January 2020

Impacts of Driving Factors on Annual Cicada Emergence in Relation to the Seasonal Abundance of Eastern Copperheads (Agkistrodon contortrix)

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Recommended Citation
Sockman, Jesse Christian, "Impacts of Driving Factors on Annual Cicada Emergence in Relation to the Seasonal Abundance of Eastern Copperheads (Agkistrodon contortrix)" (2020). *Online Theses and Dissertations*. 762.
https://encompass.eku.edu/etd/762

IMPACTS OF VARIABLES ON ANNUAL CICADA EMERGENCE IN RELATION TO THE SEASONAL ABUNDANCE OF EASTERN COPPERHEADS (*AGKISTRODON CONTORTRIX*)

BY

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IMPACTS OF DRIVING FACTORS ON ANNUAL CICADA EMERGENCE IN RELATION TO THE SEASONAL ABUNDANCE OF EASTERN COPPERHEADS (*AGKISTRODON CONTORTRIX*)

BY

JESSE C. SOCKMAN

Submitted to the Faculty of the Graduate School of
Eastern Kentucky University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
2020

DEDICATION

I would like to decide this work to my great grandmother, Thelma Alley, whose belief in me and wise words guide me each day of my life.

ACKNOWLEDGEMENTS

I would like to thank my advisor and mentor, Dr. Stephen Richter, for always offering guidance through each challenge. I extend thanks to my committee; Dr. Valerie Peters for invaluable statistical advice and Dr. Luke Dodd for limitless enthusiasm and methodological input. The support and encouragement of my parents and family have been invaluable. I owe gratitude to my dearest Lindsey, lab mates, cohort, vivarium staff, and patient friends who offered advice, laughs, and compassion. Special thanks to my fantastic team of field assistants: Renae Steinberger, Josh Hendricks, Kaitlyn Cowley, Kyle Meunnich, Jacob Stark, David Smith, Antwanai Seay, Austin Owens, and Henderson Gull. I owe thanks to the Louisville Zoo and Kentucky Reptile Zoo for offering training and assistance. Thank you to the United States Forest Service (USFS), especially Christy Wampler, for financial and on the ground support. I would like to recognize those that laid the ground work for this study prior to Eastern Kentucky University's (EKU) involvement: Raymond Little (Big South Fork, TN), Danna Baxley (Nature Conservancy, KY), Will Bird (Louisville Zoo), Sandie Kilpatrick (USFS), Christy Wampler (USFS), and John McGregor (Kentucky Department of Fish and Wildlife Resources). Thank you to EKU, the Department of Biological Sciences, Division of Natural Areas, and faculty of EKU for ensuring I had the gear, funds, and support I needed. I must acknowledge those that made me who I am: Dr. Jason Courter, Kristen Beck, Kim Bowes, Steve Irwin, Ryan Palmer, Greg Lipps, and again my parents (Jim and Vicki Sockman). Lastly, I would like to thank those who made my goals possible, my grandparents, my Mimi supporting me both prayerfully and financially as well as the kindness of Drs. Rachel and Alex Szekely. I hope to show the same compassion and endless support given to me to the wildlife and people I interact with

each day. This research was approved by the EKU Institutional Animal Care and Use Committee, Protocol 06-2018.

ABSTRACT

For many species, life history events are cyclical and often correspond to specific environmental conditions. As a result of environmental variability, the optimal conditions that regulate the range and activity of highly regulated cyclical organisms, like cicadas, are subject to temporal change. Variability in cicada emergence and abundance has been shown to impact the species that rely on the rapid influx of nutrients. One such predator is the Eastern Copperhead (*Agkistrodon contortrix*) that has been noted feeding on emerging cicadas throughout their range. In eastern Kentucky, observations of copperheads congregating to feed on cicadas has been documented in recreational areas. This creates an urgency to understand the driving factors of the timing of this relationship to reduce negative human-copperhead interactions. The objective of this research was to investigate variables (temperature, humidity, precipitation, moon phase, photoperiod, and growing-degree days) in connection with the timing of copperhead movement and cicada emergence. Nightly visual encounter surveys were conducted to determine copperhead and cicada relative abundances while observing behavioral interactions. Climatic data and environmental factors were collected during each survey or through the Midwestern Regional Climate Center and US Naval Observatory. Each year copperheads congregated consistently after the initial rush of cicada emergence with arrival fluctuating only a day across three years. The initial arrival of copperheads at the site was positively related to increases in growing degree day accumulation and cicada abundance. Increases throughout the season in copperhead abundance was positively associated with temperature, growing degree day accumulation, and cicada abundance. In contrast, initiation of cicada emergence was negatively related to temperature and relative humidity. This may be due to the pulsating nature or presence of a thermal minimum threshold for initial cicada emergence. Increased cicada abundance throughout the season was positively related to humidity and negatively related to moon phase. Higher humidity has often been associated with successful ecdysis of cicadas inferring more successful emergence on higher humidity nights. Overall, analyses suggest that cicada emergence at the site is a preemptive indicator of copperhead abundance, and growing degree day accumulation may have management implications for predicting copperhead arrival at foraging sites within the Daniel Boone National Forest.

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Introduction

For many species, life history events are cyclical and often correspond to specific environmental conditions (Visser, Hollemann, and Geinapp, 2006). As environmental conditions change from year to year, the optimal period for these events varies annually (Visser, Hollemann, and Geinapp, 2006). With the impacts of global climate change (GCC) altering the phenology of many species, it is important to understand the annual plasticity of species to reveal how they will respond to long-term change (Parmesan and Yohe, 2003). For example, many avian species are advancing nesting events earlier in the spring in response to warming temperatures and altered peak food availability (Halupku and Halupka, 2017). Environmental factors such as growing-degree days (GDD), precipitation, and temperature impact the circadian rhythms of species, perhaps even differentially. Climate change induced shifts in phenology can lead to environmental asynchronies, which can be detrimental to the persistence of populations (Saino et al., 2011).

Insect species, such as cicadas (Family Cicadidae), alter their range and active seasons due to changing patterns of precipitation and temperature (Ogawa-Onishi and Berry, 2013). Although most research within this group has focused on periodical cicadas (*Magicicada* spp.) that are primarily hard-wired for simultaneous emergence every 13 or 17 years responding to environmental conditions to fine tune emergence (Oberdorster and Grant, 2006), annual cicadas (*Neotibicen* spp.) are a consistent nutrient resource and readily respond to environmental cues (Callaham et al., 2000). In Kentucky, initial periodical nymph emergence typically begins when soil temperatures reach 17.8° C (Johnson and Townsend, 2003). Periodical cicadas tend to emerge earlier in the summer than annual cicadas, which tend to emerge in higher numbers in late summer (Newton, 2008; Williams and Simon, 1995). Annual cicadas become most active and experience emergence as the imago life-stage between June and September (Hendricks, 2019; Johnson and Townsend, 2003; Newton, 2008).

Despite the role annual cicadas play in nutrient and energy transfer in the ecosystem, little is known about their habitat associations or response to environmental cues in the United States, especially in comparison to periodical cicadas (Chiavacci, Bednarz, and McKay, 2014). Studies have shown that stochastic weather events resulting from climate change can lead to shifts in cicada lifecycle events (Chiavacci, Bednarz, and McKay, 2014; Moriyama and Numata, 2011; Ogawa-Onishi and Berry, 2013). In Japan, Moriyama and Numata (2011) reported that the annual cicada species *Crytotympana facialis* advanced hatching within the rainy season as a result of shifts in hatch date caused by climate warming over the last century. A study in Arkansas found the response of cicadas to flooding varied based on timing and species, whereby flooding may advance or delay the emergence of cicadas dependent on the rising water's influence on other variables (Chiavacci, Bednarz, and McKay, 2014). Some cicadas also synchronize their emergence with the rainy season (Moriyama and Numata, 2019). Similarly, several cicada species have been noted to hatch when humidity is high to avoid desiccation (Moriyama and Numata, 2006). In Japan, two cicada species (*C. facialis* and *Playpleura kaempferi*) have advanced first song dates each decade since 1956 in response to temperature, while the Large Brown Cicada, *Graptopsaltria nigrofuscata,* showed the inverse trend singing later in the year (Ogawa-Onishi and Berry, 2013). The potential responses to climatic variables in differing environments by annual cicadas remain little understood.

Cicadas tend to have higher emergence densities in well-lit or open areas indicating a preference toward thermoregulation or oviposition sites in younger trees (Chiavacci, Bednarz, and McKay, 2014). Research on periodical cicadas suggests the selection of younger trees is due to the females need for softer bark for oviposition, preference toward thinner branches, and well-lit canopy for egg development (Chiavacci, Bednarz, and McKay, 2014). Likewise, nymphs of this species benefit from the roots of young trees because they grow in edge habitat for emergence; alternatively, the benefit may arise from faster root growth on young trees producing more nutrients that promote nymph growth (Chiavacci, Bednarz, and McKay, 2014; Smits, Cooley, and Westerman, 2010; Yang and Karban, 2009). While female oviposition locations are related to nymph root selection, female oviposition sites may only determine the general area of nymph densities as nymphs may establish on root masses of nearby trees (Smits, Cooley, and Westerman, 2010). After emergence from the ground, cicadas ascend into trees or other vegetation and vertical structures to molt into the imago phase where they remain vulnerable for several hours until their wings and body harden (Johnson and Townsend, 2003). Subsequently, males typically fly to higher, well-lit branches of edge habitat trees to chorus together to attract females for mating (Johnson and Townsend, 2003).

The mass emergence and congregation of cicadas at chorusing epicenters can lead to an increase in food abundance and influx of nutrients that are used by many species (Callaham et al., 2000; Karban, 1982). Cicadas represent a shift in biomass that links productivity of their host plants with secondary consumers promoting ecosystem health by altering soil composition and providing nutrients to various taxa (Smith, Kelly, and Finch, 2006; Yang, 2004). Mammals, fish, reptiles, other insects, and birds are all known to consume cicadas (Williams, Smith, and Stephen, 1993). For example, Powell and Powell (2011) observed eight species of fish feeding on cicadas that fell into the water. Further, birds are considered one of the main predators of cicadas, consuming 15–40% of annual crop at low densities and exhibiting nesting success in relation to cicada abundance in some habitats (Chiavacci, Bednarz, and McKay, 2014; Williams, Smith, and Stephen, 1993). Finally, turtles, including Eastern River Cooters (*Pseudemys concinna*), False Map Turtles (*Graptemys pseudogeographica*), Wood Turtles (*Clemmys guttata*), and Red-eared Sliders (*Trachemys scripta*), opportunistically prey upon cicadas and in some cases form mixed-species aggregations to eat cicadas (Powell and Powell, 2012; Reid and Nichols, 1970).

Specific to our investigation, snakes are known predators of cicadas (Beaupre et al., 2011; Hamilton Jr. and Pollack, 1956). Schalk et al. (2018) reported one instance of a Cottonmouth (*Agkistrodon piscivorus*) consuming a cicada, but considered it merely opportunistic. However, typically arboreal and active hunting species, including the Coachwhip (*Coluber flagellum*), have been observed feeding on cicadas more regularly (Hanson and Hanson, 1997). In contrast, Eastern Copperheads (*Agkistrodon contortrix*) are ambush predators that shift their hunting tactics to feed on cicadas (McKnight et al., 2014). Hendricks (2019) noted copperheads congregating in large numbers to feed on emergent annual cicadas in eastern Kentucky; showing a shift in their foraging behavior to active foraging methods using visual and vomeronasal cues to pursue cicadas even up into trees.

Historically, copperhead diet has been considered primarily mammalian-based (Lagesse and Ford, 1996). Fitch (1960) suggested that their primary food source was voles and other rodents as they dominated the total biomass consumed by the species, but occurrence of prey items in the study suggests cicadas account for the second most prevalent item behind only voles. McKnight et al. (2014) found that from April to August the copperheads in southeastern Oklahoma were consuming insects, mostly cicadas, with mammals, anurans, other snakes, and lizards as additional food sources. The wide array of prey taken by copperheads is likely a result of prey availability across their range and seasonal differentiation (Fitch, 1960; Schalk et al., 2018). Even so, copperheads are documented consuming cicadas in much of their range including Arkansas, Ohio, West Virginia, Texas, Louisiana, Georgia, Oklahoma, Kansas, and Kentucky (Beaupre et al., 2001; Blair and Richter, 2016; Conant, 1938; Fitch, 1960; Hendricks, 2019; McKnight et al., 2014; Mengak, 2001; Reid and Nichols, 1970; and Schalk et al., 2018). While predation on cicadas has been noted, it has been primarily anecdotal without prior research directed at connecting the lifecycle movements of the two species.

Copperhead movement and habitat usage exhibit seasonal variation as they emerge from winter hibernacula and travel to a transitional habitat before entering their summer home range (Fitch, 1960; Smith et al., 2009). Movement and habitat selection are affected by thermoregulatory needs and food availability (Row and Blouins-Demers, 2006). Both sexes of the snake move in mid to late June in their northern-most range (the Connecticut River Valley) to summer foraging areas which consist of grassy glades and open canopy areas (Smith et al., 2009). In Tennessee, peak activity and food intake typically occur in June and August, but show decline in July suggesting that they feed irregularly (Garton and Dimmick, 1969). The timing of copperhead movement within their active season remains understudied, but may be connected to local environmental influences such as habitat structure and climatic cues (Smith et al., 2009).

Currently, little is known about the importance of cicadas in the diet and spatial ecology of the copperhead. McKnight et al. (2014) suggested cicadas serve a larger role in the copperhead diet. Hendricks (2019) stated that the spatial and temporal predictability of localized high-density annual cicada emergences may produce a high energy, reliable food source that leads to accelerated growth, maturation, and increased fecundity in snakes. Blair and Richter (2017) concluded a strong selective element for cicadas must be present due to copperhead congregations coinciding with cicada emergence. The increased energy expenditure of active foraging for cicadas by copperheads means that the behavior must have a net profit to persist (Hendricks, 2019). Barbour (1962) found a large congregation of copperheads at Robinson Camp, Kentucky feeding on the emergent cicadas. Similarly, at Koomer Ridge campground in Kentucky, copperheads were found to strictly use the site for foraging and all observed feedings were on cicadas (Hendricks, 2019). Cicada emergence may cause a seasonal differentiation in copperhead diet due to fluctuations in prey availability (Fitch, 1960; Garton and Dimmick, 1969), which might drive copperhead movement.

Our study focused on the spatial and foraging ecology of copperheads at Koomer Ridge Campground in the Daniel Boone National Forest (DBNF) with particular interest in their relationship with cicadas. Prior data have shown that copperhead arrival at the site coincides with cicada emergence. Our objective was to investigate variables (temperature, precipitation, humidity, photoperiod, moon phase, and GDD) in connection with the timing of copperhead movement and cicada emergence. We hope to identify driving forces behind this phenomenon to inform future management decisions by the U.S. Forest Service (USFS) and in accordance with the mission of the USFS to foster a better relationship between the public and copperheads through habitat preservation, education, and limiting human-copperhead interactions.

Methods

Study Area

Copperhead surveys and cicada collection were conducted at Koomer Ridge Campground primitive site (37.7845607, -83.636487), a recreational forest opening and surrounding forest within the Cumberland District of the DBNF. The study site is a small (~0.1 ha), grassy opening that is regularly mowed and has sporadic groves of trees, two vault toilets, several trail heads, and five gravel tent pads within the main opening. The climate is temperate continental with high humidity (Kalisz and Powell, 2003). The site is surrounded by forested ridgetops and ravines composed of mostly oaks (*Quercus*), pines (*Pinus*), Red Maple (*Acer rubrum*), and Sourwood (*Oxydendrum arboreum*) (Kalisz and Powell, 2003). The Koomer Ridge primitive site is composed of mostly White Ash (*Fraximus americana*), Red Maple, Tulip Polar (*Liriodendron tulipifera*), White Pine (*Pinus strobus*), Black Walnut (*Juglans nigra*), American Beech (*Fagus grandifolia*), Dogwood (*Cornus spp.*), Redbud (*Cercis canadensis*), Shagbark Hickory (*Carya ovata*), American Hickory (*Carya tomentosa*), *Pinus* spp., and several immature oak saplings.

Climatic Variables

Climactic variables were acquired based on readings from the Koomer Kentucky Weather Station (37.7689, -83.6333) and Stanton 2W Weather Station (37.8604, -83.897) via the Midwestern Regional Climate Center by the National Oceanic and Atmospheric Administration Regional Climate Center (available at https://mrcc.illinois.edu/). The Koomer Kentucky Weather Station was used to obtain maximum, minimum, and mean daily temperatures, and growing degree day accumulations. Daily precipitation data were gathered from the nearest weather station providing precipitation data (Stanton 2W Weather Station). Growing degree days are heat index units accrued over time based on the average daily temperature above a baseline value (Murray, 2008; Wang, 1960). In this study, GDD accumulations were calculated using a base 10°C and March 1 start date (Pruess, 1983; Trudgill et al., 2005). Midwestern Regional Climate Center data were partnered with nightly visual surveys at Koomer Ridge; air, ground, and soil (15 cm below surface) temperatures and nightly humidity readings were taken inside the campground and under the forested canopy using a Kestrel 3000 wind meter (Kestrel Meters, Minneapolis, MN). Temperature readings were taken at the beginning and end of each survey round starting at dusk (see below). In order to gather temperature and relative humidity throughout the day and under the soil level, HOBO dataloggers (HOBO Pro v2 Internal Temperature/Relative Humidity Datalogger) were used to collect temperatures and humidity every 30 minutes (Smith, Kelly, and Finch, 2006); a pair of dataloggers were placed both in and outside of the forest. At each location, one datalogger was above ground and the other buried at 5cm below the ground according to a prior study investigating soil temperature in relation to emergence (Smith, Kelly, and

Finch, 2006). Temperature and humidity data were compared from above sources. The averages of nightly temperature and humidity were found to not differ from any of the sources using unpaired Wilcoxon tests, so averages of nightly data collected at the site were used in all statistical evaluations.

Cicada Emergence

Cicada emergence (defined as the number of exuvia or active individuals found per night) was quantified using several techniques. Visual surveys and collection of fresh exuvia were conducted nightly by multiple observers (Sato and Sato, 2015; Oberdorester and Grant, 2006), before and during copperhead surveying because copperheads tend to knock down exuvia, which could affect accuracy of counts. Visual surveys were completed by walking the site (the forest gap) along circular transects. The area surveyed included the entire primitive campground and a 3-m buffer into the forest on all sides. Transects were split into an outer transect and inner transect, each surveyed simultaneously by two observers. The outer transect ran along the border of the site and was used to survey 3 m into the forest, the edge, and an additional 3 m on the other side of the transect line. The inner transect covered the inside of the site so that no area was missed. When performing a survey lap, the observers walked in a zig-zagging pattern stopping to check all trees, shrubs, and the ground for exuvia and emerging cicadas using a flashlight (Nitecore MH25, Nitecore). For trees and shrubs, surveyors checked the trunk, branches, and leaves (both sides) to reduce error. Data collected regarding exuvia included GPS location, sex, date, and plant species or structure type. Sex was determined from exuvia using the 8th sternite: in females, two cylindrical processes extend from the 8th sternite to each side of the tip of the 9th sternite. Exuvia were removed as they were counted to avoid recounting. Actively molting cicadas were not disturbed as to not bias copperhead behavior, but the exuvia locations were georeferenced so they could be removed later. In the case of an actively climbing cicada, data were collected, the tree was flagged, and the location of the cicada on the tree was described using height and cardinal direction so that exuvia could be obtained when fully molted. Exuvia located high in trees were knocked down using a telescoping pole (Mr. LongArm Pro-Lok 8.4-ft-23.2 ft Telescoping Threaded Extension Pole), snake hook (Midwest tongs), or ladder for cicadas out of reach. All collected exuvia were then cataloged chronologically by time observed.

