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POPULATION DEMOGRAPHICS AND UNIQUE FORAGING BEHAVIOR OF
COPPERHEADS (*AGKISTRODON CONTORTRIX*) AT A RECREATIONAL SITE IN
EASTERN KENTUCKY

BY

JOCELYN J. HENDRICKS

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Date: 4/5/2019

POPULATION DEMOGRAPHICS AND ACTIVE FORAGING BEHAVIOR OF
COPPERHEADS (*AGKISTRODON CONTORTRIX*) AT A RECREATIONAL SITE IN
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JOCELYN J HENDRICKS

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

2019

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DEDICATION

I would like to dedicate this work to my wife, Courtney, whose attention to detail far surpasses my own and whose patience is undeserved.

ACKNOWLEDGEMENTS

I would first like to thank my advisor, Dr. Stephen Richter, whose experience provided structure for this research and whose guidance allowed me to develop and improve my own ideas. I thank Dr. Charles Elliott and Dr. Luke Dodd, whose detailed comments have greatly improved this manuscript. I'd like to acknowledge Raymond Little (Big South Fork, TN), Danna Baxley (Nature Conservancy, KY Chapter), John MacGregor (Kentucky Department of Fish and Wildlife Resources), Sandie Kilpatrick [United States Forest Service (USFS)], Christy Wampler (USFS), and Will Bird (Louisville Zoo) for providing the initial effort for this study. A number of ECU students and volunteers contributed to the conceptual and practical aspects of the study: Jesse Sockman (EKU), Austin Owens (EKU), Kyle Muennich (EKU), Peyton Blair (EKU), Matt Mineo (KY Reptile Zoo), Sarah Phillips (EKU), David Smith (EKU), Dr. Kelly Watson (EKU), Callie Boggs (EKU), and Renae Steinberger (EKU). Dr. David Brown (EKU) and Alex Baecher (EKU) provided assistance with demographic analyses. Funding and support was provided by the USFS, Kentucky Society of Natural History, National Science Foundation, Kentucky Herpetological Society, The Louisville Zoo, Kentucky Reptile Zoo, ECU-Battelle Scholarship, and the ECU Department of Biology. This research was approved by the Eastern Kentucky University Institutional Animal Care and Use Committee, Protocol 06-2018.

ABSTRACT

Recreational areas represent a significant source of human-wildlife interaction, which can have an especially negative effect on organisms, like snakes, that are generally perceived as dangerous by the public. Considering the projected increase in recreation rates in the United States, the threat to this already vulnerable group of organisms deserves attention. While habitat factors associated with recreational areas—fragmentation, decreased canopy cover, altered vegetation composition—have been shown to affect snake thermoregulatory behavior and abundance, detailed studies of wild snake behavior are uncommon due to their cryptic nature. The goal of this study was to reduce human-wildlife conflict at a recreational site in Kentucky where copperhead snakes (*Agkistrodon contortrix*) are known to aggregate and forage. Capture-recapture data were used to 1) describe the demographic structure of the population and 2) construct models that quantify the probability of apparent survival (S) and recapture (p) as it related to snake sex and weight. In addition, copperhead foraging behavior was closely observed in order to 1) quantify individual behaviors, 2) calculate movement rates, and 3) describe the copperhead's general foraging strategy at the site. From 2015 to 2018, 84 individual copperheads (male = 46; female = 38) were captured, weighed, and PIT-tagged. The average number of snakes caught each year ranged from 18 to 45, and the total number of captures (including recaptures) was 261. The probability of apparent survival varied 5–49%, and the probability of recapture varied 0–15%, depending on the sampling year. The greatest difference in apparent survival attributable to sex was 3% and the greatest difference in recapture was 1%. Apparent survival varied as a function of mass, 9–20% for both males and females. Recapture did not vary as a function of mass for males or

females. In 2018, 72 nightly surveys were conducted to assess copperhead behavior at the study site. Individuals were observed using visual and vomeronasal cues to forage for newly emerged annual cicadas (*Tibicen* spp.) on the ground and in patches of vegetation and small trees. On average, snakes were non-mobile for 61.00 ± 8.44 min (59%) and mobile for 42.69 ± 7.51 min (41%). The average distance traveled during a single foraging event was 30.20 ± 6.98 m, at an average speed of 0.40 ± 0.11 m/min. The number of directional changes during a foraging event ranged from 0 to 24 with a mean of 6 ± 1 changes, and the average amount of time individuals spent climbing was 13.1 ± 4.80 min. The number of cicadas eaten per individual ranged from 0 to 3 and the average handling time was 3.17 ± 0.60 min. Based on the importance of human safety and snake conservation at the study site, these data will be used to 1) inform educational programs and resources that facilitate public understanding of copperhead ecology, and 2) reinforce copperhead conservation by implementing management techniques that reduce copperhead occupancy and allow future monitoring at the study site.

