relative humidity values recorded by our weather stations (Vaisala 2013. Humidity Conversion Formulas: Calculation Formulas for Humidity. Available from http://forms.vaisala.com/LP=1194 [Accessed 20 June 2016]). We defined annual seasons based on the Northern Hemisphere meteorological seasons of three months each, as follows: spring from March-May, summer from June-August, fall from September-November, and winter from December-February (National Oceanic and Atmospheric Administration. 2013. Meteorological versus astronomical summer–what's the difference? Available from https://www.ncdc.noaa.gov/news/meteorological-versus-astronomical-summer%E2%80%94what%E2%80%99s-difference [Accessed 2 August 2016]). In addition to referencing seasons, when we wish to show higher temporal resolution, we indicate specific months.

Statistical analyses.—We constructed multiple generalized linear models to assess frog activity in program R, as follows: (1) total activity across the entire year; (2) activity during the most active months (April-October; when activity was > 33%); (3) activity during the daytime (sunrise-sunset, entire year); and (4) activity during the nighttime (sunset-sunrise, entire year). We investigated the following daily variables: average, minimum, and maximum ambient temperature; average, minimum, and maximum vapor pressure gradient; and total precipitation. We excluded variables with high co-linearity (Zuur et al. 2007), and therefore considered average temperature, minimum and maximum vapor pressure gradient, and total precipitation in the models. We fitted the global model with all the parameters and considered all subset models as well as the null model. To prevent overfitting and unnecessary complexity, we only included parameter main effects. We selected the best-fit models with the lowest Akaike information criterion (AIC) values (ΔAIC < 2.0; Burnham and Anderson 2002). To determine which covariates explained the most variation in activity, we calculated a model-averaged measure or a summed model weight for each covariate (Burnham and Anderson 2002).

To compare daytime and nighttime activity, we conducted a generalized least squares analysis in program R. We assessed average monthly activity (averaged across 2009–2013) using the following variables (main effects only): photoperiod (daytime or nighttime), month, and season. We added a correlation structure to the model to control for temporal correlation or non-independence between months (Zurr et al. 2009). Preliminary results revealed a significant season effect (t = 3.29, P = 0.005) but non-significance for photoperiod (t = −0.65, P = 0.526) and month (t = 1.32, P = 0.206). Therefore, we subsequently analyzed activity in individual seasons (spring, summer, fall, and winter) while considering photoperiod and month as explanatory variables.

To compare activity between adult and juvenile frogs, we conducted an additional generalized least squares analysis in program R using average monthly activity of adults (n = 10) and juveniles (n = 6) in 2012. We included the main effects of frog age (adult or juvenile), month, and season (meteorological), and controlled for non-independence between months (see above; Zurr et al. 2009). Similarly, we assessed differences among individual frogs with a final least squares analysis using average monthly activity of the four longest monitored frogs (two adult males, an adult female, and a juvenile) in 2012. We included the main effects of frog identity, month, and season, and controlled for non-independence between months (Zurr et al. 2009).

Table 2. Results of the generalized linear models constructed to explain Crawfish Frog (*Lithobates areolatus*) total activity from 2009–2013 (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana, USA). These candidate models consider all combinations of the following explanatory variables (main effects only): daily average ambient temperature, minimum and maximum vapor pressure gradient, and precipitation. The response variable is frog activity: the percentage of photos during which a frog was active on a given day, averaged for all frogs (n = 17). Abbreviations are TempAvg = average temperature, VPGMin = minimum vapor pressure gradient, VPGMax = maximum vapor pressure gradient, Precip = precipitation, df = degrees of freedom, L = likelihood, AIC = Akaike's Information Criterion, and ω_i = Akaike weights.