Tree Survey

Before the sampling season began, all trees within the site were mapped and assigned an identification number and GPS location using a Bad Elf GNSS Surveyor (https://bad-elf.com). Each individual tree (defined as a woody, perennial plant taller than 6m at maturity) were identified to species, measured for diameter at breast height (DBH) using a DBH tape and height using a clinometer (PM-5/360 PC Compass, Suunto). Trees were marked using a numbered tag attached with aluminum nails. Additional measurements, such as canopy cover and distance to edge from each tree, were also collected. Canopy cover estimates were collected by using a point intercept method with a GRS densitometer along three 100-m transects spaced 10 m apart taking a reading every 5 m.

Mark Recapture

Copperhead abundance (number of individuals per night) was visually surveyed throughout their active season beginning in May and concluding when the snakes left their summer feeding grounds in September (Hendricks, 2019). Active capture methods were used to locate free-ranging snakes (Mullin and Seigel, 2009), and methods described by Greenbaum (2003) were used to capture and handle new (i.e., unmarked) individuals. Copperheads were captured using tongs (Gentle Giant Tongs MT Pro Series, Midwest Tongs) and placed into snake bags lining 26.5-L buckets with locking lids (Greenbaum, 2003). Copperhead surveys were performed following the survey methods described for cicadas checking both ground and trees for copperheads and scanning for each individual located for the presence of a passive integrated transponder (PIT) tag. Surveys continued from dusk until three rounds occurred without a new individual being located.

New captures were held overnight and measured the following morning for mass (g), SVL (cm), total length (cm), and sex of each copperhead. Snakes were held overnight to reduce risk to personnel when collecting data on the snake. Captures were made as late in the evening as possible or when snakes exited the site to allow copperheads to feed and not interfere with foraging behaviors. The GPS location of each capture and initial sighting location were also logged using a Bad Elf GNSS Surveyor.

If a copperhead was not marked, a passive integrated transponder (PIT) tag was inserted for mark-recapture purposes. PIT tags are injected or surgically implanted as a permanent marker unique to the individual with minimal to no risk, no alteration of behavior, and lowered sampling/misidentification error (Gibbons and Andrews, 2004). A

PIT tag reader (Biomark HPR Reader, Biomark) was used to identify recaptured individuals based on the unique identification code on each PIT tag (Gibbons and Andrews, 2004). Captured individuals that were placed in buckets during the survey were removed using snake tongs and placed in a large plastic bin. They were coaxed into clear polycarbonate restraining tubes (Midwest Tongs) to immobilize them and enable safe handling. Latex gloves were worn to limit risk of venom transfer from any surfaces before sterilization using 70% ethanol to reduce disease transfer between individuals. After immobilization, copperheads were gently stretched out to be measured using a meter stick to collect both snout-to-vent length and total body length. Sex was determined using lubricated cloacal probes inserted into the cloaca and down the tail. If the probe penetrated more than 3–4 scale rows, the snake was documented as a male; shorter distances indicated female (Dodd, 2014). Prior to PIT tag insertion, the location was swabbed with an alcohol pad to maintain sterile conditions. PIT tags were inserted by isolating the posterior region of the snake and using a veterinary 12-gauge N125 Injector Needle (Biomark) and MK10 Implanter (Biomark) (Gibbons and Andrew, 2004). The PIT tag was inserted beneath the skin outside of the muscle surrounding the peritoneal cavity on the lateral side of the snake, 2–3 scale columns up from ventral scutes (Gibbons and Andrews, 2004). The injector was angled to break the skin and then twisted to lay the PIT tag along the muscle wall of the body. Medical glue was applied to the injection location to reduce infection risk and loss of PIT tags. The location of the tag was massaged to confirm that the PIT tag was under the skin away from the insertion point and then tested using the Biomark HPR Reader by scanning the PIT tag along the body of the snake before releasing the individual. Identification error was reduced by scanning the tag prior to insertion, documenting the number on the datasheet, and then reading back the tag number to the data recorder after injection by scanning through the snake body wall. Snakes were released into the forest surrounding the site closest to the point of capture, but away from human trafficked areas. All equipment including the table, buckets, PIT tags, and clear polycarbonate tubes were disinfected between snakes using a 70% ethanol solution to prevent the spread of disease such as snake fungal disease (*Ophidiomyces ophiodiicola*).

Statistical Analysis

Normality was tested using both a qqnorm plot of residuals and a Shapiro-Wilk test to verify results while differences in variance was accessed with an F-test or Levene's test. All correlations were determined using Pearson correlation for normal data and Spearman correlation when non-normal variables were present. The influence of environmental data on copperhead abundance and cicada emergence were separately compared using hurdle models in the R statistical program (R Core Team, 2014) to account for non-Gaussian distribution, over dispersion, and a surplus of zeroes. Correlation tests followed by a VIF test with a cutoff of 2 were used to assess which variables would be included in the models. Both alternative distributions and candidate models were compared using adjusted Akaike's Information Criterion (AIC_C) (Bolker et al., 2008). Candidate model sets were composed of all variables individually, all combinations of 3-variable models, as well as the null and full model giving 28 candidate models for copperheads and 27 for cicadas. Cicada models included all duo combinations since the copperhead variable was not included in their candidate set. Model averaging was performed when there was no top model with weight > 0.90 using all models with weights ≥ 0.01 (Burnham and Anderson, 2001). Hurdle models addressed frequent zeros in the dataset and differentiated between variables predicting the initiation and the abundance of copperheads or cicadas found at the site. Hurdle models evaluated which variables (air temperature, humidity (Rh %), daily precipitation, moon phase, photoperiod, and GDD accumulation) best explained initial occurrences and fluctuating abundances of copperheads and cicada emergence. Hurdle models used the “hurdle” function from the “pscl” package in R. Because the complex nature of hurdle models is not supported in AICmodavg package in R, candidate models were evaluated using the AIC function in R and then model-averaging calculations were completed manually using Microsoft Excel. Model results were interpreted using 85% confidence intervals to accurately infer statistical significance because 95% confidence intervals likely overlook significant results by conflicting with the AIC selection method parameters (Arnold et al., 2010).

Additional questions were addressed using supplemental statistical methods. Tree species preference during cicada emergence was investigated using a Chi-square test. Chi-square was used to compare the number of each tree species used by cicadas to the number of trees of each species expected to be used. This was determined by taking the actual number of trees of each species divided by the total number of trees available to get the proportion available; the proportion available for each species was independently multiplied by the total number of trees used to get the value for how many of each species would be expected to be used. Following this, tree height, species, and DBH were included as explanatory variables of nightly cicada abundance in a glm using function “lme4.” The same AIC protocol as described above was used in the selection of models and distribution. The best fitting distribution was Poisson as the data failed the Shapiro-Wilk test. Model averaging was performed in accordance with the above specifications using the “MuMIn” package in R.

I investigated whether cicadas emerged in even sex ratios using the non-parametric, two-sample Wilcoxon test because the data were non-normal based on normality tests and did not differ in variance. To determine if male or female cicadas had different tree species preferences for emergence an unpaired Wilcoxon Test was performed because data were non-normal based on normality tests, but the variances were not different. The cicadas eaten were compared to both tree variables and copperhead size demographic variables of biological importance. To evaluate the readiness of copperheads to climb trees to feed, the relationship between DBH and the number of cicadas consumed on a tree was evaluated by performing analyses with and without zeros (only trees climbed by snakes). The number of cicadas consumed on each tree at the site was analyzed using simple regression with a response variable of number of cicadas eaten in the tree and the explanatory being DBH. The AIC protocol methodology above was used in the selection of glm models and distribution. The best fitting distribution was negative binomial. Zeros were then removed from the dataset to only consider trees climbed. Considering only trees climbed by copperheads addressed if the DBH of the tree impacted the number of cicadas consumed. The glm with Poisson distribution had best fit with the response variable cicadas eaten and the DBH of trees climbed was the explanatory variable. Lastly, the number of cicadas eaten in 2019 was analyzed as to whether it varied with SVL and mass of copperheads measured at the beginning of the season using a linear model (lm) because cicadas eaten was normally distributed.

Results

A total of 102 survey nights were completed at Koomer Ridge Primitive Campground during 2018 to 2019 sampling a total of 65 copperheads and 1057 cicadas across the two years. Copperhead yearly abundance remained consistent across both years with 42 and 43, respectively. Cicada emergence increased from 233 cicadas observed in 2018 to 824 in 2019 (Table 1). Most of these cicadas were identified as *Neotibicen tibicen tibicen* (Swamp Cicadas), with 2 individuals identified as a periodical species (*Magicicada* spp.).

Table 1. Cicada total emergence abundances from 2018 to 2019 at a recreational area in the Cumberland Ranger District, Daniel Boone National Forest, KY. Sex was not determined prior to 2019.

	2018	2019
Male	-	354
Female	-	317
Unknown	233	153
Total	233	824

Copperhead Site Usage

Copperhead arrival at the site was measured in two ways each year, initial occurrence of an individual and initial congregation, which was defined as when a group of 10 or more copperheads first arrived at the site. Copperhead arrival has been measured each year during 2017–2019, revealing initial occurrences of one snake on 06/20/2017, two on 06/16/2018, and one on 06/12/2019, respectively. The initial congregation dates were remarkably consistent over the 3 years: 06/30/2017, 06/30/2018, and 07/01/2019 with 10 snakes located on each date. Growing degree day accumulation on the above dates ranged from 1667 to 1720 GDDs, but in 2018 and 2019 both arrived synchronously between 1667–1671 GDDs. In 2018–2019, initial arrival of copperheads at the site occurred after 1460 GDDs had accumulated. In both years, the increased nightly abundance of copperheads comes just after the initial pulse of cicada emergence and aligns closely with the peak emergence of cicadas (Figure 1). In 2019, the night of first congregation was the same as the season high for cicada emergence with a total of 29 cicadas (Figure 1).

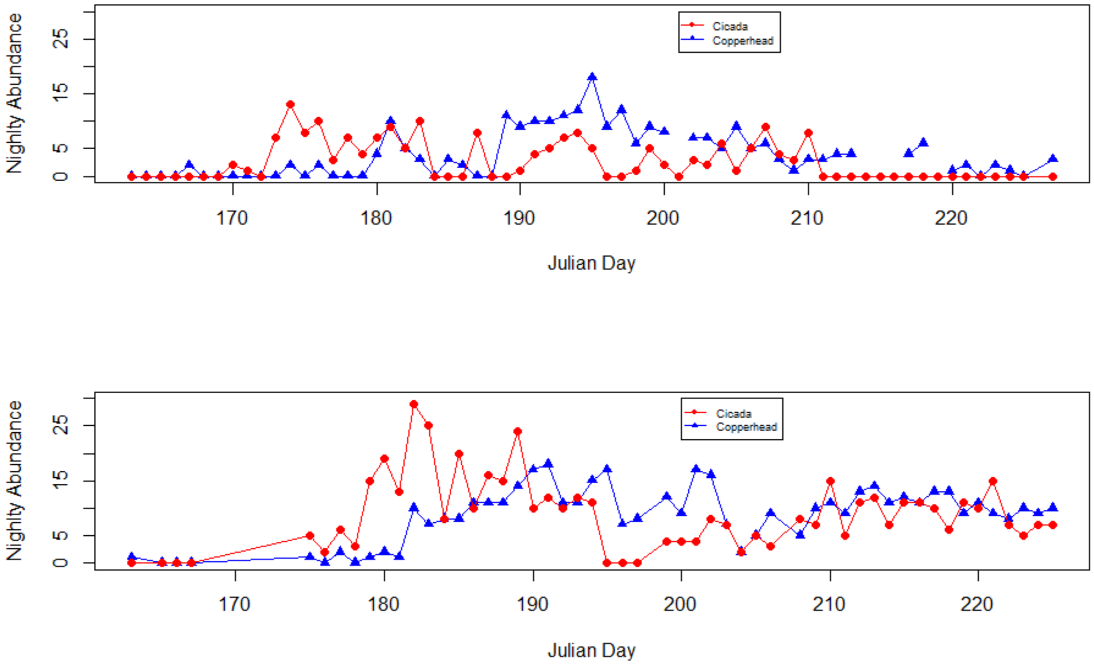


Figure 1. Nightly abundance of Eastern Copperhead (*Agkistrodon contortrix*) (blue) and annual cicadas (red) in 2018 (top) and 2019 (bottom) in survey events at a recreational area in the Cumberland Ranger District, Daniel Boone National Forest, KY. As cicada emergence pulses, copperhead abundance within the site grows and then stays relatively consistent until cicada numbers decrease at the end of the season.

Copperheads within the site had a male-skewed sex ratio each of the last two years (2018 = 2:1, male = 28, female = 14, juvenile = 1; 2019 = 3.88:1, male = 31, female = 8, juvenile = 2) (Table 2). Of these individuals, 15 males were observed eating 68 individual cicadas, while 3 females were observed eating 3 cicadas with 7 eaten by individuals with an unknown sex (Table 3; Figure 2). Four of the males were observed eating 5 or more cicadas (Table 3; Figure 2). A simple linear regression was performed on only male copperheads observed feeding (n =15) to determine if SVL influenced feeding rate (Figure 3). Female snakes were excluded from this model due to small sample size (n = 3). Mass was not included in the model because it was too highly correlated with SVL (r = 0.87) and because SVL had a higher explanation of variation with cicadas eaten (SVL-cicadas, $R^2 = 0.27$; Mass-cicadas, $R^2 = 0.16$). Results indicated that that SVL was not significantly related to the number of cicadas consumed by copperheads ($t_{12} = 1.271$, $p = 0.2039$) (Figure 3). Of all 78 cicadas observed being eaten by copperheads, the sex of the cicada was only able to be determined for thirteen individuals, 11 of which were males. This small sample size precludes statistical analysis, so this should be a point of future research.

Table 2. Sex ratio of Eastern Copperheads (*Agkistrodon contortrix*) at a recreational area in the Cumberland Ranger District, Daniel Boone National Forest, KY from 2015 to 2019. More intensive efforts were established in 2017. The population using the site has shifted to more male dominated, but the overall ratio remains consistent with that of the initial survey conducted.

	2015	2016	2017	2018	2019	Total
Male	11	20	25	28	31	50
Female	8	12	15	14	8	36
Ratio	1.38	1.67	1.67	2	3.88	1.39

Table 3. The observed number of annual cicadas consumed by copperheads based on sex at a recreational area in the Cumberland Ranger District, Daniel Boone National Forest, KY. Males consumed more than females, but it may be a representation of population demographics.

Sex of copperhead	Number of cicadas consumed
Male	68
Female	3
Unknown	7
Total	78

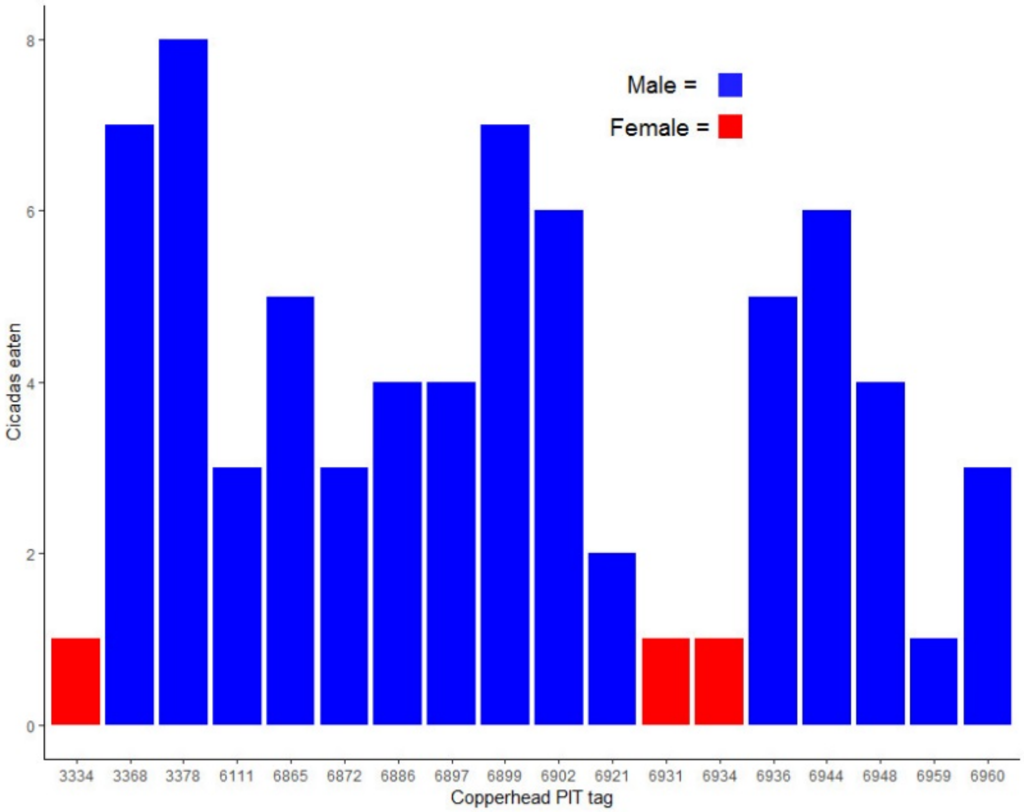


Figure 2. Number of cicadas eaten by individual male (blue) and female (red) Eastern Copperheads (*Agkistrodon contortrix*) at an eastern Kentucky recreational site between June and August of 2019. Males foraged at the site more frequently and thus feed on more annual cicadas.

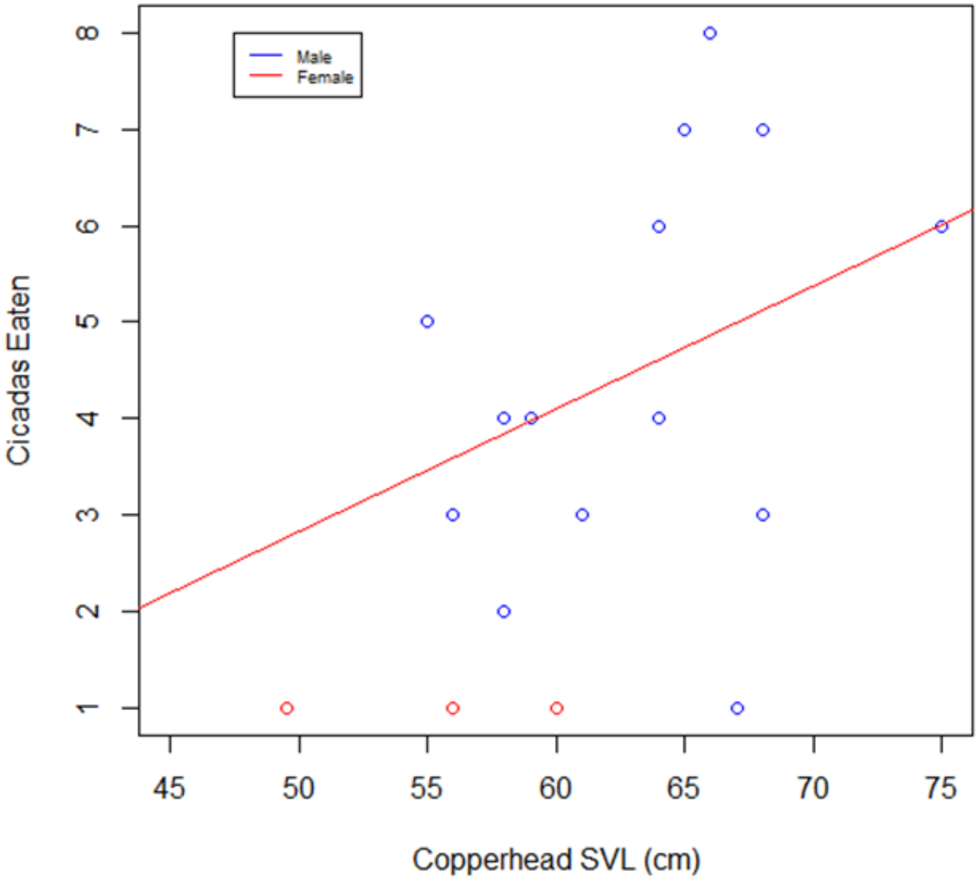


Figure 3. Eastern Copperhead (*Agkistrodon contortrix*) snout-vent-length (mm) as a predictor of number of annual cicadas consumed observed during visual surveys between June and August 2019 at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

The GLM performed indicated trees with lower DBH were more often climbed by snakes as more cicadas were consumed in smaller trees ($z_1 = -2.074$, $p = 0.025$). However, when only trees climbed were compared (all zeroes removed), there was no relationship between DBH and climbing frequency by copperheads ($r = 0.01$; $z_1 = -1.103$, $p = 0.2437$) (Figure 4). This indicated that DBH does not impact the quantity of cicadas consumed, but larger trees may limit the ability of copperheads to climb.