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CHAPTER I

INTRODUCTION

One of the most fundamental threats to wildlife is their interaction with humans (Treves et al. 2006; Dickman 2010; Sullivan et al. 2014); recreational areas represent a significant source of this interaction (Losos et al. 1995; Papouchis et al. 2001; Taylor and Knight 2003; Reed and Merenlender 2008; Marzano and Dandy 2012).

Paradoxically, recreational areas also serve as a useful tool for wildlife-related public outreach, education, and conservation, while simultaneously increasing the probability of human-wildlife interactions (Sorice et al. 2003). Interactions with humans can have an especially negative effect on organisms, like snakes, that are generally perceived as dangerous by the public (Kellert et al. 2003; Shine and Koenig 2001; Dickman 2010). In light of the projected increases in recreation in the United States (Bowker et al. 2012), the threat to this already vulnerable group of organisms deserves attention (Gibbons et al. 2000; Gardner et al. 2007; Bohm et al. 2013; Meiri and Chapple 2016).

Predicting the spatial distributions and habitat associations of organisms is a central theme in ecological studies (Arthur et al. 1996; Boyce et al. 2003; Johnson et al. 2006; Beyer et al. 2010), and an important component of conservation planning and wildlife management programs (Aldridge and Boyce 2007; Sullivan et al. 2014; Allen and Singh 2016). While it is generally accepted that snakes select habitats at multiple scales (Reinert 1993; Moore and Gillingham 2006; Sutton et al. 2017; Buchanan et al. 2017), their life history is seldom studied according to this paradigm (McGarigal et al. 2016). Further, while landscape-level data can provide important insights related to coarse spatial patterns and general habitat associations (Steen et al. 2012), these patterns

should not be generalized to explain finer-scale ecological processes (Tischendorf 2001). This concept is especially important in cases where organisms, like viperid snakes, rely heavily on microhabitats (Harvey and Weatherhead 2006). Consequently, studies with conservation or management objectives should carefully examine habitat use as a dynamic network of interrelated life history functions (Johnson 1980; Reinert 1993) that vary across spatial and temporal scales (Boyce et al. 2003; Semlitsch et al. 2017).

Habitat use in snakes is directly related to physiological constraints imposed by their ambient environment (Arnold and Bennett 1984; Huey 1991). Structural variation in a habitat provides an environmental gradient that allows individuals to regulate their physiological and behavioral state (Webb and Shine 1998; Beaupre 2002). For example, fragmentation can increase the thermoregulatory potential of a site (Blouin-Demers and Weatherhead 2002), as well as the quantity and availability of prey (Blouin-Demers and Weatherhead 2001). Similarly, canopy gaps in forested habitats can affect snake thermoregulatory behavior (Pringle et al. 2003; Webb et al. 2005) and overall abundance (Carter et al. 2014). Changes in vegetative composition and structure due to fire can affect the relative abundance of forest-dwelling snakes (Howey et al. 2016). Changes in habitat composition can also increase exposure to predators (Blouin-Demers and Weatherhead 2002; Shoemaker and Gibbs 2010; Steen et al. 2014), which may cause an individual to alter its foraging behavior (Rugiero et al. 2013; DeGregorio et al. 2015). While habitat disturbance has been shown to significantly affect snakes at different spatial scales, behavioral responses to habitat change over time are less well known (Reinert et al. 2011).