Covariates	df	-2log(L)	ΔAIC	ω_i
TempAvg, VPGMin, VPGMax	4	816.6	0.0	0.711
Global	5	816.4	1.8	0.289
TempAvg, VPGMax, Precip	4	852.0	35.4	< 0.001
TempAvg, VPGMax	3	856.2	37.5	< 0.001
TempAvg, VPGMin, Precip	4	859.6	43.1	< 0.001
TempAvg, VPGMin	3	864.8	46.2	< 0.001
TempAvg, Precip	3	889.0	70.5	< 0.001
TempAvg	2	901.2	80.7	< 0.001
VPGMin, VPGMax, Precip	4	1,066.8	250.2	< 0.001
VPGMax, Precip	3	1,070.6	252.1	< 0.001
VPGMin, VPGMax	3	1,086.8	268.3	< 0.001
VPGMax	2	1,094.6	274.0	< 0.001
Precip	2	1,185.2	364.7	< 0.001
VPGMin, Precip	3	1,185.0	366.4	< 0.001
Null	1	1,199.4	376.8	< 0.001
VPGMin	2	1,199.8	379.1	< 0.001

Results

We monitored 17 Crawfish Frogs: 11 adults and six juveniles (Table 1). We monitored the highest number of animals (10 adults, six juveniles) for the longest period in 2012, after field-site conditions allowed us to discover and monitor Crawfish Frog burrows. Specifically, in fall 2011, an intense, late-season, prescribed burn removed all vegetation in a 32-ha area and revealed the locations of 5,903 burrows.

We monitored individual Crawfish Frogs until we had to remove our cameras or frogs vacated their burrows. At least one frog vacated its burrow involuntarily after being preyed upon by a Common Garter Snake (*Thamnophis sirtalis*). The disappearances of two other adults and one juvenile Crawfish Frog were associated with the presence of either a Common Garter Snake or a Black Racer (*Coluber constrictor*), but we did not observe predation. Two adult Crawfish Frogs relocated to new burrows after crayfish occupied and capped their burrows. Two other adult frogs relocated to new burrows and were known from breeding surveys to be alive at the end of this study. Four adults and five juveniles disappeared; we do not know their fate.

We observed Crawfish Frogs outside their burrows every month of the year, although they were most active (mean monthly activity > 33%) from April to October. Crawfish Frogs were not, however, uniformly active during this time (Fig. 1). Our data suggest a consistent pattern of circumdiel activity with one peak occurring in the late spring, centered in May, and one in early fall, centered around early September. There was a consistent mid-summer plateau in activity associated with nocturnal activity preferences.

Frogs were active in at least one image on days characterized by the following averages: average temperature of 19.4° C (95% Confidence Interval = 18.8–19.9° C); minimum vapor pressure gradient of 1.2 hPa (1.1–1.4 hPa); maximum vapor pressure gradient of 23.3 hPa (22.2–24.4 hPa); and total precipitation of 3.1 mm (2.5–3.7 mm). We detected no differences between the activity patterns of adults and juveniles ($t = -0.42$, df = 18, $P = 0.686$; although this result may be confounded by small sample sizes, and the subsequent lack of resolution necessary to detect subtle variation) and no monthly or seasonal effects between adult and juvenile activity. Similarly, there were no differences between the activity patterns of the two male adults, the female adult, and the juvenile ($t = 1.25$, df = 32, $P = 0.225$) and no monthly or seasonal effects among individual frog activity (Fig. 2). While most Crawfish Frogs did not interact with other individuals while occupying burrows, we observed two instances of two frogs cohabiting a single burrow (in one case, two juveniles; in the other, an adult and a juvenile) in 2012.