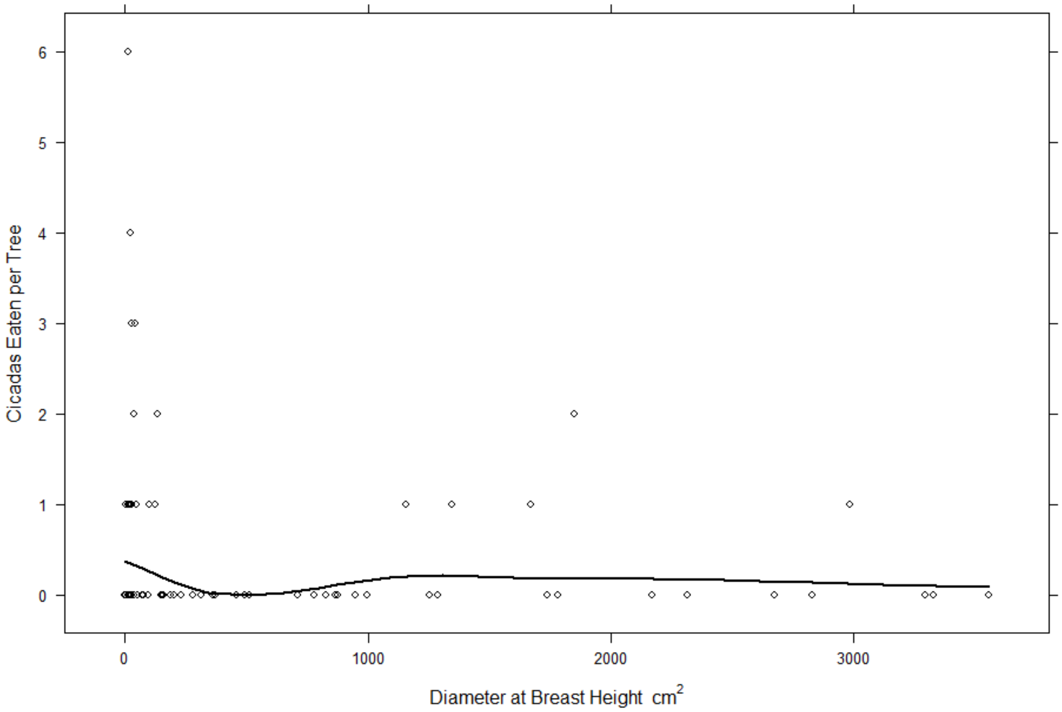


Figure 4. Number of annual cicadas eaten by Eastern Copperheads (*Agkistrodon contortrix*) based on the DBH (cm^2) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. This considers all trees within the site and displays copperhead climbing preferences. Overall, there was a slight trend toward copperheads climbing smaller trees. However, when zeros are removed the relationship is no longer significant.

Copperheads & Climate

Copperhead abundance data were analyzed for 2018 and 2019 from 12 June to 15 August in 2018 and 12 June through 13 August in 2019. Hurdle models were used to assess the effects of climatic variables and cicadas on copperhead abundance. The prospective set of explanatory variables to be included in the models were average temperature, average relative humidity, daily precipitation, GDD, moon phase, and cicada abundance (Figure 5). Photoperiod and GDD were correlated (r = -0.95), so photoperiod was excluded from the model set because it explained less variation in the response (Photoperiod-copperhead: $R^2 = 0.0441$; GDD-copperhead: $R^2 = 0.16$). Further, the VIF test performed determined all other variables could be retained in the models.

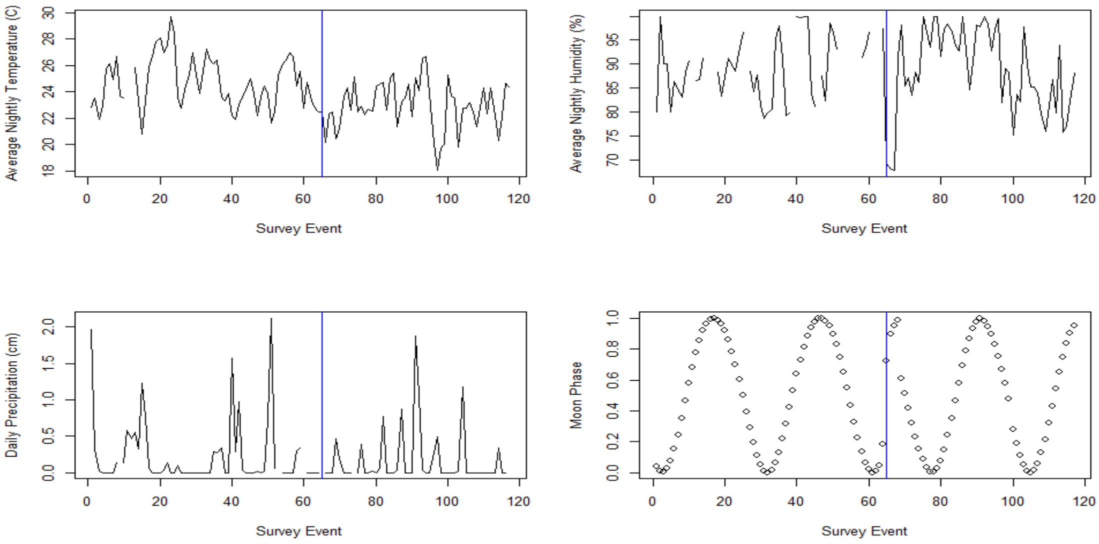


Figure 5. Climatic variables and moon phase for 2018–2019 aligned by survey event at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. Survey Event 65 represents the shift to 2019 which is signified by a blue line.

The set of 28 candidate models best fit to negative binomial hurdle models, and after AIC model selection, the top 5 models were model averaged (Table 4; Table 5). Based on the model-averaged, zero-hurdle coefficients, GDD and abundance of cicadas had a direct impact on the initial arrival of copperheads at the site (Table 6) (Figure 6; Figure 7). The count model indicated average nightly temperature, GDD, and cicada abundance were directly related to copperhead abundance throughout the season (Table 6). This indicated that GDDs and cicada abundance were an initial cue for copperheads to arrival at their summer foraging habitat while temperature and cicada abundance influenced nightly abundance of copperheads (Table 6) (Figure 6; Figure 8).

Table 4. Full models compared using AIC scores to determine the best fitting distributions for further analysis for both Eastern Copperhead (*Agkistrodon contortrix*) models (left) and the cicada models (right) both model sets contained all climate variables and moon phase. The best fit distributions in both cases were hurdle models using negative binomial distributions.

Copperhead		Cicada	
Distribution	AIC	Distribution	AIC
Hurdle (neg. bin.)	512.63	Hurdle (neg. bin.)	491.70
Negative binomial	538.28	Hurdle	532.94
Hurdle	545.59	Negative binomial	540.00
Poisson	557.2	Gaussian	594.70
Gaussian	615.94	Poisson	776.91

Table 5. All candidate hurdle negative binomial models with Eastern Copperhead (*Agkistrodon contortrix*) abundance as the response variable and predictor variables assigned individually, in triplets and contained in a full and null model. The top five models were selected for model averaging.

Copperhead Models	K	Log-likelihood	AIC	Δi	W	Copperhead Models	K	Log-likelihood	AIC	Δi	W
Average_TA+Cicada+GDD	4	-238.1	494.11	0.00	0.82	Average_TA+RHA+Cicada	4	-257.8	533.64	39.53	0.00
GDD+Cicada+Moon	4	-240.6	499.22	5.11	0.06	RHA+Cicada+Moon	4	-257.9	533.87	39.76	0.00
GDD+Cicada+Precip	4	-240.7	499.37	5.26	0.06	Precip+Cicada+Moon	4	-258.3	534.65	40.54	0.00
RHA+Cicada+GDD	4	-241	500.10	5.99	0.04	RHA+Cicada+Precip	4	-258.6	535.24	41.13	0.00
GDD	2	-246.4	502.78	8.67	0.01	Average_TA+Cicada+Precip	4	-258.8	535.58	41.47	0.00
Average_TA+GDD+RHA+Precip +`Moon Illumination`+ Cicada	7	-237.3	504.59	10.48	0.00	null	1	-268.8	543.57	49.46	0.00
Average_TA+GDD+Moon	4	-244	506.03	11.92	0.00	Moon Illumination	2	-267	544.07	49.96	0.00
GDD+Precip+Moon	4	-244.8	507.64	13.53	0.00	Precip	2	-268.2	546.40	52.29	0.00
Average_TA+GDD+Precip	4	-244.8	507.68	13.58	0.00	Average_TA	2	-268.3	546.56	52.46	0.00
GDD+RHA+Moon	4	-245.1	508.23	14.12	0.00	RHA	2	-268.4	546.72	52.61	0.00
Average_TA+RHA+GDD	4	-245.3	508.64	14.53	0.00	Average_TA+Precip+Moon	4	-265.8	549.61	55.50	0.00
GDD+Precip+RHA	4	-245.6	509.25	15.15	0.00	Average_TA+RHA+Moon	4	-266.3	550.52	56.41	0.00
Cicada	2	-259.9	529.73	35.62	0.00	RHA+Precip+Moon	4	-266.3	550.56	56.45	0.00
Average_TA+Cicada+Moon	4	-257.6	533.11	39.00	0.00	Average_TA+RHA+Precip	4	-267.3	552.67	58.57	0.00

Table 6. Model-averaged estimates and confidence intervals for response variables used in Eastern Copperhead (*Agkistrodon contortrix*) hurdle modeling used to determine which variables contributed significantly to copperhead initial occurrences (zero) and abundance of copperheads at the site (count). The model-average estimate and unconditional standard error (UnSE) depict directionality of the relationship, and bold variables represent those that were significant based on confidence intervals not overlapping zero.

			85% Confidence Interval	
	Model average estimate	**UnSE**	**Lower**	**Higher**
Zero				
Average Temperature	0.0141	0.1753	-0.2383	0.2666
Cicadas	**0.1937**	**0.1224**	**0.0174**	**0.3699**
Growing Degree Days	**11.7450**	**3.3661**	**6.8978**	**16.5923**
Precipitation	-0.0368	0.0898	-0.1660	0.0925
Relative humidity	-0.0008	0.0040	-0.0066	0.0051
Moon Phase	-0.0693	0.1287	-0.2546	0.1160
Count				
Average Temperature	**0.0716**	**0.0316**	**0.0262**	**0.1171**
Cicadas	**0.0363**	**0.0117**	**0.0194**	**0.0531**
Growing Degree Days	**1.1524**	**0.4595**	**0.4908**	**1.8140**
Precipitation	-0.0076	0.0119	-0.0247	0.0095
Relative humidity	-0.0001	0.0004	-0.0006	0.0005
Moon Phase	-0.0082	0.0136	-0.0278	0.0115

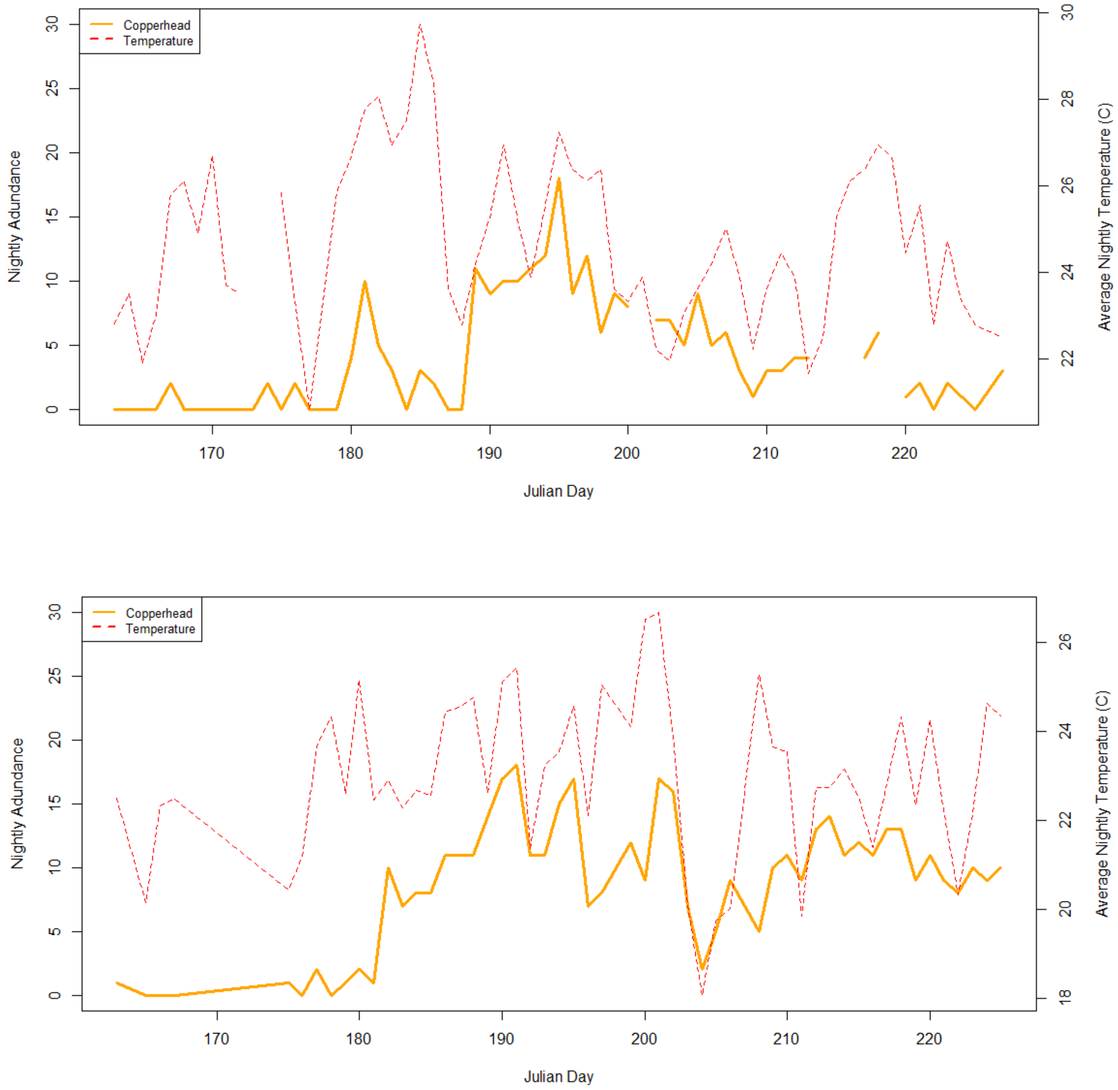


Figure 6. Eastern Copperhead (*Agkistrodon contortrix*) nightly abundance was it relates to average nightly temperature over the course of our study period from 2018 (top) to 2019 (bottom) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. As temperature increases throughout the season, the copperhead abundance increases.

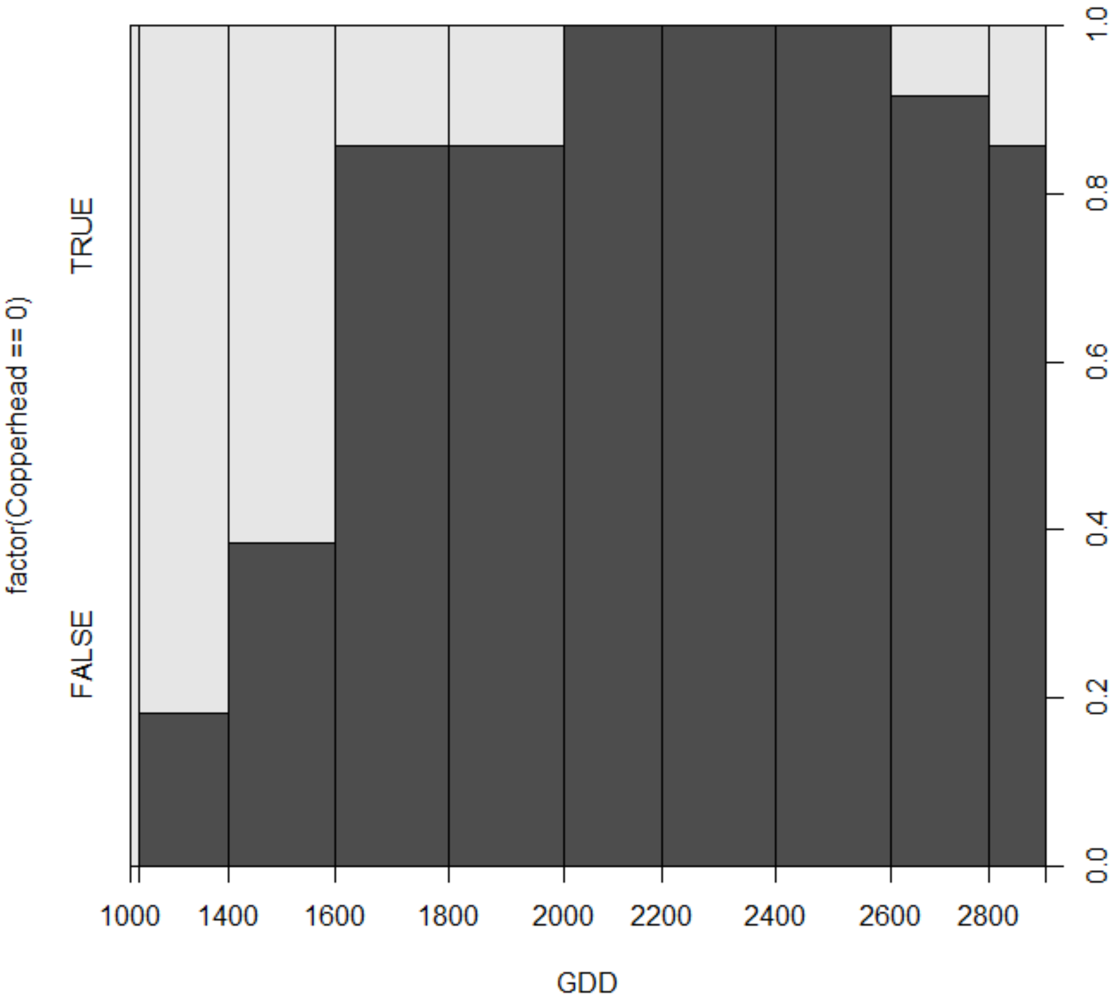


Figure 7. Initiation of Eastern Copperhead (*Agkistrodon contortrix*) arrival at the foraging site based on growing degree day accumulation. The increase in GDD accumulation was associated with the arrival of copperheads at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. The value “True” corresponds to the predicted snake arrival at the site while false expects no snakes.