Copperhead snakes (*Agkistrodon contortrix*) are a widely distributed viperid endemic to eastern North America. Although they are notably more docile than the other North American viperids, they are historically no less feared by humans (Garman 1883). Copperheads are ambush predators and feed mainly on small mammals, occasionally eating amphibians, birds, and insects (Fitch 1960; Garton and Dimmick 1969). Although copperheads have been observed throughout their range to forage in considerable numbers for newly emerged cicadas (Surface 1906; Heinze 1934; Fitch 1960; Barbour 1962), this behavior has never been formally studied. These snakes inhabit rocky hillsides, areas with woody debris and leafy ground cover, and interfaces between forested and open areas (Fitch 1960). For this reason, copperheads are often encountered by humans at recreational sites near hiking trails, picnic areas, scenic overlooks, and campgrounds (Fitch 1960; Barbour 1962, Carter et al. 2014; Sutton et al. 2017). Their leaf-like skin pattern provides excellent camouflage, making them even more susceptible to accidental encounters with humans (Fitch 1960). As a consequence, copperhead bites are the second most commonly reported envenomation in the United States (Walker and Morrison 2011).

The overall objective of this study was to reduce conflict at a recreational site in Kentucky where copperheads are known to aggregate and forage. Capture-recapture data were used to 1) describe the demographic structure of the population and 2) quantify the probability of survival and recapture as it related to snake sex and weight. In addition, copperhead foraging behavior was closely observed in order to 1) quantify behaviors, 2) calculate movement rates, and 3) describe the copperhead's general foraging strategy at the site. These data will be used to 1) inform educational programs

and resources that facilitate public understanding of copperhead ecology and 2) reinforce copperhead conservation by implementing management techniques that reduce copperhead occupancy at the study site and facilitate future data collection.

CHAPTER II

METHODS

Study Site

The study site is located near the southern edge of the Red River Gorge in the Daniel Boone National Forest. The Red River Gorge is managed by the United States Forest Service (USFS) and designated as a national geological area. The study area is located within Mixed Mesophytic Forest Region (Jones 2005) and is composed mainly of mixed oak and oak-pine forest (Woods et al. 2002). The site is within the Cumberland Plateau Physiographic Region (Jones 2005) and has a complex topology of ridges, valleys, and cliff-faces. The extent of the study area (~0.6 km²) is based on opportunistic radiotracking data gathered in 2015, 2017, and 2018 (Figure 1). The study site is ca. 1000 m² and lies adjacent to a southwest-facing slope, just below the top of a ridge (elevation 366 m). The site is characterized by patches of mowed grass, several patches of small vegetation and trees, and several gravel trails and gravel tent pads. The site is used for recreational purposes from March to September and receives daily use during the summer months.

Visual Encounter Surveys

Copperheads were located, beginning at dusk, by conducting visual surveys of the study site (Dodd 2016). A complete search of the site was conducted wherein one person searched a 3 m portion along the edge while another person simultaneously searched the inner portion of the site. Surveys were repeated until three consecutive searches of the campground produced no new captures. Copperheads were captured



Figure 1. Map illustrating the spatial and topological context of the study area (larger rectangle) and study site (smaller rectangle). The study site is shown in the top right.

using tongs (Midwest Tongs, tongs.com) and placed in 26.5 L buckets lined with a snake bag. A knot was tied in the snake bag after a locking lid was placed on the bucket. Environmental conditions were recorded before and after each survey; relative humidity was determined using a Kestrel 3000 wind meter (KestrelMeters, Minneapolis, MN), ground surface temperature using an HDE infrared laser thermometer, and soil temperature using a soil thermometer left in the ground throughout the survey. Air and ground temperatures were also recorded at a randomly selected location in the forest approximately 5m from the edge of the site.

Capture-recapture procedure

Individual copperheads and bags containing snakes were handled with tongs and tubes during the measuring and marking process. Bags containing individuals were grasped with tongs and transported to a digital scale to determine the weight of the individual, corrected for the weight of the bag. After weighing, the snake was transported in the bag to a 190 L plastic bin, and tongs used to release the snake into the bin. Individuals were guided into clear polycarbonate tubes (Midwest Tongs, tongs.com) to be immobilized. Individuals were measured [total length (TL), snout-vent length (SVL)] and their sex determined using a lubricated cloacal probe (Dodd, 2016). A Passive Integrated Transponder (PIT) tag was implanted after measurements were taken. PIT tags (BioMark HPT12) were injected using a 12-gauge N125 Injector Needle (Biomark, Boise, ID) and an MK10 Implanter (Biomark, Boise, ID), following the procedure outlined in Dodd (2016). Recaptured individuals were scanned and identified using a BioMark HPR Reader (BioMark, Boise, ID). Capture-recapture surveys were conducted 3–5 times each season (May–September) in 2015 and 2016. In 2017–2018, sampling was more intensive— 12 surveys in 2017 and continuous monitoring from 2 June to 18 August in 2018.