Our best-fit generalized linear models (ΔAIC < 2.0; Table 2; Burnham and Anderson 2002) for all four analyses (total, April-October, daytime, and nighttime activity) included daily average temperature, minimum vapor pressure gradient, maximum vapor pressure gradient, and precipitation as explanatory variables (Tables 2–5). Frogs were more active when average temperature was higher (for a given vapor pressure gradient and precipitation), when minimum and maximum vapor pressure gradients were lower (and therefore the risk of desiccation was lower for any given temperature and precipitation), and when precipitation was greater (for a given temperature and vapor pressure gradient). The summed model weights for average temperature and minimum vapor pressure gradient were 1.000 for all four analyses. Maximum vapor pressure gradient had a summed weight of 1.000 for total, April-October, and daytime activity analyses, and a weight of 0.989 for nighttime activity. The summed weight for precipitation varied among the analyses, as follows: total, 0.289; April-October, 0.344; daytime, 0.277; and nighttime, 0.274. While each of the environmental variables we measured (temperature, vapor pressure gradient, and precipitation) was important to explain

Table 3. Results of the generalized linear models constructed to explain Crawfish Frog (*Lithobates areolatus*) total activity during the most active months, April-October, 2009–2013 (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana, USA). Consideration of explanatory variables is explained in Table 2. The response variable is frog activity: the percentage of photos during which a frog was active on a given day, averaged for all frogs (n = 17). Abbreviations as in Table 2.

Covariates	df	-2log(*L*)	ΔAIC	ω_i
TempAvg, VPGMin, VPGMax	4	696.0	0.0	0.646
Global	5	695.2	1.2	0.354
TempAvg, VPGMax, Precip	4	727.4	31.4	< 0.001
TempAvg, VPGMin, Precip	4	729.8	33.7	< 0.001
TempAvg, VPGMax	3	732.8	34.7	< 0.001
TempAvg, VPGMin	3	736.0	37.9	< 0.001
TempAvg, Precip	3	755.0	57.0	< 0.001
TempAvg	2	768.0	68.0	< 0.001
VPGMin, VPGMax, Precip	4	805.6	109.5	< 0.001
VPGMax, Precip	3	814.6	116.6	< 0.001
VPGMin, Precip	3	815.2	117.2	< 0.001
VPGMin, VPGMax	3	815.4	117.4	< 0.001
Precip	2	822.0	122.0	< 0.001
VPGMin	2	822.6	122.6	< 0.001
VPGMax	2	828.8	128.8	< 0.001
Null	1	833.2	131.2	< 0.001

activity, temperature and vapor pressure gradient were better predictors than precipitation (Fig. 3).

Our generalized least squares analysis comparing day and night activity confirmed that frog activity was tied to photoperiod in the spring (t = -3.61, df = 6, P = 0.037) and summer (t = 3.78, df = 6, P = 0.033), but not in the winter (t = -0.28, df = 6, P = 0.799; Fig. 4). Frogs were more active during the day in the spring, with total activity increasing during this season (t = 8.73, df = 6, P = 0.003). In contrast, during the summer, frogs were more active during the night (Fig. 5). In the fall, frogs were active during both the day and night (t = -3.05, df = 6, P = 0.055), and total activity decreased during this time (t = -6.65, df = 6, P = 0.007). Total frog activity did not vary significantly throughout the summer (t = -0.26, df = 6, P = 0.814) or winter (t = -2.30, df = 6, P = 0.105).