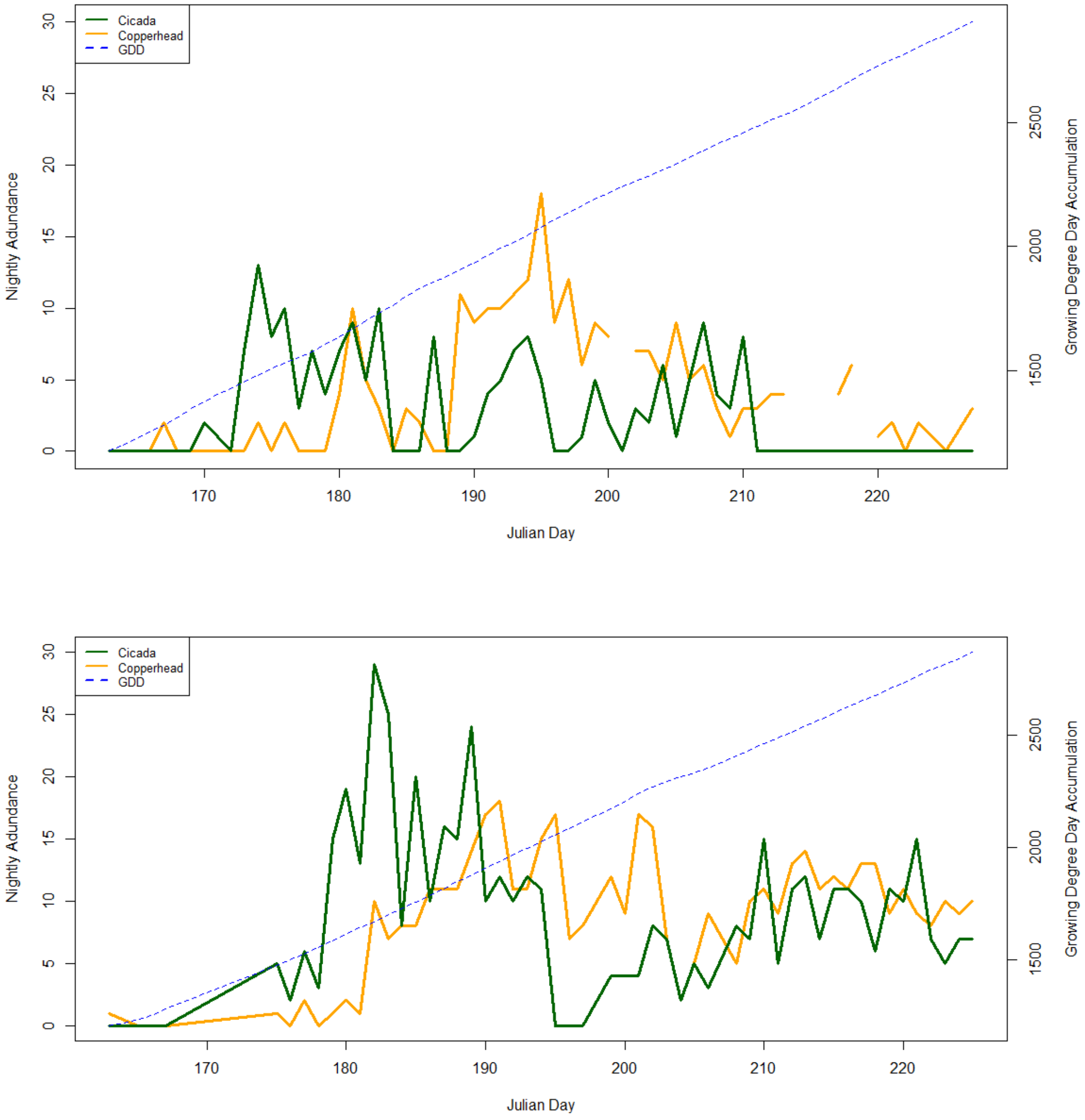


Figure 8. The nightly abundances of Eastern Copperheads (*Agkistrodon contortrix*) and annual cicadas overlaid with the fluctuations in GDDs across 2018 (top) and 2019 (bottom) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Cicada Emergence

Cicada emergence began in mid to late June and lasted until mid-August in 2018, when a total of 233 cicadas emerged, and in 2019, when a total of 824 cicadas were observed (Table 1; Figure 9). The 2018 emergence began later and ended earlier than 2019 and was more sporadic. Overall patterns in 2018 were consistent with emergence in 2019, with the exception of late July to early August with two distinct peaks (Figure 9). In 2019, male cicadas emerged 4 days prior to females at the start of each emergence event (Figure 10). However, the final sex ratio in 2019 was 52% male (345 individuals) and 48% female (317 individuals), which is not statistically different from 1:1 (D = 0.2449, p = 0.1058) (Figure 11).

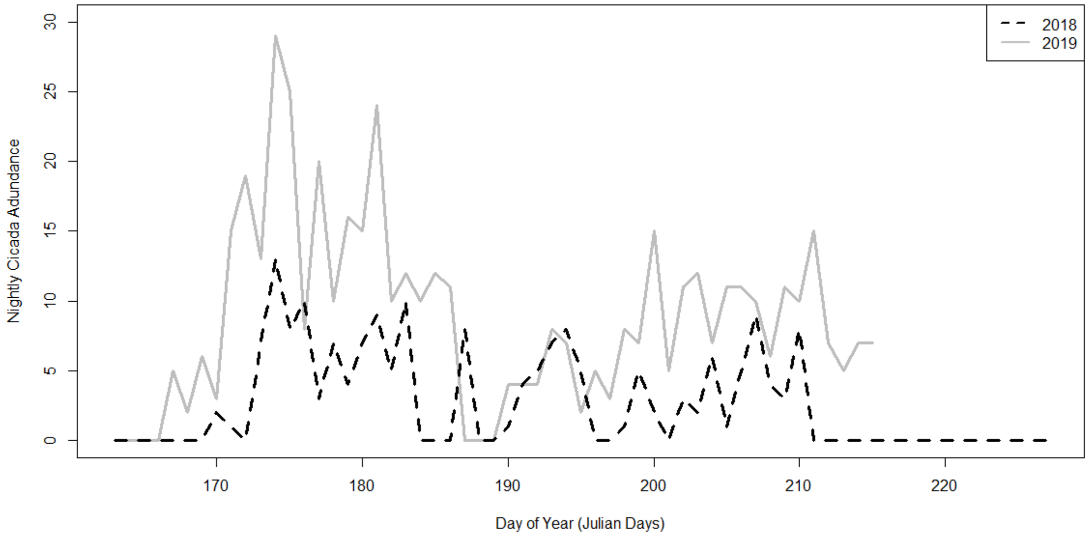


Figure 9. Nightly abundance of cicadas across the summers of 2018–2019, visualized using Julian days, at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

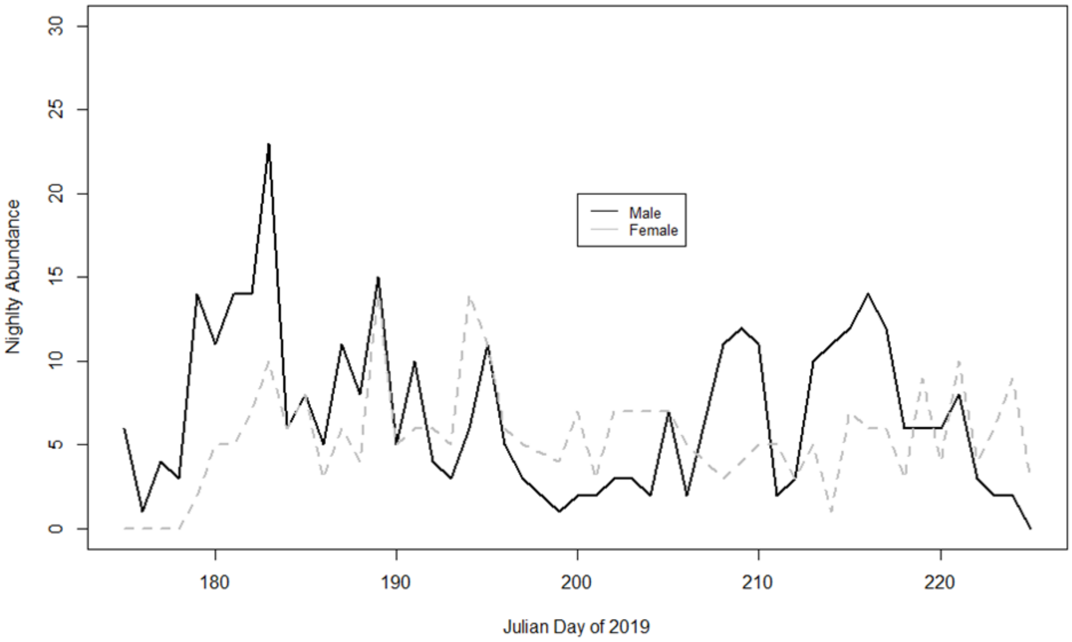


Figure 10. Nightly abundance of male and female cicadas throughout the summer of 2019 at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. While there was no difference between male and female abundances, male cicadas emerged four days prior to female cicadas, and an influx of males always preceded spikes in female emergence.

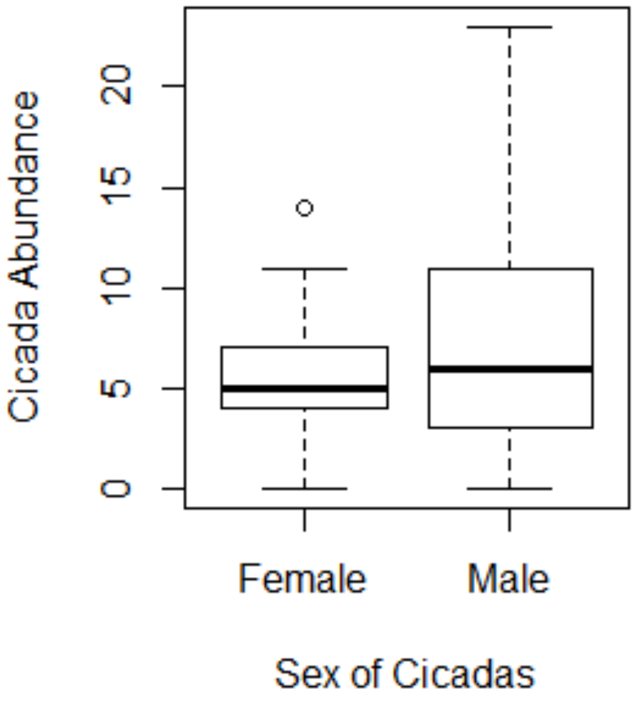


Figure 11. Box-Whisker plot visualizing the nightly abundances of female and male annual cicadas using median as central tendency and completing the box with upper and lower quartiles before extending out to the maximum and minimum extremes leaving only outliers as individual points. Exuvia were collected during visual surveys from June to August 2019 at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. This shows that there is no difference between male and female abundances.

Cicadas & Climate

The AIC model selection approach described for copperheads was also used for cicadas. Because GDD and photoperiod were correlated (GDD-photoperiod, r = -0.95; GDD-cicada, $R^2 = 0.026$; photoperiod-cicada, $R^2 = 0.002$), only photoperiod was included in the model because it had a better explanation of variation in cicada abundance. Like the copperhead models, the best fitting distribution was a negative binomial (Table 4). A set of 27 candidate models were compared using AIC model selection and model averaging was performed using the top 20 models whose weights accounted for at least 0.99 of the total weight (Table 7). Based on the zero-hurdle coefficients, average temperature and relative humidity negatively related to cicada emergence (Table 8). This indicates that temperature and humidity may cue initial cicada emergence (Figure 12; Figure 13; Figure 14). Based on the count-hurdle coefficients, relative humidity has positive, direct impact on cicada emergence abundances (Table 8). This indicated that relative humidity may cue higher emergence rates in annual cicadas (Figure 16). Moon phase was found to be negatively related to cicada emergence in the count-hurdle coefficients (Table 8). This indicates that illuminated moon phases may be a cue for nightly cicada emergence rates throughout the season (Figure 15).

Table 7. All negative binomial hurdle candidate models for annual cicadas with all predictive values assigned individually, in triplets, and in a full and a null model. The data was collected from visual surveys from June to August in 2018–2019. The top 20 models were included in model averaging.

Model	K	Log-likelihood	AIC	Δi	W	Model	K	Log-likelihood	AIC	Δi	W
Average_TA+RHA+Moon Phase	4	-266.3	507.087	0	0.35894	Photoperiod+Precip+Moon Phase	4	-244.8	515.414	8.3265	0.00558
Average_TA+Precip+Moon Phase	4	-265.8	508.765	1.6778	0.15513	Photoperiod+Moon Phase	3	-241.4	515.449	8.3614	0.00549
Average_TA+Photoperiod+RHA+Precip+Moon Phase	6	-230.8	509.135	2.0478	0.12893	RHA	2	-268.4	515.453	8.3659	0.00548
RHA+Moon Phase	3	-238.6	510.11	3.0229	0.07918	Average_TA	2	-268.3	515.738	8.6508	0.00475
RHA+Precip+Moon Phase	4	-266.3	510.464	3.3765	0.06635	Average_TA+Photoperiod+Precip	4	-244.8	515.977	8.8893	0.00421
Average_TA+Moon Phase	3	-239.5	511.285	4.1974	0.04401	Average_TA+RHA+Photoperiod	4	-245.3	516.883	9.7956	0.00268
Average_TA+RHA+Precip	4	-267.3	511.833	4.7457	0.03346	null	1	-268.8	517.398	10.3107	0.00207
Moon Phase	2	-267	512.755	5.668	0.0211	Precip	2	-268.2	517.885	10.7971	0.00162
Precip+Moon Phase	3	-240.8	512.888	5.8005	0.01975	Average_TA+Photoperiod	3	-239.9	517.914	10.8265	0.0016
Average_TA+RHA	3	-238.9	513.1	6.0122	0.01776	RHA+Photoperiod	3	-241	519.159	12.0712	0.00086
Photoperiod+RHA+Moon Phase	4	-245.1	513.917	6.8292	0.01181	Photoperiod+Precip+RHA	4	-245.6	519.319	12.2316	0.00079
Average_TA+Precip	3	-240.5	514.024	6.9368	0.01119	Photoperiod	2	-246.4	519.601	12.5136	0.00069
Average_TA+Photoperiod+Moon Phase	4	-244	514.324	7.2369	0.00963	Photoperiod+Precip	3	-240.7	519.838	12.751	0.00061
RHA+Precip	3	-241	515.159	8.0712	0.00634						

Table 8. Model-averaged estimates and confidence intervals for response variables used in annual cicada hurdle modeling used to determine which variables contributed significantly to cicada initial emergences (zero) and abundance of cicadas at the site (count). The model-average estimate and unconditional standard error (UnSE) depict directionality of the relationship, and bold variables represent those that were significant based on confidence intervals not overlapping zero.

			85% Confidence Interval	
	Model average estimate	**UnSE**	**Lower**	**Higher**
Zero				
Average Temperature	**-0.275**	**0.127**	**-0.458**	**-0.092**
Photoperiod	0.028	0.151	-0.189	0.246
Precipitation	-0.518	0.382	-1.067	0.032
Relative humidity	**-0.050**	**0.033**	**-0.097**	**-0.003**
Moon Phase	0.888	0.704	-0.126	1.903
Count				
Average Temperature	-0.005	0.034	-0.053	0.043
Photoperiod	-0.001	0.047	-0.069	0.067
Precipitation	-0.076	0.122	-0.252	0.100
Relative humidity	**0.015**	**0.009**	**0.003**	**0.028**
Moon Phase	**-0.567**	**0.203**	**-0.860**	**-0.274**

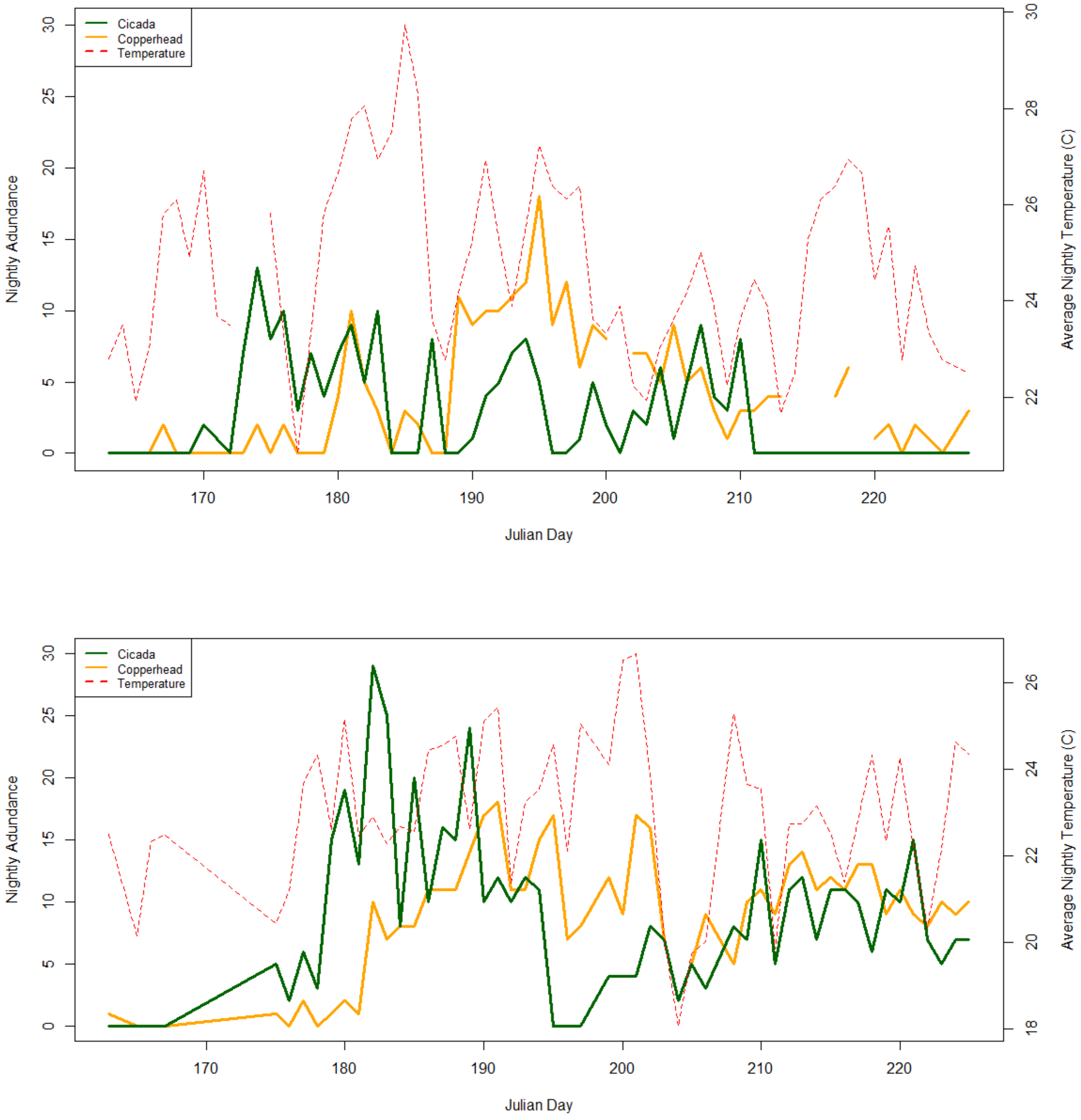


Figure 12. The nightly abundances of Eastern Copperheads (*Agkistrodon contortrix*) and annual cicadas overlaid with the fluctuations of average temperatures across 2018 (top) and 2019 (bottom) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Figure 13. The interaction between Eastern Copperhead (*Agkistrodon contortrix*) abundance and annual cicada emergence with precipitation over time considering the summer of 2018 (top) and 2019 (bottom) at a recreational site within the Cumberland Ranger District, Daniel Boone National Forest, KY. The cicada abundance was found to only correspond to precipitation inversely with the initiation of emergence. However, both initiations of emergence occurred on a night with precipitation following days without rain.