Behavioral observations

In 2018, the focal sampling method (Altmann 1974) was employed to document the foraging behavior of 24 individual copperheads throughout the season (June–September). To ensure non-interference with behaviors, headlamps were used on a dim setting and the observer always remained 3–4 m away from the individual. Using a

stopwatch, the total amount of time individuals were mobile, non-mobile, climbing, eating, observed in combat, and reproducing was recorded. Mobile behavior was defined as sustained movement for at least 10 seconds. Non-mobile behavior was defined as remaining immobile for at least 10 seconds. Climbing was defined as parallel contact and/or movement along any structure with height, including branches of trees. Eating was defined as the amount of time from initial contact with a prey item until the snake's mouth was able to fully close. Combat was defined as contact with an individual of the same sex, wherein the individuals intertwined the anterior portions of their bodies (Fitch 1960). Reproduction was defined as contact with an individual of the opposite sex, wherein the posterior portions of the individuals are intertwined (Fitch 1960). The sampling frame for an individual foraging event was defined as the time an individual was seen entering the site to the time it either moved out of the site or remained in a coiled position with its head down for a minimum of 30 minutes. In order to quantify the spatial component of individual foraging events, all locations where a behavior or movement direction changed were recorded. Behavioral points of interest (POI) were defined as the location of a change in either behavior or direction.

Data Analysis

In order to determine the effect of sex and mass as it relates to population demography and site utilization by copperheads, capture-recapture models were constructed to estimate the probability of survival and recapture within a Robust Model framework (Pollock 1982), using Huggins parameterization for initial and subsequent capture probabilities (Huggins 1989). Data were analyzed from 4 primary sampling

occasions (i.e. 2015–2018), and 27 secondary (within-year) occasions (i.e. 3, 5, 12, 7, respectively) (Figure 2). To account for the continuous sampling structure during the last year of the study, secondary occasions for that year ($n = 49$) were evenly binned by week. Discretizing sampling occasions may result in low-biased estimates of survival and recapture in some models (Barbour et al. 2013), as well as confound various time-dependent and movement parameters (Kendall and Bjorkland 2001). As a result of the copperhead’s relatively slow-moving, ‘migratory’ foraging behavior (Smith et al. 2009), movement parameters (temporary emigration and immigration) are unlikely to be confounded with apparent survival and recapture during secondary occasions. Additionally, the nature of the copperhead’s active foraging behavior at the study site increases the probability of overall capture during a secondary occasion, thus also decreasing potential bias as a result of non-instantaneous capture intervals. The effect of sex on survival and recapture probabilities may remain biased due to the tendency of females to be more sedentary and hidden during the breeding season (Smith et al. 2009).

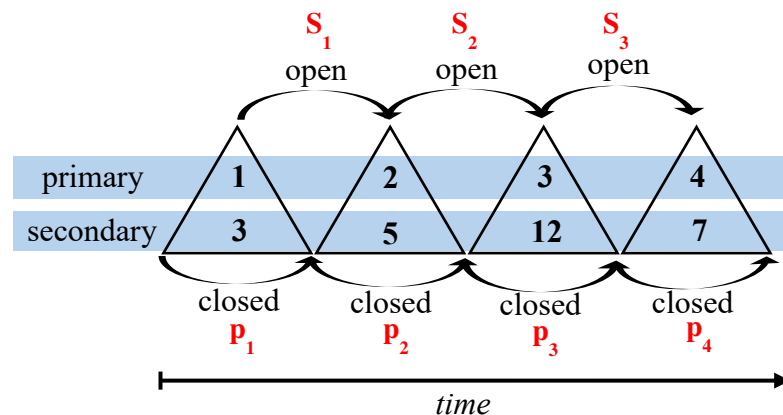


Figure 2. Robust design model structure (adapted from Kendall 2009) illustrating open and closed population assumptions and associated parameters (S_i , p_i) derived from primary and secondary sampling periods.