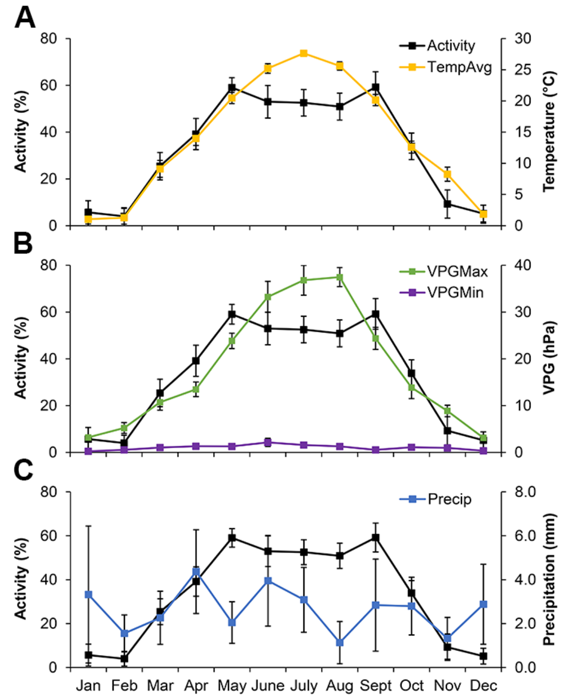

Figure 3. Monthly activity of Crawfish Frogs (*Lithobates areolatus*; n = 17) and weather variables recorded near Hillenbrand Fish and Wildlife Area-West (Greene County, Indiana, USA), 2009–2013. We measured activity as the percent of photos during which a frog was active on a given day, averaged for all frogs and then averaged for each month. We included the following variables in our generalized linear models to explain activity: (A) TempAvg, daily average ambient temperature; (B) VPGMax, daily maximum vapor pressure gradient, and VPGMin, daily minimum vapor pressure gradient; and (C) Precip, total daily precipitation. Error bars represent 95% Confidence Intervals.

Discussion

Our results generally confirmed our hypothesis that Crawfish Frog daily activity is tied to the environmental variables of temperature, vapor pressure gradient between the atmosphere and frog skin, and precipitation, with some surprising deviations from the perspective of stereotypically perceived activity patterns. We found that Crawfish Frogs could be diurnal, nocturnal, or circumdiel depending on seasonally consistent environmental variations. In particular, cold nighttime temperatures resulted in increased diurnal activity in the early spring and late fall, while hot, desiccating daytime conditions stimulated more nocturnal activity in mid-summer. Absent temperature and desiccating extremes, Crawfish Frogs are circumdiel.

The peaks in Crawfish Frog activity that consistently occurred in late spring and early fall indicate circumdiel activity patterns as was previously documented (Hoffman et al. 2010). In contrast, earlier in the spring and later in the fall when nighttime temperatures were lower, Crawfish Frogs were less active overall because they reduced nocturnal activity (although fall activity was circumdiel, there was a tendency towards diurnal activity). Crawfish Frog activity plateaued during the summer (June-August), when frogs became nocturnal. Our data suggest this was to avoid desiccating daytime conditions. The Crawfish Frog activity patterns we observed may parallel anuran activity patterns more generally. Bider (1968) noted temporal shifts in daily activity in related species of ranids living at the