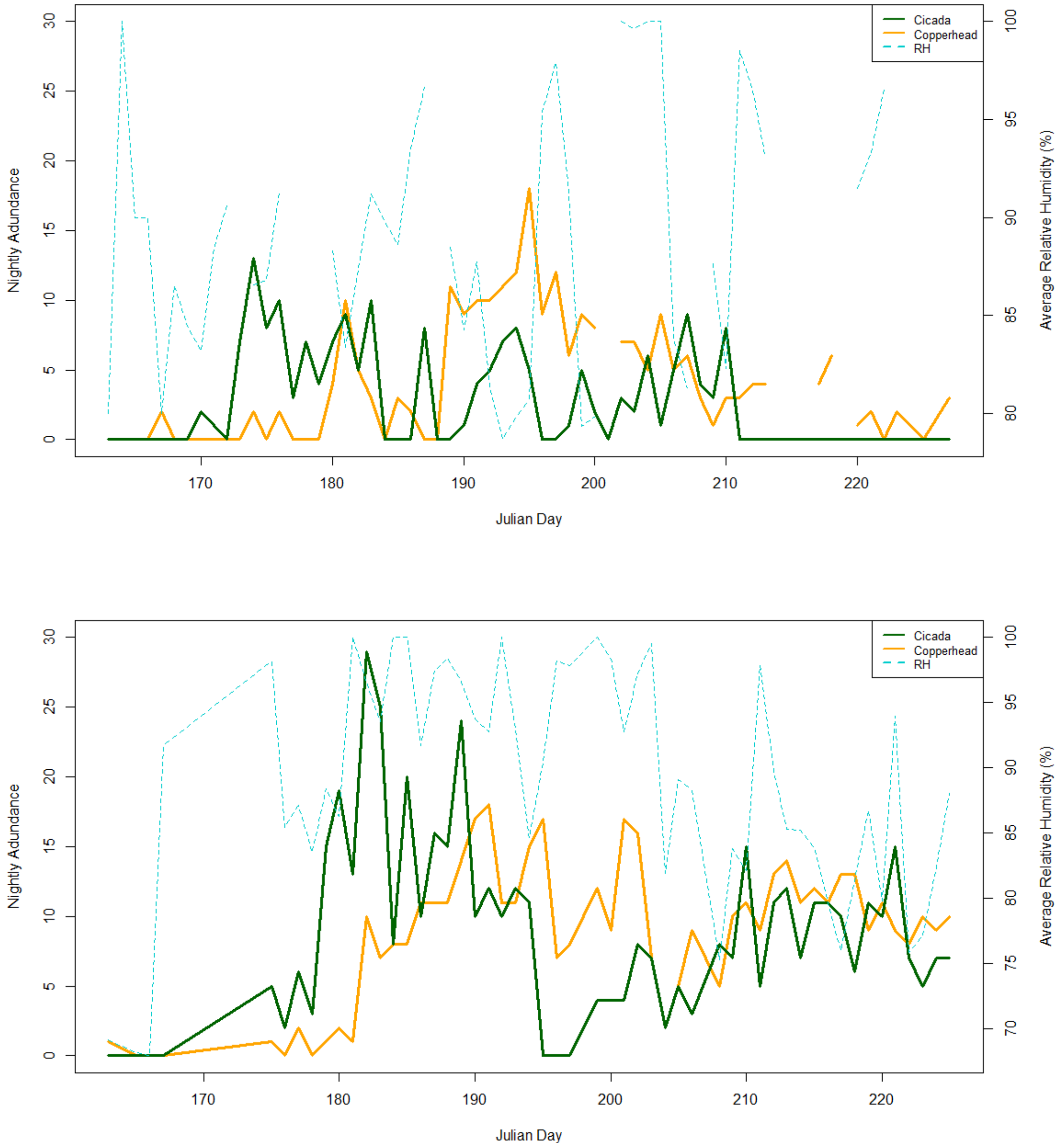
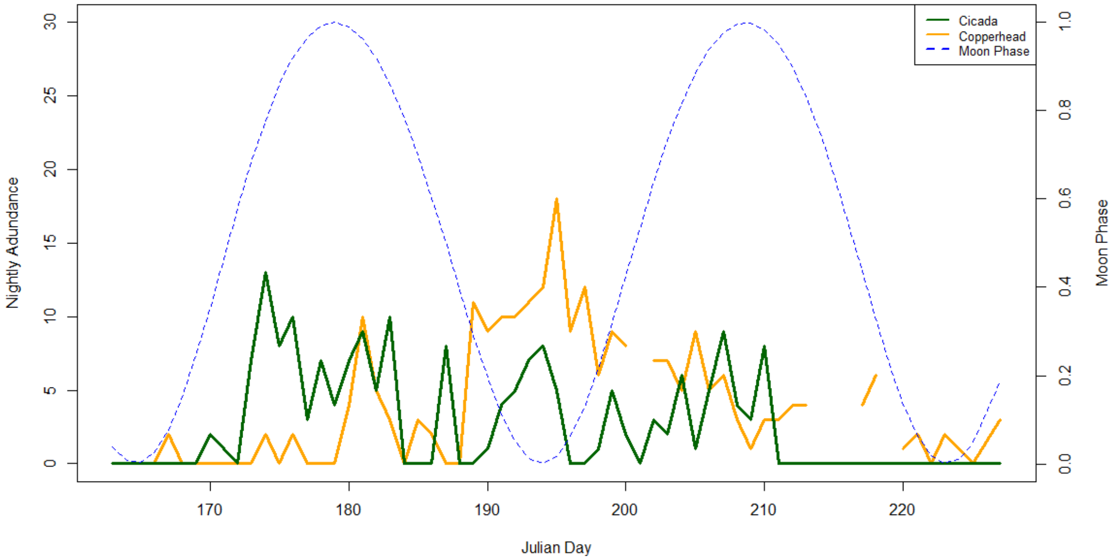


Figure 14. The nightly abundances of Eastern Copperheads (*Agkistrodon contortrix*) and annual cicadas overlaid with the shifts in averages relative humidity across 2018 (top) and 2019 (bottom) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



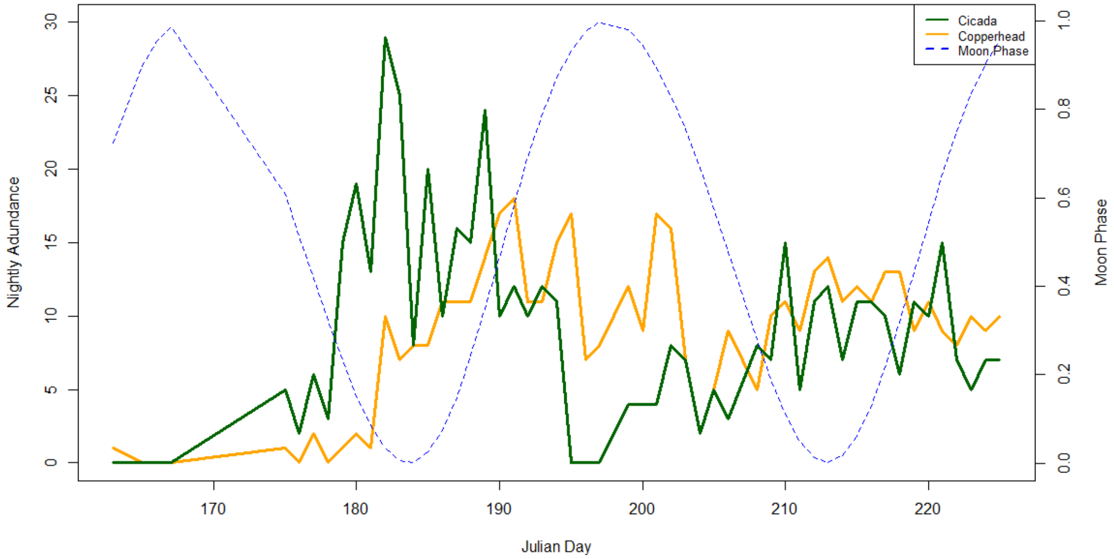


Figure 15. The nightly abundances of Eastern copperheads (*Agkistrodon contortrix*) and annual cicadas overlaid transitioning of moon phase across the summers of 2018 (top) and 2019 (bottom) at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Cicada Tree Preference

When evaluating cicada preference within the site, cicadas did not emerge preferentially on any tree species, emerging within expected ratios on all trees (X^2_{10}= 25.46, p = 0.99; Table 9). Most exuvia (237 of 824; 28.8%) were found in White Ash Trees (*Fraxinus americana*), but this was the most abundant tree species within the site (36 of 79; 45.6%) (Table 9). No difference was found between male and female cicadas in tree species selection (w_{47} = 42, p-value = 0.152) (Figure 16).

Cicada emergence preference within the habitat was also examined using a generalized linear model with cicada abundance as the response variable and DBH, tree species, and tree height as potential predictor variables. DBH was removed due to high correlation with tree height (r = 0.89) and low explanation of variation in cicada abundance (DBH-cicada, R^2 = 0.004; Tree height-cicada, R^2 = 0.0064). While the best fitting model was the null model, competing models were included in model averaging to find that DBH, species, and tree height did not significantly impact trees selected for ecdysis (Table 10; Table 11). Additionally, no trends were observed when accessing overall directional emergence on the tree trunk using all primary cardinal directions (Figure 17).

Table 9. Number of cicadas observed emerging on each tree species, how many of each tree were climbed, and expected number of trees to be climbed based on available trees at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. Cicadas were found to not select for specific trees during emergence and cicada abundances on each tree species were within the expected ranges. Proportion represents the frequency of that tree species within the site.

Tree Species	Cicadas	Tree Counts	Proportion	Expected Tree Use
American Beech	28	2	0.03	1.76
Black Walnut	17	2	0.03	1.76
C Dogwood	8	1	0.01	0.88
Red Maple	102	12	0.16	10.54
Pinus spp.	10	1	0.01	0.88
Redbud	8	2	0.03	1.76
Shagbark Hickory	3	1	0.01	0.88
Tulip Poplar	81	12	0.16	10.54
White Ash	237	36	0.49	31.62
White Pine	27	4	0.05	3.51
American Hickory	0	1	0.01	0.88

df = 10

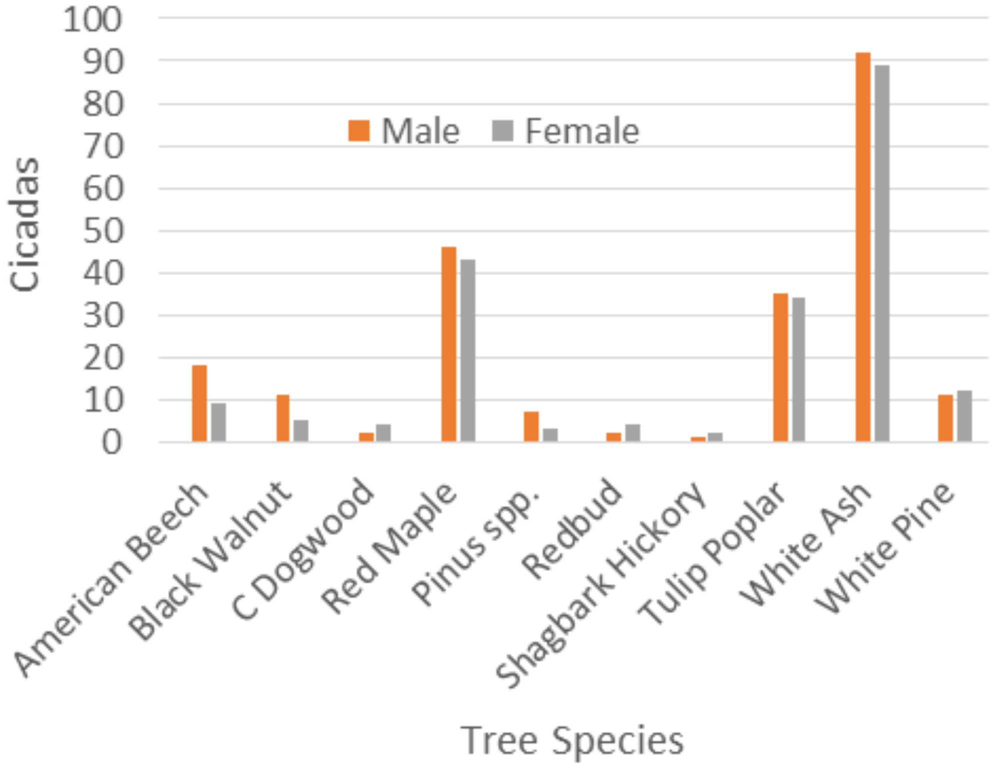


Figure 16. Number of male and female cicadas observed emerging on each tree species at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. There was no difference between the sexes in terms of emergence tree location.

Table 10. All candidate GLM models with Annual Cicada abundances as the response variable and predictor variables assigned individually, as a full, and a null model. All models were included in model averaging.

Model	K	Log-likelihood	AIC	Δi	W
null	1	-506.9277	1015.9	0	0.50519
Tree Height	2	-506.8029	1017.6	1.7	0.215926
Tree Species	2	-506.8818	1017.8	1.9	0.195378
Tree Species + Tree Height	3	-506.774	1019.5	3.6	0.083507

Table 11. Model-averaged estimates and confidence intervals for response variables used in the GLM to determine if any preferences in emergence location of Annual Cicada existed across two tree characteristics. The model-averaged estimate and standard error (SE) depict directionality of the relationship, and bold variables represent those that were significant based on confidence intervals not overlapping zero.

			85% Confidence Interval	
	Model-averaged Estimates	**Std. Error**	**Lower**	**Upper**
Tree Height	0.0005467	0.002486	-0.006944	0.01169
Tree Species	0.0013358	0.009869	-0.034313	0.04687

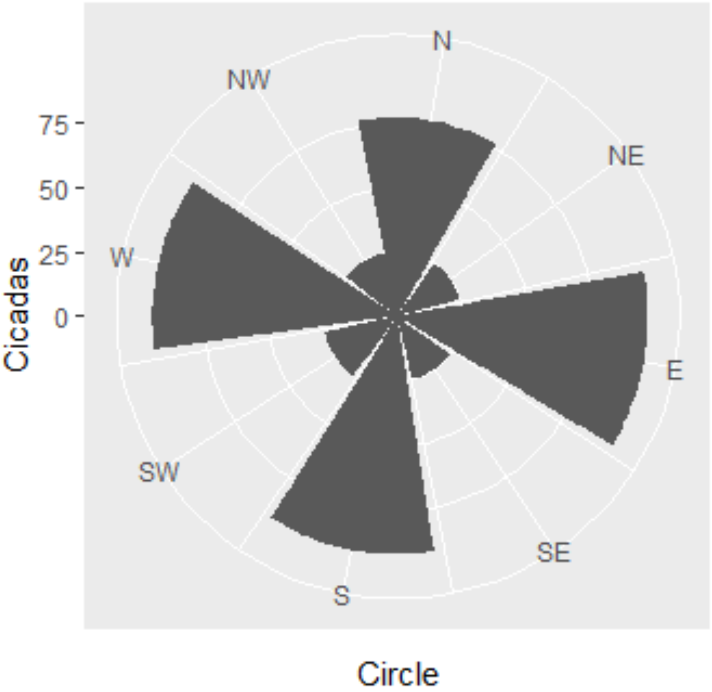


Figure 17. Number of cicadas observed emerging based on the cardinal direction that nymphs were found emerging on the vertical trunk of the tree or surface, June to August 2019 at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Discussion

Climate and Copperheads

To fully understand the foraging ecology of the Eastern Copperhead, it is important to understand the factors cuing copperheads to move to the site and remain there to feed. The initiation and fluctuations of copperhead abundances at foraging areas were predicted by climatic variables and cicada emergence. Snakes have long been understood to utilize environmental factors, especially temperature, in the management of their activity regiment (Buchanan et al., 2016). Past studies have noted the importance of environmental conditions on the spatial ecology of copperheads (Novak, 2017; Smith et al., 2009; Sutton et al., 2017). This effect of temperature on abundance is supported broadly as increased temperature often relates to increased activity, digestive function, and extended above-ground periods in many snakes (Eskew and Todd, 2017; Needleman, Neylan, and Erickson, 2018; Sanders and Jacobs, 1981). As ectotherms, copperheads use environmental temperatures to thermoregulate their own body temperatures, which likely impacts their activity budget (Mueller and Gienger, 2018). Similarly, some snake species respond to increased temperatures by becoming more active during cooler periods or more active nocturnally like copperheads (Butler, Malone, and Clemann, 2005; Sperry, Ward, and Weatherhead, 2013). Carter (2012) found that copperheads limited nocturnal behavior on nights below 21° C and that foraging behaviors were exhibited on nights exceeding 25° C. In Kentucky, copperhead preferred temperatures were found to be right around the foraging threshold ranging from 24.9 to 27.9° C (Mueller and Gienger, 2018). Copperhead thermoregulation has been considered more similar to thermoconformity, supporting that warmer temperatures would be more conducive to greater movement and abundances of copperheads while cooler days coincide with copperheads seeking refugia to reduce energy costs (Mueller and Gienger, 2018).

Copperheads may use the Koomer Ridge Campground primitive site because of the role of habitat structure on the thermal attributes of the site (Pringle, Webb, and Shine, 2003; Shoemaker, Johnson, and Prior, 2009). Open habitat or artificial canopy openings have increased thermal qualities making them crucial habitat for thermoregulation in many reptile species (Carter, 2012; Shoemaker, 2007; Shoemaker, Johnson, and Prior, 2009). Sartorius, Vitt, and Colli (1999) found that *Ameiva ameiva*, a tiied lizard, preferred anthropogenically disturbed habitat surrounded by forest due to increased temperatures experienced in the opening allowing them to increase foraging activity above that possible in forested habitat. This may reveal possible explanation for how copperheads are utilizing the site nocturnally. Artificial canopy openings are regularly used by many snake species for thermoregulation such as copperheads, Timber Rattlesnakes (*Crotalus horridus*), Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*), and Eastern Hognose Snakes (*Heterodon platirhinos*) (Carter, 2012; Plummer et al., 2000; Sisson, 2017; Shoemaker, 2007). However, snakes are noted to most commonly use canopy openings to thermoregulate when gravid, while non-gravid individuals tend to avoid these habitats likely due to predation risks unlike tiied lizards (Sartorious, Vitt, and Colli, 1999; Sisson, 2017; Shoemaker, 2009). Carter (2012) found that copperheads selectively used power-line right-of-ways (ROW) possibly due to the increased temperature. A powerline ROW provides an artificial canopy opening similar to our study site in the Daniel Boone National Forest.