Three general models with different movement parameters were evaluated— ‘No Movement’, ‘Random (classical) Movement’, and ‘Markovian Movement’ (see Lukacs 2009)— and compared based upon Akaike Information Criteria (AIC) corrected for small sample size (AIC_c) (Hurvich and Tsai 1989). Both the ‘Markovian Movement’ and ‘Random Movement’ models lacked numerical convergence, resulting in several inestimable parameters and confidence bounds. Because standard parameter constraints (Lukacs 2009) were imposed to eliminate structural confounding, the lack of convergence is most likely a combinative effect of data sparseness and model complexity. Alternatively, the ‘No Movement’ model resulted in numerical convergence for all parameters and error terms. A median \hat{c} goodness of fit test (Kendall et al. 2013) for this model structure indicated no overdispersion; therefore, the ‘No Movement’ model was chosen as a general model. The ‘No Movement’ design is a constrained version of Markovian movement that fixes $\gamma'' = 0$ and $\gamma' = 1$, effectively eliminating the movement parameters from the model. In the absence of these movement parameters, survival estimates are ‘apparent’, meaning they are confounded with temporary movement to and from the study site. Based upon previous observations and scarcity of vegetational cover within the site, movement ‘on’ and ‘off’ the site is highly probable and may result in low-biased estimates of survival and recapture.

For the Huggins parameterization, the probability of initial capture (p_i) and subsequent capture (c_i) are confounded; therefore, one parameter must be constrained to be a function of the other (Lukacs 2009). Based upon *a priori* reasoning and previous observations, a time-varying recapture structure was used, constraining $p_t = c_t$ (for model notations see Otis et al. 1978; Lebreton et al. 1992) (Table 1). Applying

knowledge of copperhead biology and foraging ecology to this general model, *a priori* hypotheses were developed and time-dependent models were constructed to estimate the effect of time, sex, and mass on the probability of survival and recapture. All

Table 1. Definitions of parameters used in constructing capture-recapture models.

Parameter	Definition
S_i	Probability of an individual being marked, released, and surviving from session i to $i + 1$.
γ''	Probability of an individual being unavailable during session i , given that the individual was <i>available</i> during session $i-1$.
γ'	Probability of an individual being unavailable during session i , given that the individual was <i>unavailable</i> during session $i-1$.
p_i	Probability that an individual is encountered, conditional on survival and availability within the superpopulation.
c_i	Probability that an individual is encountered, conditional on survival, availability, and having been previously encountered.

analyses were performed using Program MARK version 9.0 (White and Burnham 1999).

Basic demographic statistics (sex ratio, size and length distributions, frequency of captures) were calculated from 2015 to 2018. For individuals captured in 2018, the average amount of time individuals were observed in different behavioral states was determined and compared across snake sex and size. Individual demographic effects on foraging behavior were assessed by comparing the amount of time individuals of a certain sex and size class were mobile and non-mobile, as well as the rate of foraging and total distance traveled during a single foraging event. Individuals that remained non-mobile for 30 min upon sighting were excluded from behavioral analyses. The effect of mass on foraging distance and mobile behavior was determined using simple linear regression models. Information from individuals with multiple observations over

time was averaged in order to avoid pseudoreplication. A Shapiro-Wilk test was used to test the normality assumption. For individuals that were observed eating, the average handling time was determined. A t-test was used to compare the seasonal air and ground temperatures in the study site and forest.

CHAPTER III

RESULTS

From 2015 to 2018, 84 individual copperheads were captured, weighed, and PIT-tagged. The average number of snakes caught each year ranged from 18 to 43 ± 10 snakes (Table 2), and the total number of captures (including recaptures) was 261.

Table 2. Recapture array for copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Release year	Number released (R_i)	Number recaptured (m_{hi}) in year i			
		2016	2017	2018	Total
2015	18	10	5	0	15
2016	29		22	0	22
2017	43			15	15
2018	30				0

The overall sex ratio of the population was 1.2:1 ($n_{\text{male}} = 46$; $n_{\text{female}} = 38$). The weight range for male copperheads was 141.7–196.2g, with an average weight of 156.2 ± 11.3 g; the female weight range was 110.8–147.7g, with an average weight of 115.8 ± 6.4 g (Appendix A). The average SVL of a male during the study ranged from 56.5 to 62.5cm, and the average SVL of a female ranged from 50.9 to 56cm (Appendix B). Results of model comparisons of the *a priori* copperhead capture-recapture models revealed appreciable support for several models (Appendix C); therefore, model averaging was used to determine the average parameter estimates for each sampling period (Burnham and Anderson, 2002). Model-averaged parameter estimates supported the hypothesis that survival and recapture are dependent on the sampling period (Table 3).