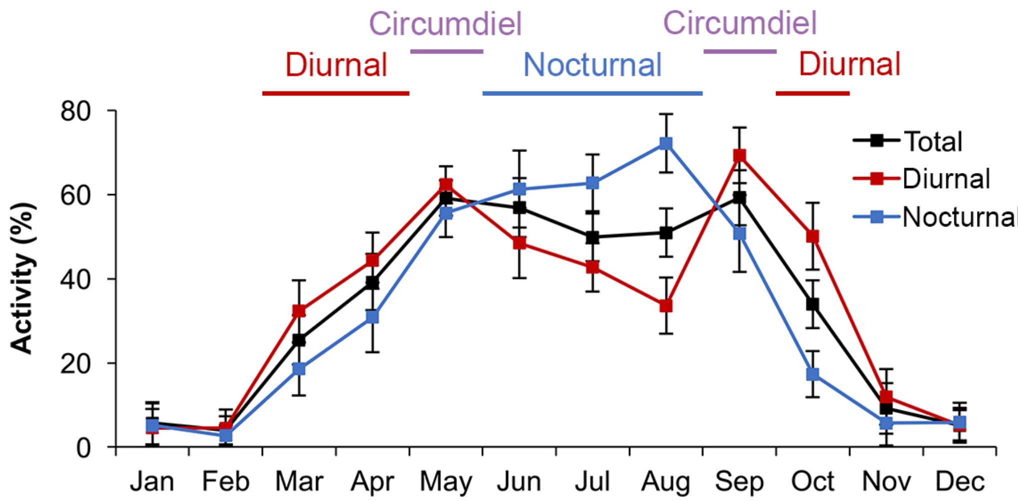

Figure 4. Crawfish Frogs (*Lithobates areolatus*) shift activity patterns. Here, we show mean monthly activity of 17 frogs at Hillenbrand Fish and Wildlife Area-West (Greene County, Indiana, USA) in 2009–2013, sorted by total activity, diurnal activity (sunrise-sunset), and nocturnal activity (sunset-sunrise). We measured activity as the percent of photos during which a frog was active on a given day, parsed into daytime or nighttime hours. We then averaged these data for all frogs by month. Activity peaks corresponded to around-the-clock (circumdiel) activity in the late spring (May) and early fall (September; although at this time frogs were more diurnal than nocturnal). Early spring increases (March-April) in activity and late fall decreases (October) in activity are due to animals being primarily diurnal, likely due to cool nighttime temperatures. The summer plateau in activity (centered in July) corresponds to decreased diurnal activity, likely due to desiccating mid-summer conditions (when the vapor pressure gradient is the greatest; Fig. 3). See also Figure 5. Error bars represent 95% Confidence Intervals.

Table 4. Results of the generalized linear models constructed to explain Crawfish Frog (*Lithobates areolatus*) activity during daytime, 2009–2013 (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana, USA). Consideration of explanatory variables is explained in Table 2. The response variable is frog activity: the percentage of photos during which a frog was active during daytime (sunrise-sunset) on a given day, averaged for all frogs (n = 17). Abbreviations as in Table 2.

Covariates	df	-2log(L)	ΔAIC	ω_i
TempAvg, VPGMin, VPGMax	4	919.4	0.0	0.731
Global	5	919.4	2.0	0.269
TempAvg, VPGMax	3	938.8	17.3	< 0.001
TempAvg, VPGMax, Precip	4	937.6	18.3	< 0.001
TempAvg, VPGMin, Precip	4	976.8	57.4	< 0.001
TempAvg, VPGMin	3	981.4	60.1	< 0.001
TempAvg, Precip	3	990.4	68.9	< 0.001
TempAvg	2	997.6	74.3	< 0.001
VPGMin, VPGMax, Precip	4	1092.4	173.0	< 0.001
VPGMax, Precip	3	1095.2	173.8	< 0.001
VPGMin, VPGMax	3	1104.4	183.1	< 0.001
VPGMax	2	1108.8	185.4	< 0.001
Precip	2	1149.0	225.5	< 0.001
VPGMin, Precip	3	1149.0	227.6	< 0.001
Null	1	1158.0	232.7	< 0.001
VPGMin	2	1158.0	234.5	< 0.001

Table 5. Results of the generalized linear models constructed to explain Crawfish Frog (*Lithobates areolatus*) activity during nighttime, 2009–2013 (Hillenbrand Fish and Wildlife Area-West, Greene County, Indiana, USA). Consideration of explanatory variables is explained in Table 2. The response variable is frog activity: the percentage of photos during which a frog was active during nighttime (sunset-sunrise) on a given day, averaged for all frogs (n = 17). Abbreviations as in Table 2.

Covariates	df	-2log(L)	ΔAIC	ω_i
TempAvg, VPGMin, VPGMax	4	655.0	0.0	0.713
Global	5	655.0	1.9	0.276
TempAvg, VPGMin	3	666.0	9.0	< 0.001
TempAvg, VPGMin, Precip	4	666.0	11.0	< 0.001
TempAvg, VPGMax	3	690.8	34.0	< 0.001
TempAvg, VPGMax, Precip	4	690.4	35.4	< 0.001
TempAvg, Precip	3	724.2	67.3	< 0.001
TempAvg	2	727.0	68.1	< 0.001
VPGMin, VPGMax, Precip	4	1,087.2	432.2	< 0.001
VPGMax, Precip	3	1,089.2	432.2	< 0.001
VPGMin, VPGMax	3	1,091.2	434.2	< 0.001
VPGMax	2	1,094.2	435.1	< 0.001
VPGMin, Precip	3	1,129.6	472.6	< 0.001
VPGMin	2	1,132.6	473.5	< 0.001
Null	1	1,136.8	475.7	< 0.001
Precip	2	1,135.0	476.1	< 0.001