Copperheads with Precipitation and Humidity

Copperhead arrival and abundance at the foraging site was not affected by precipitation or humidity. Larger clutch sizes or increased reproductive output have been observed with increased precipitation (Mengak, 2001; Seigel and Fitch, 1985; Smith et al., 2019). However, parturition does not occur within the site so this effect remains unknown within our population. Brown and Shine (2002) had similar results concluding that weather variables, including precipitation and humidity, were not good predictors of numbers of individuals. Precipitation, humidity, and other weather variables may be more important cues in tropical snake species where variation in precipitation is greater compared to more consistent temperatures (Brown and Shine, 2002; Daltry et al., 1998; Marques, Almeida-Santos, and Rodrigues, 2006). Tropical climates have more sporadic or seasonal rain and more dramatic variation in humidity so coordinating activity in these systems may be beneficial to prevent dehydration or to locate prey dependent on rainfall (Daltry et al., 1998; Eskew and Todd, 2017). Temperate climates tend to have more evenly distributed rainfall and consistent humidity, so it is likely less limiting for copperhead behavior (Daltry et al., 1998; Eskew and Todd, 2017). However, Eskew and Todd (2017) did find a negative relationship with precipitation and snake activity in temperate snake assemblages. Similar to copperheads, Tiger Snake (*Notechis scutatus*) activity did not change due to relative humidity or precipitation (Butler, Malone, and Clemann, 2005).

Copperheads and Moon Phase

Copperheads did not show any changes in abundance in relation to moon phase. These results are similar to what was found in ratsnakes (Sperry, Ward, and

Weatherhead, 2013). However, Florida Cottonmouths (*A. piscivorus conanti*) and Water Python (*Liasis fuscus*) activity was correlated with moonlight levels (Brown and Shine, 2002; Lillywhite and Brischoux, 2012). Some visual hunting snakes theoretically benefit from the presence of moonlight (Lillywhite and Brischoux, 2012; Sperry, Ward, and Weatherhead, 2013); however, copperheads locate cicadas through stimulations from chemosensory, acoustic, tactile, and visual cues (Fitch, 1960; Hendricks, 2019). Likewise, nocturnal predators have been shown to adapt to well-lit nights by being more cryptic (Lillywhite and Brischoux, 2012). Since copperheads are not completely reliant on visual cues, it is logical that moon phase does not affect behavior. Some snakes do experience reduced activity when there is increased moon illumination, but relationships were weak and likely due to predation risk caused by visibility (Eskew and Todd, 2017). Finally, copperheads do not have many nocturnal predators so predation risk is not likely a concern on highly illuminated nights (Lillywhite and Brischoux, 2012; Sperry, Ward, and Weatherhead, 2013). Additionally, nocturnal predators may be deterred by the volume of humans camping in the recreational areas further alleviating this pressure. Like Eskew and Todd (2017), the measure of moon phase does not consider cloud cover so it may be that true moon illumination influences copperhead activity, especially with the effect of moon phase on cicadas. This will be evaluated as part of a future study at the site.

Copperhead GDD

Copperhead abundance was not correlated with photoperiod. While annual cycles in many species such as birds are cued by changes in day length, snakes using underground hibernacula are not exposed to photoperiod enough to observe changing conditions indicating copperheads do not utilize photoperiod as a critical initiator of spring emergence (Lutterschmidt, LeMaster, and Mason, 2006). Rather than cuing on temperature alone, copperhead's initial arrival and fluctuations in abundance throughout the season were better explained by the accumulation of growing degree days (Figure 12). While temperature is consistently tied to the activity season of reptiles (Nelson, et al., 2000), other thermal variables have been found to serve as a zeitgeber for circannual cycling in snakes (Girons, 1982; Lutterschmidt, LeMaster, and Mason, 2006). Guisan and Hofer (2003) found that reptilian distribution was largely determined by temperature-related factors. Red-sided Gartersnakes (*Thamnophis sirtalis parietalis*) cue emergence using a critically low temperature during hibernation rather than increased ground temperatures (Lutterschmidt, LeMaster, and Mason, 2006). Eastern Ribbonsnakes (*T. saurita*) emerge when temperatures steadily increase indicating that an accumulation or increase in heat is more important than simply warm temperatures to cue emergence (Todd, Amiel, and Wassersug, 2009). The impact of GDDs on growth and development has been considered for decades by entomologists and agriculturalists, so it should be no surprise the role thermal integrals have on the growth and activity of ectotherms (Neuheimer and Taggart, 2007). Neuheimer and Taggart (2007) state GDDs allow life cycle elements to be scaled to the physiology driving ectotherms. Additionally, GDDs have been used to link and predict the life events of birds, primarily nesting, and overlay them with emergence or hatching of pest species for agricultural management which may be a useful application for copperheads and cicadas (Courter, 2012; Sockman and Courter, 2018).

Copperheads and Cicadas

Annual cicada abundance predicted the arrival and increased abundance of copperheads within our study site. Copperheads forage on cicadas throughout their range and may selectively choose them based on seasonal availability (Lagresse and Ford, 1996; Schalk et al., 2018). Recent observations indicate this relationship plays a larger role in the lifecycle of copperheads than previously understood (Hendricks, 2019; Lagresse and Ford, 1996). Annual cicadas are consistently important food sources (Chiavacci, Bednarz, and McKay, 2014). Increased fecundity in copperheads has been found in years with periodical cicada emergence (Smith et al., 2019). Due to the large influx of nutrients of periodical cicadas, Smith et al. (2019) suggested this relationship is limited to periodical cicadas. Contrary to this, Hendricks (2019) observed copperhead congregations arriving yearly to feed upon annual cicadas at our study site. Schalk et al. (2018) found that dietary composition of copperheads was related to abundance of prey. The emergence of annual cicadas appears to be a preemptive indicator of copperhead congregations, suggesting that annual cicadas are both a consistent food source for copperheads and may represent a larger portion of their diet in regions where accessible. Fitch (1960) noted the regularity of copperheads feeding on a species of annual cicadas (*N. pruinosus*), which were the second most abundant prey item consumed by copperheads. Cicadas have been considered a seasonal element of copperhead diet (Ditmars, 1907; Fitch, 1960; Lagresse and Ford, 1996). Consistent with that would be the increased abundances or activity of copperheads when cicadas are emerging; similar findings noted ratsnakes’ nocturnal behavior increasing seasonally with the transition between avian and mammalian prey (Fitch, 1960; Sperry, Ward, and Weatherhead, 2013).

The seasonality of the large influx of nutrients associated with annual cicada emergence allows copperheads to focus in on this prey source and consume larger quantities. Likewise, Santos et al. (2006) found that the viperine snake, *Natrix maura*, selected their prey species based on prey abundance and that they will opportunistically or seasonally alter their diets to match what is most abundant. Contrary to snake species eating primarily large-mass prey items, copperheads are consuming low-mass prey in higher quantities likely due to the decreased energy expenditure of catching relatively immobile cicadas and their high availability (Shine et al., 2004). Emergent cicada nymphs typically only move a short distance before beginning ecdysis leaving them stationary until fully molted and dried. Similar behaviors are documented in Turtle-Headed Sea Snakes (*Emydocephalus annulatus*) as they actively foraged for small, immobile, defenseless prey, which were typically eggs of several fish species (Shine et al., 2004). Shine et al. (2004) noted that many snakes share this trait of consuming eggs, larvae of insects, and amphibians in multitudes including venomous species such as the Black Mamba (*Dendroaspis polyepis*).

Overall, there is likely an interplay between thermoregulation and prey availability in determining nightly foraging copperhead abundances (Sperry, Ward, and Weatherhead, 2013; Weatherhead et al., 2012). Copperheads remained active through the entire emergent period of cicadas; some level of copperhead foraging activity was observed even on suboptimal temperature nights (e.g., < 25° C). This is likely due to the copperheads synchronizing their activity with that of their prey over thermoregulation

(Sperry, Ward, and Weatherhead, 2013). While this study was performed in Kentucky, similar congregations of copperheads with cicadas have been noted throughout copperhead ranges anecdotally throughout scientific literature and news outlets. Because the timing of these congregations is linked to yearly emergence peaks of annual cicadas, understanding the cues that predict the timing, distributions, and fluctuations in cicada emergence will lead to better predicting the timing of copperhead abundances and activity.

Cicada Emergence

Cicadas were found to emerge in a near-even sex ratio in 2019. Similar trends have been seen in various cicada species, including *Cicadette calliope* and *M. cassini* (Callaham et al., 2000; Karban, 1983). While it is typical for the ratio to be even upon the completion of the season, the sex ratio does vary throughout the season for both annual and periodical cicadas (Sato and Sato, 2015; Whiles et al., 2001). Male cicadas at Koomer Ridge emerged 4 days prior to the surge of female cicadas (Figure 10). Likewise, each additional emergence surge was initiated by male cicadas with a reciprocate surge of females. *Tibicen aufifera*, *C. facialis*, *G. nigrofascata*, and *M. cassini* display protandrous emergence with males initially emerging, likely to establish chorusing epicenters, before females emerge (Callham et al., 2000; Sato and Sato, 2015; Whiles et al., 2001). Watanabee, Mori, and Yoshitaka (1999) found that this is also true for the emergence of mayflies (*Ephoron shigae*).

Increased emergence volume in 2019 may be due in part to the continued management of the campsite, allowing the gap to remain open and increasing the habitat stability for cicada population growth and potentially increasing brood overlaps.

Managed areas have been considered beneficial for periodical cicadas due to the reduced effects of succession sustaining it as preferred habitat longer (Oberdorster and Grant, 2006). Alternatively, weather variables could be influencing emergence rates; several large storms depositing over 5 cm of rain could have impacted emergence in 2018 or the impact of humidity being maintained at higher volumes longer in the 2019 season which may have influenced the sustained increasing volume of cicadas (Figure 5). The most likely explanation is the “boom and bust” cycle of annual cicada abundances is that they take 2–4 years to proceed through nymphal stages, spreading their emergence across years and having annual overlap of other broods increasing volume some years compared to others (Saljoqi et al., 2010).

Climate and Cicadas

Cicada emergence was initiated by early season temperature variation. The negative relationship is likely due to the reaching of a thermal minimum threshold allowing for emergence. Heath (1968) states that periodicals likely time their emergence in part by using a minimum thermal threshold. Periodical cicadas are known to emerge after soil temperatures reach approximately 17.8 °C; their average body temperature upon emergence is 18°C (Heath, 1968). Andersen (1994) noted that annual emergence is likely driven in part by soil temperature due to its influence on development. Earlier emergence has been linked to increases in soil temperatures and delayed emergence in colder temperatures (Heath, 1968; Smith et al., 2006). Sato and Sato (2015) found that for *C. facialis* and *G. nigrofascata*, two annual cicada species, temperature accounted for 47–64% of variation in exuvia counts suggesting that late spring temperature predicts emergence phenology. Similarly, Sato and Sato (2015) found that while initiation of emergence was related to temperature, there seemed to be no relationship with fluctuations in abundance.

Thermal tolerance in cicadas impacts when they emerge and remain active in response to temperature (Sanborn et al., 2017). The least thermally tolerant cicadas are active earlier in the year; however, northerly cicadas with low maximum voluntary tolerances (MVT) are able to stay active longer than high MVT cicadas (Sanborn et al., 2017). The population at our site is composed of mostly *N. tibicen tibicen*, a northerly cicada, but it has a high MVT (34.55 +/- 2.30 °C) contrary to expectations when considered without minimum flight temperatures (MFT) (Sanborn et al., 2017). The MFT is the lowest temperature that an organism is able to fly. *Neotibicen tibicen tibicen* has a low MFT (19.03 +/- 1.31°C) more similar to *Magicicada* species allowing it to be active earlier in the summer and throughout the summer, optimizing its active period (Sanborn et al., 2017). When considering the heat torpor temperature (45.30 +/- 2.14 °C), the range of temperatures thermally acceptable for *N. tibicen tibicen* activity is a range of 26° C making it possible for extended summer exposure (Sanborn et al., 2017). The factor that allows this wide breadth for *N. tibicen tibicen* compared to *Magicicada* and some *Neotibicen* species is that it is ectothermic (Sanborn et al., 2017). This supports the findings that annual cicadas may initiate emergence earlier in the season due to a minimum thermal threshold because the thermal breadth would allow them to be active throughout summer remaining a consistent food source for cicadas throughout summer foraging.

Cicada Precipitation and Humidity

Precipitation was not found to predict initiation nor affect abundance rates of cicadas in the study; however, rainfall has been suspected to impact cicada densities (Kim et al., 2014). While this differed from our study, the initiation of emergence occurred on a night with precipitation following several days without recorded precipitation in each year of our study. Hatching dates have been previously linked to precipitation (Moriyama and Numata, 2006; Sato and Sato, 2015). The hatching of nymphs in five cicada species coincided with rain, in which some species hatched after the rainy season and others during, but they all avoided the driest periods of the year (Moriyama and Numata, 2011). Drying periods were found to negatively impact fitness of cicada nymphs mostly through desiccation (Moriyama and Numata, 2011; Sato and Sato, 2015). Wet soil is also more easily burrowed through to allow the cicadas to access the roots faster and with less energy expenditure and lower risk of predation (Moriyama and Numata, 2011). Our site did have a lowland portion whose soil could become saturated and sustain standing water when excessive rain fell. Precipitation may be a greater driving factor in Japanese species because of the wet seasons followed by very dry and hot summers making the wet seasons surrounding the summer dryness critical for hatching (Moriyama and Numata, 2011). Hatching cicadas likely rely more on precipitation than emergent nymphs, but emergence has been influenced by flooding (Chiavacci, Bednarz, and McKay, 2014). Possible explanation on how precipitation could indirectly relate to initial emergence of cicadas is that precipitation has a cooling effect on the soil, which would delay the onset of emergence while warm rains have the opposite effect of encouraging emergence

(Chiavacci, Bednarz, and McKay, 2014; Heath, 1968). However, this was not indicated in our study.

High humidity is also important for combatting desiccation risk and leads to higher cicada abundances throughout the season (Kim et al., 2014; Moriyama and Numata, 2011). Annual cicadas in Japan were found to hatch at increasing rates with higher humidity (Kim et al., 2014; Moriyama and Numata, 2011; Sato and Sato, 2015). *Magicicada cassini* was found to fly more often on humid, overcast days (Karban, 1981). Extended periods of low humidity revealed reduced hatchability with newly hatched nymphs perishing due to desiccation at 81% humidity at 25°C (Moriyama and Numata, 2006; Moriyama and Numata, 2011). These trends seem to continue with the emergence and ecdysis process as more cicadas emerge on high humidity nights. Other molting and shedding species, such as scorpions and snakes, suffer from dysecdysis when humidity is unsuitable and preferably enter ecdysis when humidity enters into suitable ranges (Carlson, Williams, and Langshaw, 2014; Garban and Farley, 2005). Possible explanation for the early negative relationship is the interaction with other climatic variables, such as temperature, shifting the minimum threshold to earlier in the season when humidity is still low.

Cicada Moon Phase

Cicadas had greater activity and higher emergence abundances with less moon illuminated or as the new moon approached. Moonlight reduces some insect and nocturnal arachnid activity as it makes them more vulnerable to predation (Nakamura and Yamashita, 1997; Williams et al., 2003). While less common, some insects show the opposite trend, such as some aquatic insect larvae that increase activity when the moon is brighter (Nowinsky, 2004). Bergh (1992) had similar findings in mites noting that light stimulated emergence and lead to phototactic behaviors. Cicadas have been connected to phototaxis as oviposition densities increase on the western aspect of trees for greater light exposure, thus improving egg development (Yang, 2006). Periodical cicadas typically chorus more during the day in intense sunlight, even shifting their location in the canopy to match directionality of the sun (Heath, 1968; Karban, 1981). Heath (1968) found that in the morning while coolest, cicadas basked while positioning their heads towards the zenith leaving their black thorax and abdomen exposed for the maximum thermoregulatory activity until they regress from the light to avoid overheating. Cicada nymphs exhibited negative phototaxis at night during the study when a flashlight beam was placed near to them, possibly because it was more visible than the current moon illumination (Nowinsky, 2004). Gu et al. (2016) noted that Korean Blockish Cicadas, *Hylaessa maculaticollis*, were found to be atypically calling at night in urban areas, due to the brightness of outdoor lights. Inferring that the brighter the night, the more active cicadas would become. However, this is not the trend observed in our population. It is possible as the season progressed, cicadas became more susceptible to predators, so emerging during a new moon is beneficial to avoid detection. While it is understood that some insects use the moon to guide orientation, it is unknown if cicada nymphs use the moon for directional orientation to climb upward (Nowinsky, 2004). Dacke et al. (2013) found that dung beetles used celestial cues, including moon and stars, to orient movement but were unable to move dung balls over straight line paths on overcast nights. Alternatively, the cicadas may locate trees and move in a straight line by interpreting polarized light, which increases with moon phase that bounces off of surfaces in the surrounding habitat (Dacke, 2014; Nowinshy, 2004). Polarized light has biological relevance to various taxa, including birds, herpetofauna, fish, insects, and crustaceans (Barta et al., 2014; Warren and Dacke, 2016). Although some species of insects use it to orient movement, especially nocturnal beetles, studies of use of polarized light by insects have not been consistently replicated (Dacke, 2014; Nowinsky, 2004; Warrant and Dacke, 2016). Possible indirect use of moon phase through its effects on plants are little understood, but may be important future research (Fisahn, Klingele, and Barlow, 2015; Zurcher, 2001).

Photoperiod

Photoperiod was not found to influence annual cicada emergence. Past research indicated that it could be a synchronizing factor in emergence (Heath, 1968; Kim et al., 2014). Black Cicada (*Cryptotympana atrata*) hatching rates are affected by photoperiod, but this is likely related to thermal needs during development (Kim et al., 2014). Emergence is unlikely to be directly connected to photoperiod as it begins underground (Heath, 1968; Karban, Black, and Weinbaum, 2000). Likewise, growing degree days did not predict emergence in periodical cicadas for similar reasons (Karban, Black, and Weinbaum, 2000). Indirect effects of photoperiod are not eliminated as the effects of photoperiod on trees would be interpreted by cicadas. Periodical cicadas may use phenological cycles of plants, likely cued by xylem quality, to measure seasonal cycles and time their emergence (Karban, Black, and Weinbaum, 2000; Yang, 2006). However, Heath (1968) reported it was not likely for cicadas to respond to indirect cues from host trees because the influence of climatic variables accounts for synchronization and lack of support for photoperiod as a cue.

Cicada tree preference

Annual cicadas did not prefer to emerge on trees based on tree species or height, although height might be related to chorusing locations of adult cicadas, which suggests that annual cicadas were host tree generalists, similar to periodical cicadas (Oberdorster and Grant, 2006). This is partially explained by female cicadas avoiding overlapping egg runs to limit competition and increase survival (Oberdorster and Grant, 2006). Cicada preference is less species oriented and more focused on branch width as a component of age, allowing females to oviposit successfully (Ahern, Frank, and Raupp, 2005; Dybas and Lloyd, 1974). As trees age, these smaller widths are less available, making younger trees even more preferred (Ahern, Frank, and Raupp, 2005). Cicadas may be limited by older bark as it hardens and resists oviposition (Chiavacci, Bednarz, and McKay, 2014). Younger trees have tend to have softer bark, faster root growth, and are often found in well-lit open areas with beneficial thermal qualities; these factors aid in oviposition, egg development, predator avoidance, and nymph growth (Chiavacci, Bednarz, and McKay, 2014; Dybas and Lloyd, 1974; Smits, Cooley, and Westerman, 2010;Yang, 2006; Yang and Karban, 2009).