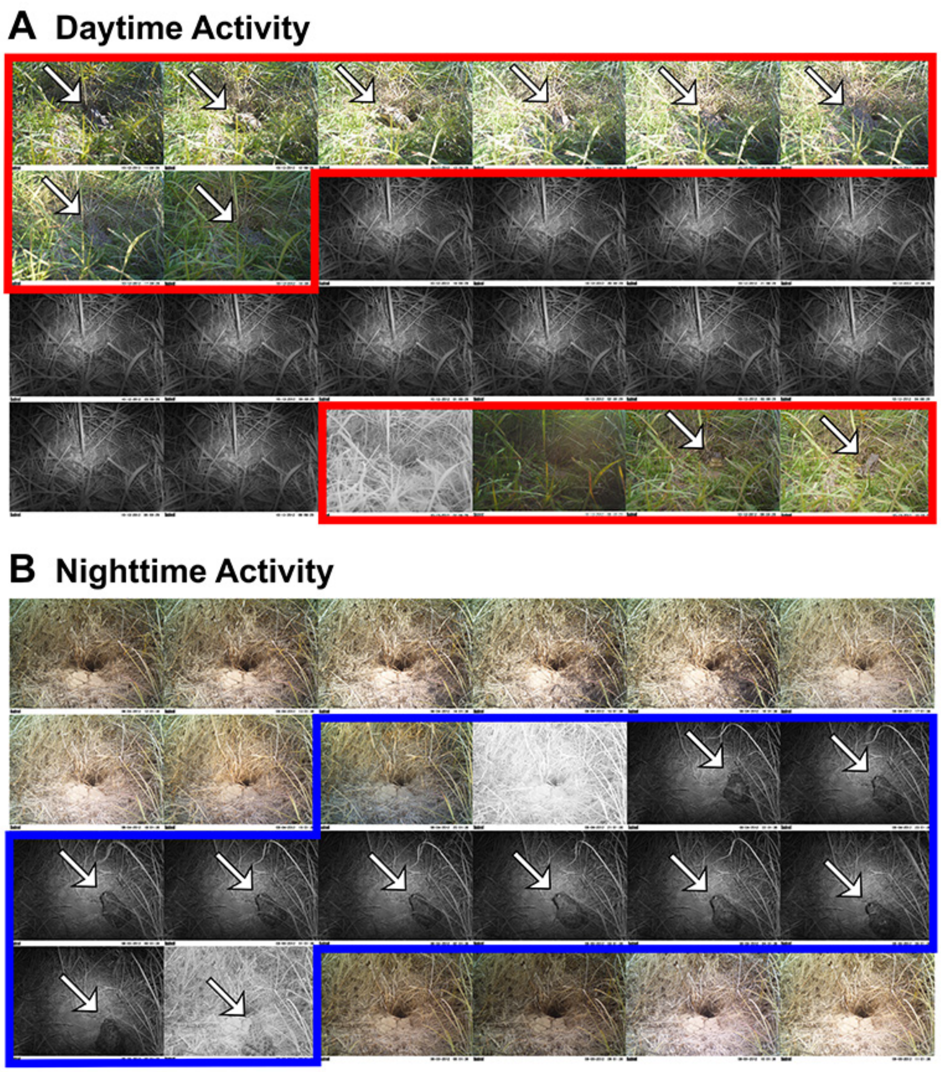

Figure 5. Wildlife camera photographs demonstrating both diurnal and nocturnal activity patterns in the same Crawfish Frog (*Lithobates areolatus*), an adult female (Frog 53) in 2012. Wildlife camera images are displayed every hour for 24 hours (from noon to noon) on 12–13 October, when this frog was active only during the day (A), and on 4–5 August, when the frog was active only at night (B). The red polygons demarcate daytime photos (noon to sunset and sunrise to noon), whereas the blue polygon indicates nighttime photos (sunset to sunrise). White arrows point to the active frog outside its burrow.

northern edge of their range, but activity was defined as movements across the landscape, with one activity peak due to adult breeding migrations and another due to post-metamorphic juvenile dispersal.

Despite living alone in burrows and typically not encountering other Crawfish Frogs except when breeding (Heemeyer and Lannoo 2012; Heemeyer et al. 2012), the responses of individual frogs to environmental variables were nearly synchronized. In 2012, we followed two adult males, one adult female, and one juvenile from late winter to late fall (February-October for animals on publicly hunted lands, February-December for the animal on private land). All four frogs exhibited the same pattern of activity observed at our study site throughout the study. This synchrony could not have been due to social factors (each burrow typically is inhabited by a single frog), and therefore was likely due to similar physiological and behavioral responses to external environmental factors or to internal homeostatic factors.

There is no surprise that temperature, water vapor pressure gradient, and precipitation each affect levels of amphibian activity. Temperature affects metabolic rates of amphibians, thereby affecting activity (Bellis 1962; Bider 1968). Minimum temperature, in particular, can present a threshold below which frogs are inactive (Bellis 1962). The vapor pressure gradient influences amphibian activity because the difference in vapor pressure between frog skin and the atmosphere dictates evaporation rates (Adolph 1932; Spotila and Berman

1976; Shoemaker and Nagy 1977; Hillman et al. 2009). Similarly, rainfall reduces the risk of desiccation (Gibbons and Bennett 1974) by increasing humidity and therefore promotes activity, including behaviors in Crawfish Frogs such as migration and dispersal (Heemeyer and Lannoo 2012; Heemeyer et al. 2012), but not calling (Williams et al. 2013).

The results of our best-fit generalized linear models suggest that the relatively simple pattern of activity we observed across years in male and female adults as well as juveniles is specifically tied to seasonal temperature and vapor pressure gradient. As mentioned above, early spring and late fall activity appears to be limited by cold nighttime conditions (Engbrecht and Lannoo 2012), whereas mid-summer activity is limited by hot, desiccating daytime conditions. Precipitation (rainfall) does not appear to be a strong driver of daily activity patterns. However, previous research has demonstrated that heavy nighttime spring rains drive adult breeding migrations (both immigrations and emigrations; Heemeyer and Lannoo 2012; Heemeyer et al. 2012), as well as mid-summer, post-metamorphic juvenile dispersal (Kinney 2011).

Frogs are interesting in that many species can be active day or night (Gordon and Hood 1976). For example, frogs are visual predators and will feed during the day, whereas they generally call and breed at night. The literature on Crawfish Frogs is riddled with confusion about their activity patterns. Prior to Hoffman et al. (2010), Crawfish Frogs were variously described as emerging only early in the morning (Smith 1950), nocturnal (Conant and Collins 1998; Minton 2001; Parris and Redmer 2005), nocturnal following rains (Johnson 2000), or crepuscular (Thompson 1915). As Hoffman et al. (2010) pointed out, these authors were not wrong, they were simply incompletely correct. Little did these authors realize that this confusion masked complex behavioral plasticity. This plasticity may permit Crawfish Frogs and other anurans to respond to the predicted hotter and drier summers resulting from anthropogenic global warming in some regions of the USA (McCarty 2001; Diffenbaugh et al. 2005; Parmesan 2006). Although we do not wish to either predict or diminish the effect climate change will have on populations of anurans (Klaus and Lougheed 2013), this conclusion supports the notion that anurans may be resilient (Beebee 2002). In particular, Reading (1998) and Urban et al. (2013) demonstrated that behavioral and phenotypical plasticity, as well as genetic adaptation, can offset some negative consequences of climate change. We suggest that the behavioral plasticity that allows Crawfish Frogs to be active day and/or night gives them some capacity to be naturally resilient to the current effects of climate extremes.

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