While cicada emergence was evenly dispersed across trees within the site considering the frequency of species, most were found emerging on low DBH, White Ash representing 46% of available trees. This is consistent with habitat preferences of cicadas primarily using younger trees (Chiavacci, Bednarz, and McKay, 2014). Ash trees (*Fraxinus*) have been found to be preferred by some periodical cicadas for oviposition due to preferences in chorusing locations (Dybas and Lloyd, 1974; Oberdorster and Grant, 2006; Speer et al., 2010). Trees with compound leaves such as ash may be preferred by cicadas because the petioles supply additional oviposition locations; for example, one periodical species, *M. septendecula*, preferred walnut (*Juglandaceae*), willow (*Sarlix* spp.), and hickory (*Juglandaceae*) (Dybas and Lloyd, 1974; Smith et al., 2006). Typically, emergence holes at our studying site were only found at the base of trees where eggs had been laid in previous years, indicating a link between parental selection and emergence location (Oberdorster and Grant, 2006). However, hatching cicadas have been noted to move to root systems of trees different from the tree their mother used for oviposition, although this dispersal is limited as larger aggregations improve survival (Oberdorster and Grant, 2006; Smits, Cooley, and Westerman, 2010). Other studies indicated cicadas prefer oviposition in oak, hickory, apple, peach, cottonwood, and pear trees and grape vines (Johnson and Townsend, 2003; Smith et al., 2006). However, most of these trees were not found or were used at our site or were saplings below DBH standards with the exception of hickory. Oberdorster and Grant (2006) also found a tendency of cicadas to emerge on ash or beech over tulip trees, which was not found in our study. Lastly, the non-selective use of trees by emergent nymphs may be due to a positive feedback loop as males will congregate where highest emergence occurs to maximize reproductive opportunities (Oberdorster and Grant, 2006).

Tree use at the site should be continually examined to build a more robust dataset over additional years, especially as the management continues and tree composition of the site change. Long term, the resistance of ash trees to the negative effects of cicada parasitism could lead to greater use at the site as the quality of the other trees diminishes more quickly (Speer et al., 2010). Additionally, the impact of Emerald Ash Borers

(*Agrilus planipennis)* and Ambrosia Beetles could greatly affect the site and nature of these relationship as their spread continues in Kentucky (Crocker et al., 2018).

Copperheads and site usage

The congregation of copperheads behaviorally is for foraging purposes as copperheads move to their summer feeding sites in mid-June (Smith et al., 2009). Males utilize the site for foraging more often than non-gravid females. No gravid females were ever located within the site. This is consistent with an Indiana study indicating that males prefer to forage in grassy openings and early successional areas, such as our location, whereas females were more often found in the forest or using rocky glades when gravid (Carter, 2012). The low ratio of females may be due to the timing of gravidity (May and June) and parturition being during the summer ranging from July to September (Carter, 2012; Mengak, 2001; Smith et al., 2019). Gravid females focus their efforts on thermoregulating as more strict thermal ranges are required for proper development of young and have been known to refrain from feeding during this time (Carter, 2012; Lorioux, Lisse, and Lourdais, 2013; Mengak, 2001). Females that are pre-ovulatory through parturition often limit their movement remaining near the hibernacula for the active season (Smith et al., 2019). The low dispersal of gravid females would explain why they have never been observed at the study site as hibernacula used by our population are in roughly 0.8 km away. This would limit the number of females seen at feeding locations because up to 60% of female copperheads in a population can be gravid during a season (Mengak, 2001).

Non-gravid females forage and behave more like males, but may use different habitats depending on the time of year (Carter, 2012). Smith et al. (2009) found that males and females used the same habitat over the summer, although this variation may not consider microhabitat preferences. At our study site, male snakes foraged on cicadas and fed more often than females. Male copperheads also tend to have slightly larger home ranges and greater annual movement in connection with increased male movement in the breeding season (Smith et al., 2009; Sutton et al., 2017). However, during the non-breeding season, males and females move relatively the same distance (Smith et al., 2009). Likewise, non-gravid females feed at similar rates to males (Smith et al., 2009). One possible explanation for why males use the site more often is yearly location fidelity which has been noted at higher rates in male copperheads than females (Smith et al., 2009). However, this is associated with a male's need to locate females, so he often returns back to locations where he had past breeding success. Food availability is a primary factor determining distribution of copperheads, but more often associated with females as they are not restricted by the need to find a mate (Smith et al., 2009). However, in the northeastern section of their range, copperheads only tend to have one breeding season occurring in late summer to fall (McDuffie, 1960; Smith et al., 2009), suggesting that during the non-breeding season food availability may be a more universal factor for both sexes. Lastly, Mengak (2001) notes that males tend to be in higher proportion of the population than females so higher foraging densities of males, may represent the population's male skew. This solution fits the sex demographics of our population (Hendricks, 2019). Additionally, male snakes may be feeding more regularly because of their larger size (Fitch, 1960). This increased size increases their thermal inertia, extending the cooling period and allowing them to forage for longer or in a habitat currently less thermally optimal (Mueller and Gienger, 2018). However, of the feeding snakes neither SVL nor mass were predictors of the number of cicadas consumed. This result may be due to a small sample size (n =15), and additional field seasons may reveal trends consistent with the literature.

Overall, the movement of copperheads each year is nearly a loop with "exploratory movements" only after arriving at summer foraging habitat (Smith et al., 2009). Hendricks (2019) described such behaviors as snakes within the foraging site would search the entire open area and surrounding edge. This active searching behavior was most often associated with the groves of young trees (Hendricks, 2019). When considering all trees in the site, copperheads were observed more often climbing trees with lower DBHs. However, when evaluating if DBH impacted how many cicadas were consumed (only climbed trees considered) there was no significant relationship. Hendricks (2019) observed similar behavior overall concluding that copperheads primarily climbed smaller trees due to the small size of copperheads compared to other arboreal snake species. Cicadas did not show preference to tree height or DBH rather emerging at expected volumes across the available trees supporting even distribution of snakes among trees climbed. A confounding factor is that most trees within the site were groves of younger trees, thus having lower DBHs and the majority of cicadas. Therefore, copperhead tree climbing is likely impacted by cicada densities around younger trees and not only DBH. While copperheads typically coil around the tree and scoot upward limiting them to lower DBH tress, one possible explanation is that smaller snakes utilize the furrows of the bark to climb vertically up the trees similar to behavior observed in Western Ratsnakes (*Pantherophis obsoletus*) (Mullen and Cooper, 2002). A third method was attempted by the largest snake described as the "chin-up" method where the snake scales the tree by reaching vertically up the tree until it hooks the first branch with its chin and then hoists its body up. These adaptive methods for climbing the trees allow snakes to overcome the general DBH restrictions. Evaluating additional factors such as bark texture, furrow depth, and frequency of low branches may be additional qualities impacting a copperhead's ability to climb a tree.

Management

Understanding the relationship between copperheads and cicadas along with the impact of climatic variables and habitat qualities on the abundances of each allows managers to guide decision making that protects people as well as copperheads within the Koomer Ridge Campground. Copperheads have had consistent usage and yearly congregations within this recreational area in the Daniel Boone National Forest. This is similar to an Indiana population showing strong associations with managed and natural gaps often used for recreation (Carter, 2012). The consistent influx of copperheads each year has shown previous management techniques to be ineffective including several culling efforts and translocation. The goal of this study was to provide practical, effective options for mitigating the negative interactions between copperheads and humans while protecting the viability of the copperheads and their habitat. Evidence indicates that selection of these methods must be carefully analyzed because snakes are killed inadvertently by land management practices (Carter, 2012).

One possible way to mitigate this relationship is by providing a managed, artificial canopy opening in between the known foraging locations and hibernacula that restricts human access. Copperheads are known to select canopy openings for foraging likely due to thermal qualities and the food availability accompanying them (Carter, 2012). Cicadas showed no preference to tree species, but have been noted to prefer young trees and canopy gaps in other studies, suggesting the artificial gap should present adequate habitat (Chiavacci, Bednarz, and McKay, 2014; Speer et al., 2010; Yang, 2006). The strategy would hopefully attract copperheads as well as cicadas facilitating this predator-prey relationship while lowering negative-interactions with people.

Management practices should be performed in early spring or fall starting in September when snakes are using intermediate forested areas or returning to their hibernacula to reduce copperhead mortality (Carter, 2012). Additionally, the application of growing degree days may allow managers to accurately predict the arrival of copperheads within recreational areas. Management could use calendar days to acquire similar results (Pruess, 1983), but GDDs will be more appropriate with the effects of climate change over time. Neuheimer and Taggart (2007) state day may account for some variation, but the parsimonious inclusion of temperature in GDDs is important when considering ectotherms. This could be used to generate greater awareness among individuals using these areas or be used to close the sites for periods of the summer to restrict the risk. Cicada abundance is another predictor of copperhead abundance and could be used as a proximate warning as to when copperhead numbers will increase and ultimately subside. However, it is unknown what will occur in periodical years as this influx will be far greater. Consideration for monitoring cicada abundance via audio recordings was attempted, but ultimately proved ineffective due to the presence of several calling insects and amphibians overlapping and interfering with cicada calls. By understanding temperature and cicada abundance as determinants of variant in daily activity of copperheads, copperheads can be more effectively located and monitored (Brown and Shine, 2002).

Lastly, educating the public and giving them simple instructions on how to be safe around snakes had promising results. Zero bites or attempted bites were reported at the study site across two years when surveyors were present at the site regardless of snake volumes. Past studies have been inconclusive on the effects of education on human conservation attitudes and behavior some indicating benefits while others find no evidence (Godinez and Fernandez, 2019; Gutiérrez de White and Jacobson, 1994; Marino et al., 2010). However, our efforts go beyond education and shift toward training venomous snake competence formation which leaves visitors feeling empowerment. Competence formation has been shown to improve conservation behavior because it integrates knowledge into attainable actions (Jensen and Schnack, 2006; Kaiser, Roczen, and Bogner, 2008). In addition to awareness, key statements to hikers and campers were to watch their steps, wear leather boots, and always use a flashlight at night. While surveyors did not alter copperhead behavior, human presence onsite may have acted like an enforcer encouraging certain actions around snakes. For example, people may be less likely to harm a snake when people are present promoting their protection.

Future research

Although not investigated in this study, evaluating cicada abundances at other locations throughout the Red River Gorge may help managers understand additional features linking the copperheads to the cicadas. Callaham et al. (2000) found that emergence varied across topography, soil type, and vegetation type influenced emergence. Additionally, adding new sites with characteristics known to attract snakes may reveal more about their distribution in the RRG. The directionality of rock faces should be considered as western ridgetops are preferential to snakes due to their thermal qualities (Webb, Pringle, and Shine. 2004). These thermal connections may be used to locate additional sites within the RRG and throughout copperhead range. When considering directionality on a nightly basis, cicadas head to the western side of trees for egg laying so identifying possible directional biases during emergence should be investigated (Yang, 2006). The movement of the moon across the sky may impact the location of the emergent cicadas on the trunk of trees. Future work concerning the impact of moon illumination on cicada emergence rates and movement may present valuable insight into emergence timing and success.

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Appendices

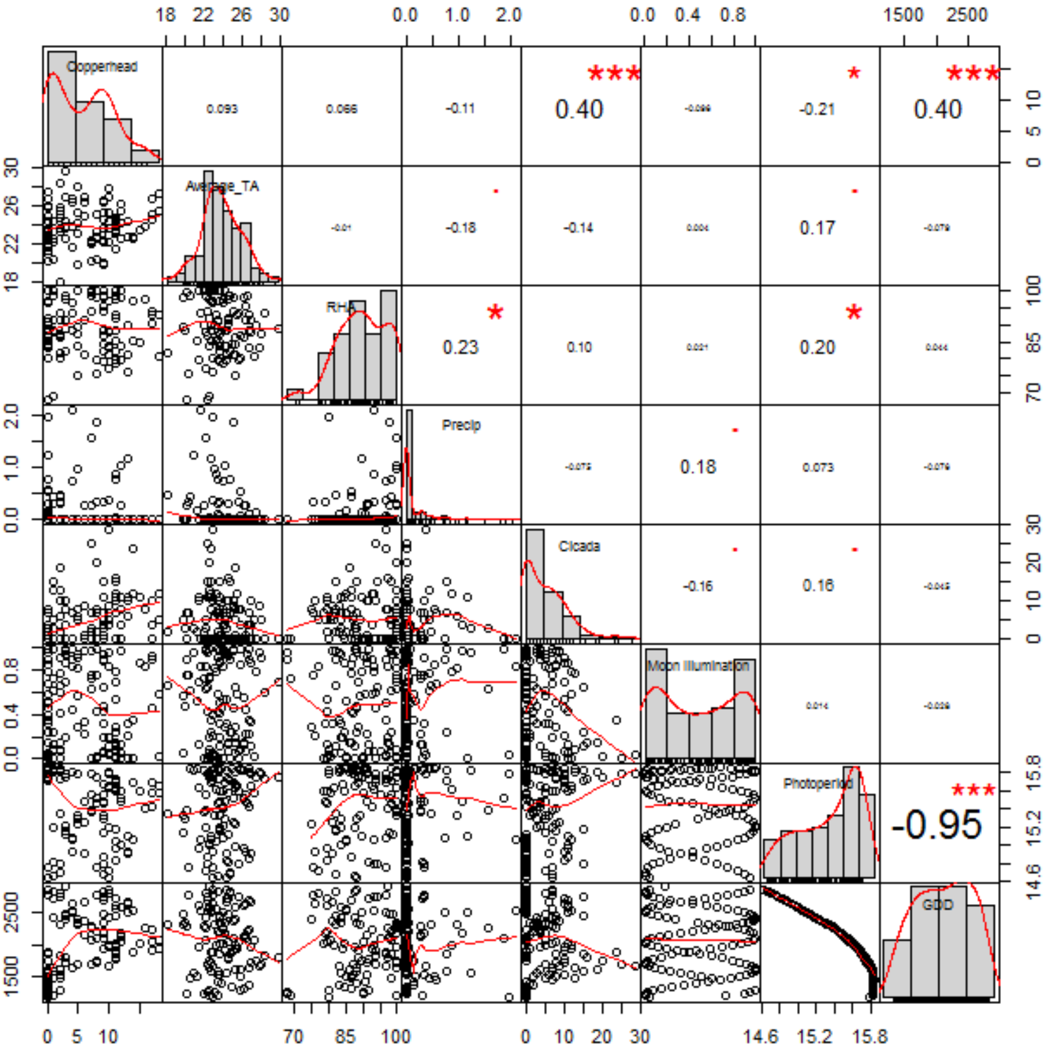
Appendix A. The tree characteristics, DBH and height, related to the number of annual cicadas found emerging on each individual tree. All surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

The tree characteristics, DBH and height, related to the number of annual cicadas found emerging on each individual tree. All surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

DBH by Species	Tree Height (m)	Cicadas
A. Beech		
15.3	23	23
30.8	3	3
Black Walnut		
4.7	1	1
41.7	15	15
C. Dogwood		
22.2	8	8
Red Maple		
17.8	8	8
19.3	4	4
21.5	4	4
26.7	5	5
27.9	29	29
31.6	6	6
34	5	5
35.9	2	2
40.9	24	24
42.2	5	5
53.2		7
Pinus spp.		
35.4	9	9
Redbud		
8.4	4	4
10.1	4	4
S. Hickory		
9.8	3	3
Tulip Poplar		
8.6	5	5
12.3	3	3
29.6	19	19
40.9	1	1
43	11	11
46.6	1	1
48.1	9	9
51.7	4	4
57.7	7	7
59.6	14	14

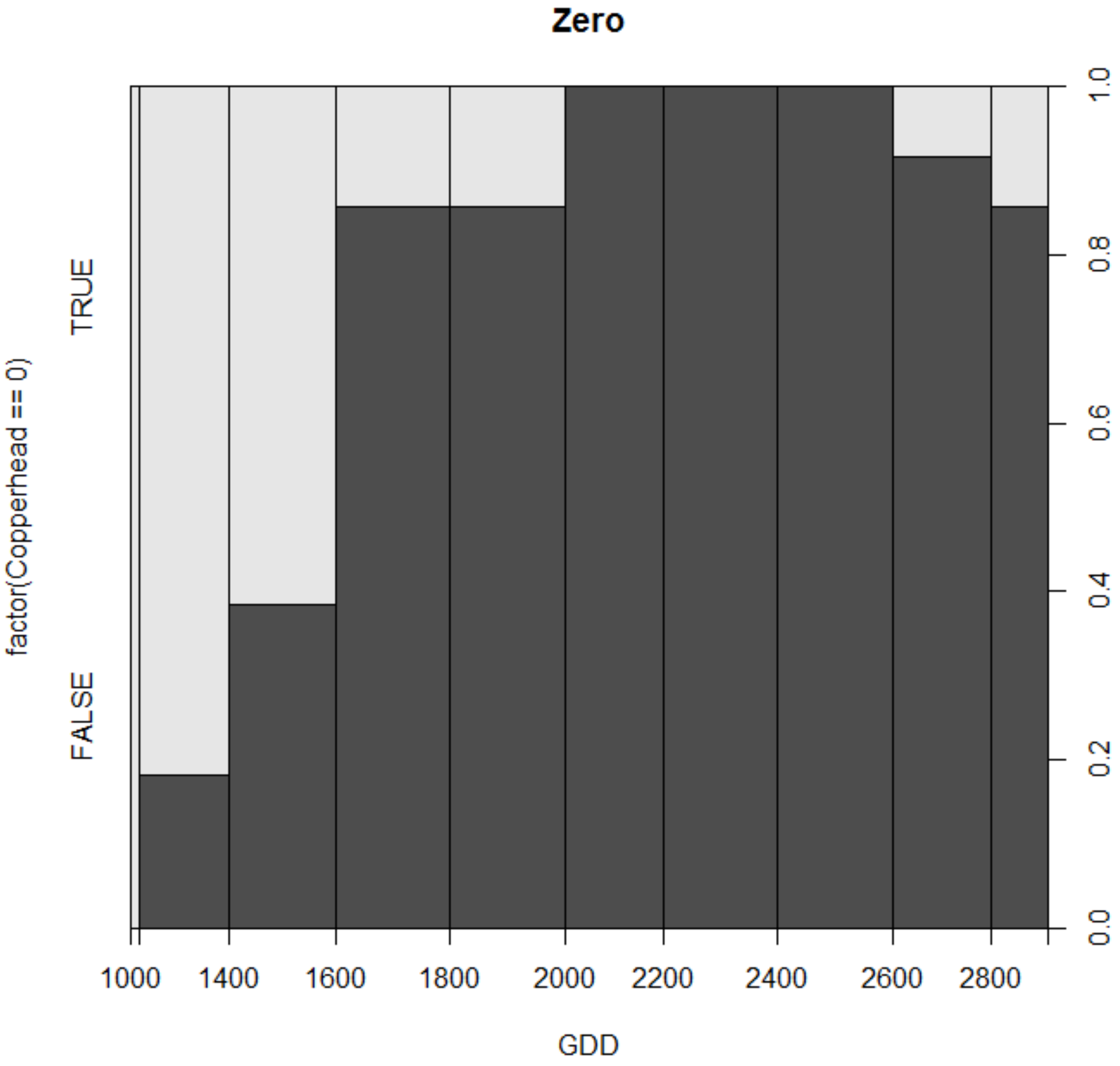
DBH by Species	Tree Height (m)	Cicadas
White Ash		
1.5	9	9
2.2	1	1
2.5		8
3.5	3	3
3.6	1	1
3.8	10	10
3.9	10	14
4	19	19
4.3	4	4
4.6	5	5
4.7	1	1
4.8	6	6
4.9	2	2
5	8	8
5.2	2	2
5.4	2	2
5.5	11	11
6.3	18	18
6.5	10	10
6.8	13	13
7.2	13	13
8.8	10	10
11.3	31	31
11.7	4	4
12.7	9	9
13.7	8	8
14.3	9	9
16.8	6	6
36.7		1
White Pine		
3.9	4	4
8.8	5	5
36.7	9	9
57.4	9	9

Appendix B. Correlations for all variables included in the models. More “*”s indicate a stronger relationship between the two variables; no relationship does not have a star, weak relationship (*), moderate (**), and strong (***). Data were collected at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



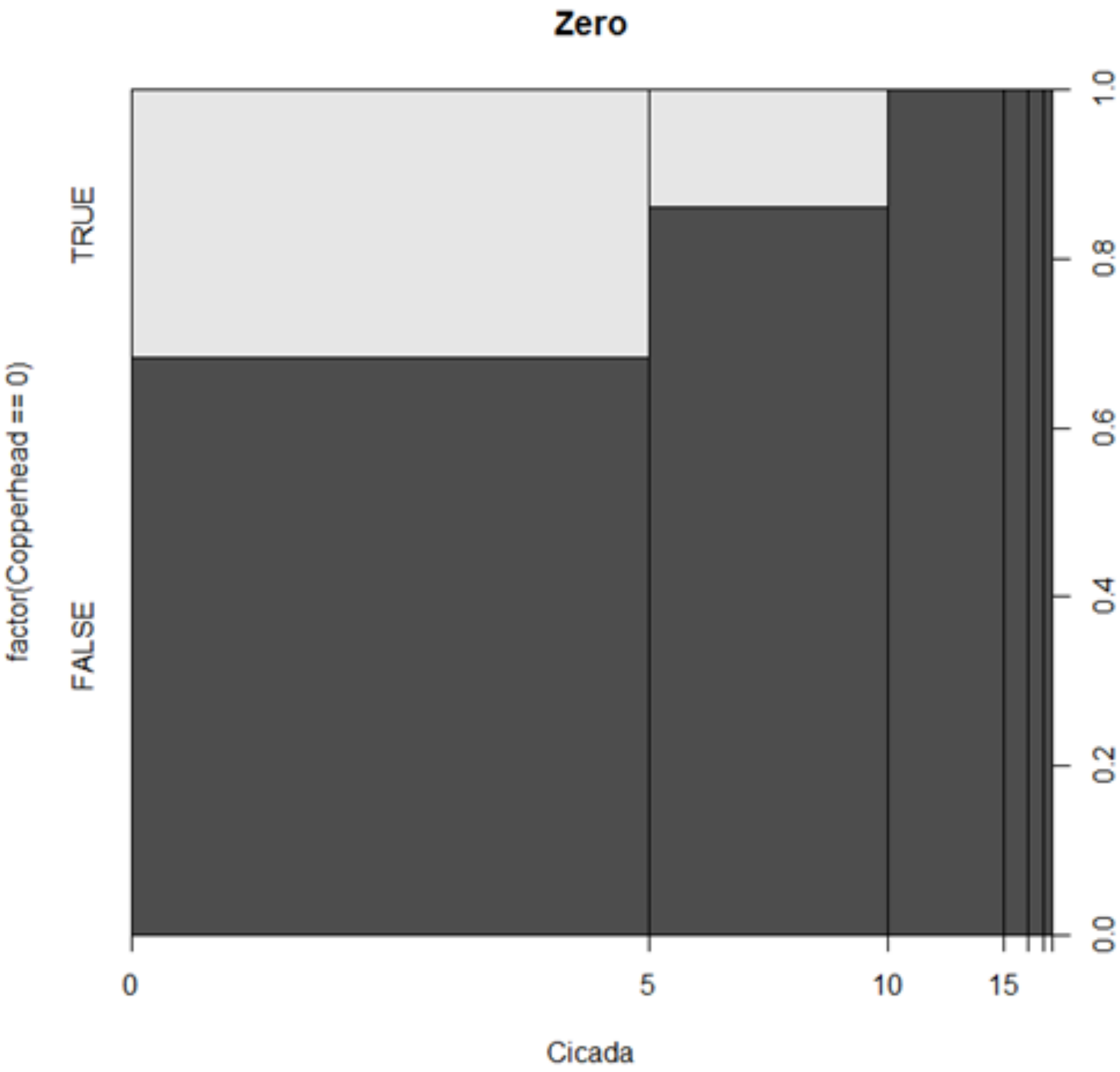
Correlations for all variables included in the models. More “*”s indicate a stronger relationship between the two variables; no relationship does not have a star, weak relationship (*), moderate (**), and strong (***). Data were collected at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Appendix C. Initiation of Eastern Copperhead (*Agkistrodon contortrix*) arrival at the foraging site based on growing degree day accumulation at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. The increase in GDD accumulation was associated with the arrival of copperheads. The value “True” corresponds to the predicted snake arrival at the site while false expects no snakes.



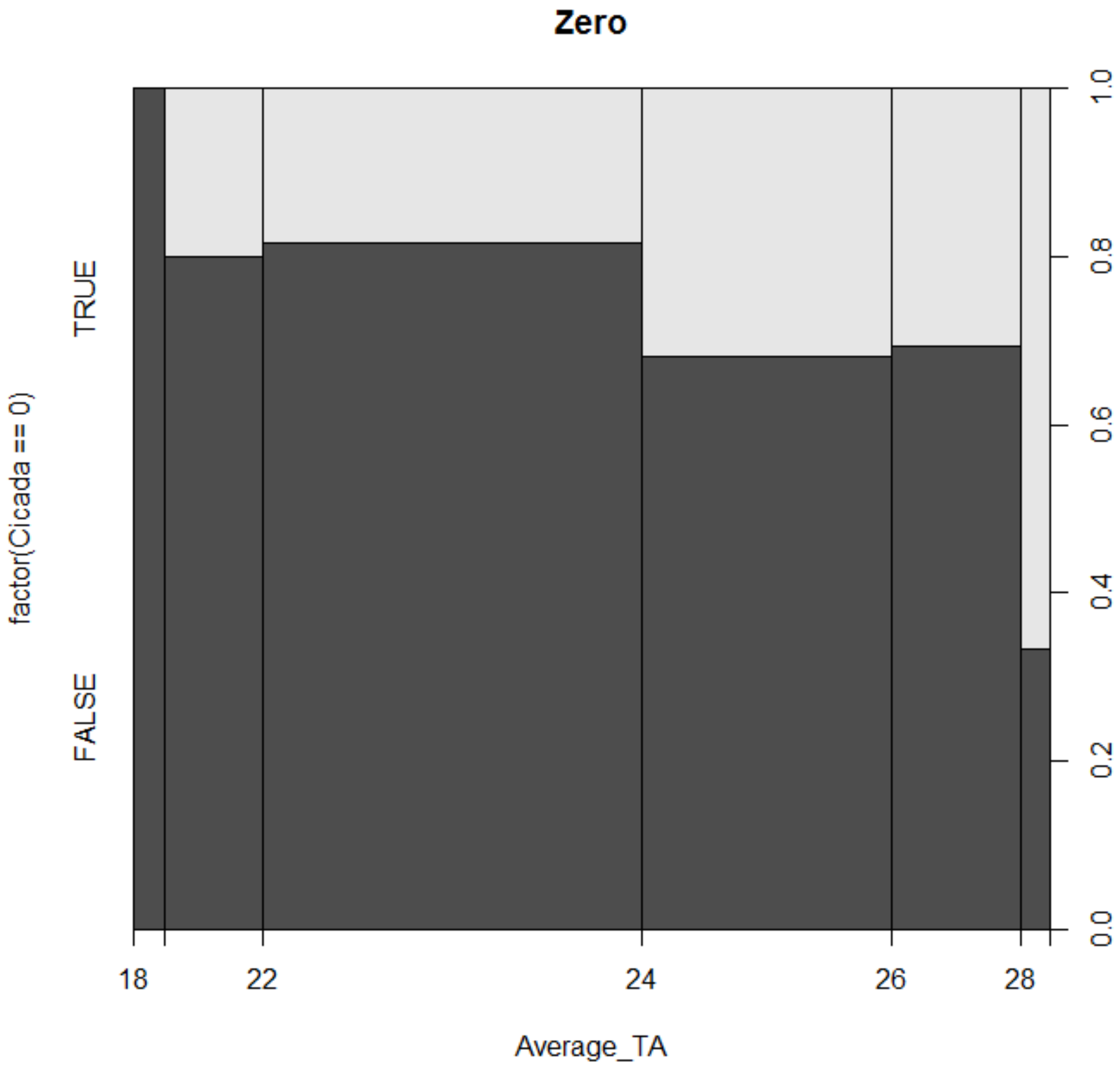
Initiation of Eastern Copperhead (*Agkistrodon contortrix*) arrival at the foraging site based on growing degree day accumulation at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY. The increase in GDD accumulation was associated with the arrival of copperheads. The value "True" corresponds to the predicted snake arrival at the site while false expects no snakes.

Appendix D. Annual cicada abundances seem to predict initial copperhead abundances, after 10 cicadas emerge copperheads will be found at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



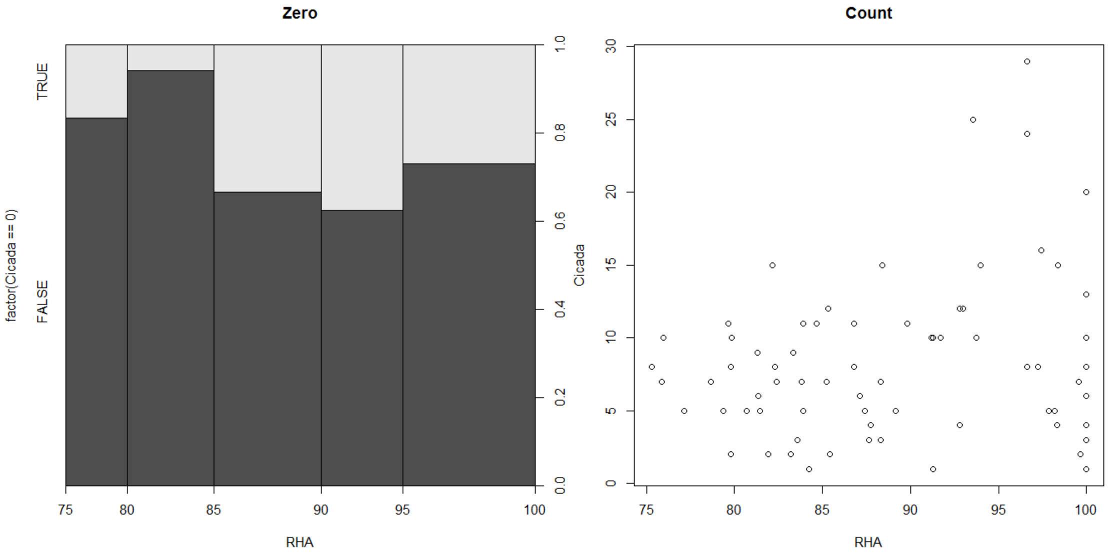
Annual cicada abundances seem to predict initial copperhead abundances, after 10 cicadas emerge copperheads will be found at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Appendix E. The graph depicted the threshold of emergence as it related to average temperature, ‘true’ indicating emergence occurred. Lower average nightly temperature predicted the initiation of emergence of annual cicadas, likely indicating a minimum thermal threshold for emergence. All the cicada surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



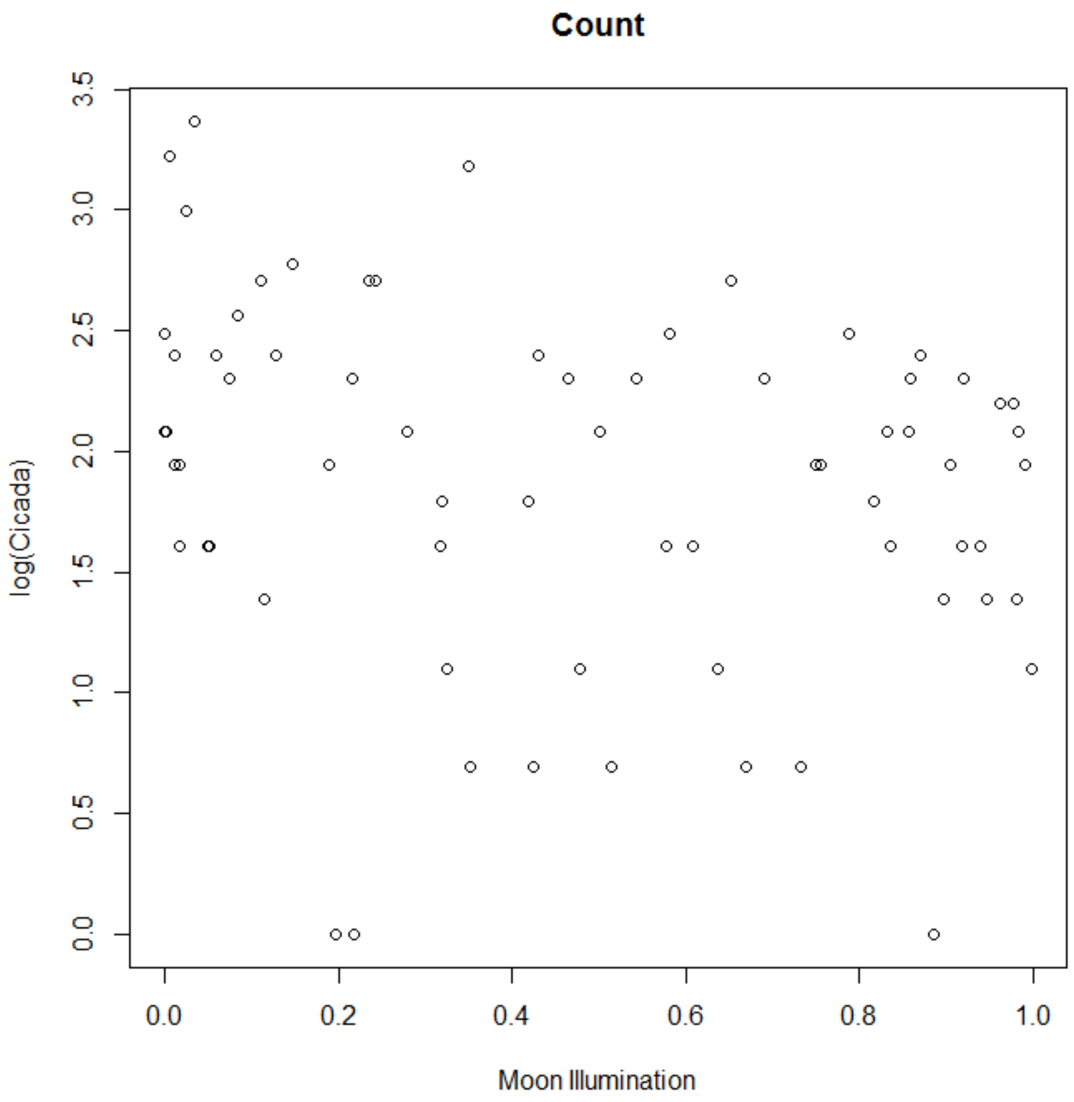
The graph depicted the threshold of emergence as it related to average temperature, ‘true’ indicating emergence occurred. Lower average nightly temperature predicted the initiation of emergence of annual cicadas, likely indicating a minimum thermal threshold for emergence. All the cicada surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Appendix F. Humidity was predictive of initial annual cicada emergence shown on the left with an inverse relationship, but this may be due to other variables timing initial emergence earlier in the season when humidity would climatically be lower (left). Annual cicada counts throughout the season fluctuated directly with relative humidity (right). All surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



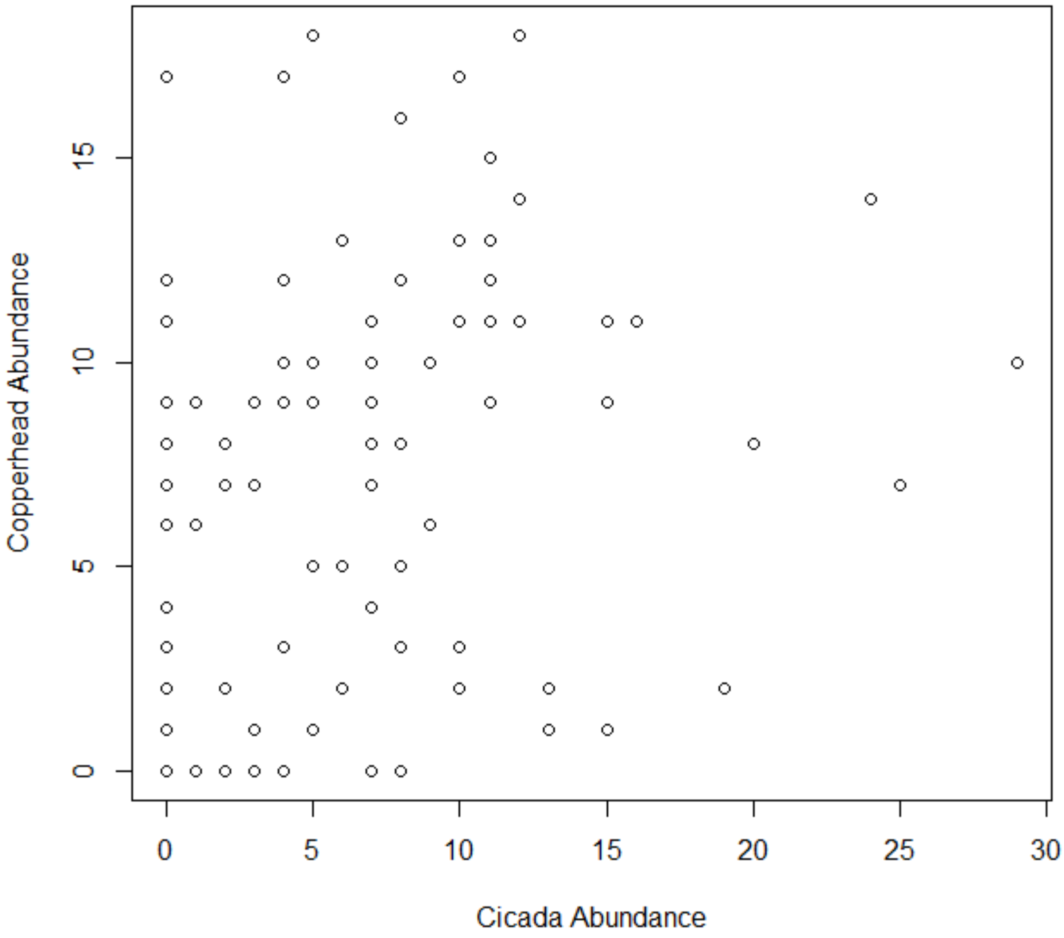
Humidity was predictive of initial annual cicada emergence shown on the left with an inverse relationship, but this may be due to other variables timing initial emergence earlier in the season when humidity would climatically be lower (left). Annual cicada counts throughout the season fluctuated directly with relative humidity (right). All surveys were performed at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Appendix G. Moon phase impacted the fluctuation of cicada emergence abundances throughout the season. Moon phase had a negative relationship with cicada abundance. Lower moon phases coincided with larger emergence events at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.



Moon phase impacted the fluctuation of cicada emergence abundances throughout the season. Moon phase had a negative relationship with cicada abundance. Lower moon phases coincided with larger emergence events at a recreational site in the Cumberland Ranger District, Daniel Boone National Forest, KY.

Appendix H. Eastern Copperhead (*Agkistrodon contortrix*) abundances and annual cicada abundances from 2018 to 2019 were positively related; greater abundances of cicadas led to the copperhead volume at the eastern Kentucky recreational site increasing.



Eastern Copperhead (*Agkistrodon contortrix*) abundances and annual cicada abundances from 2018 to 2019 were positively related; greater abundances of cicadas led to the copperhead volume at the eastern Kentucky recreational site increasing.