Table 3. List of a priori capture-recapture models for copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Model	k	AICc	Δ AICc	w_i	$-2\log(L)$
S(t+mass), $G'' = 0, G' = 1, p(t)$	8	1190.00	0.00	0.210	1173.43
S(t), $G'' = 0, G' = 1, p(t)$	7	1190.50	0.50	0.163	1176.06
S(t+mass), $G'' = 0, G' = 1, p(t+sex)$	9	1191.10	1.10	0.121	1172.39
S(t), $G'' = 0, G' = 1, p(t+sex)$	8	1191.48	1.47	0.101	1174.90
S(t+sex), $G'' = 0, G' = 1, p(t)$	8	1191.58	1.58	0.095	1175.01
S(t+sex+mass), $G'' = 0, G' = 1, p(t)$	9	1191.93	1.93	0.080	1173.22
S(t+mass), $G'' = 0, G' = 1, p(t+mass)$	9	1192.14	2.13	0.072	1173.42
S(t), $G'' = 0, G' = 1, p(t+mass)$	8	1192.63	2.63	0.056	1176.06
S(t+sex), $G'' = 0, G' = 1, p(t+sex)$	9	1192.79	2.79	0.052	1174.07
S(t+mass), $G'' = 0, G' = 1, p(t+mass)$	9	1193.73	3.73	0.033	1175.01
S(t+mass+sex), $G'' = 0, G' = 1, p(t+mass+sex)$	11	1195.06	5.06	0.017	1172.00

To detect the effect of the sex covariate, model-averaged values of apparent survival and recapture were calculated for males and females. The sex effect size is the difference between the model-averaged estimates for males and females. Although males consistently had a higher probability of survival and recapture, the size of the effect and associated standard error suggests that the probability of survival and recapture is not sex-dependent in this case (Appendix D; Figure 3). Model-averaged estimates were also used to determine the effect of mass on survival and recapture. Mass did not have a significant effect on either apparent survival or recapture during any sampling period (Figure 4; Figure 5). There were no sex-specific differences in apparent survival or recapture (Appendix E; Appendix F). In 2018, 72 nightly surveys for copperheads were conducted from 2 June to 18 August. There were 51 captures and 180 total recaptures (Appendix G). Overall captures were highest from 8 July to 26 July, when the average air temperature was $23.6 \pm 0.4^\circ\text{C}$. The recapture frequency was 23.8% for males and 21.5% for females. The mean nightly air temperature was $22.3 \pm 0.3^\circ\text{C}$ at the study site and $22.1 \pm 0.3^\circ\text{C}$ in the forest; these differences were not significantly different ($T_{82} = 0.64$; $p = 0.526$). The average nightly ground temperature

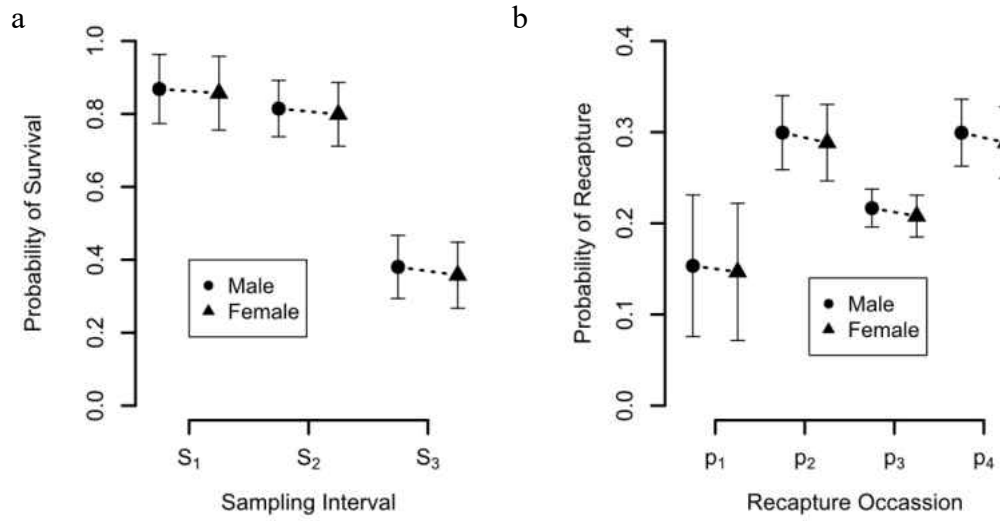


Figure 3. Model-averaged estimates of apparent survival (a) and recapture (b) for a population of copperheads utilizing a recreational site at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

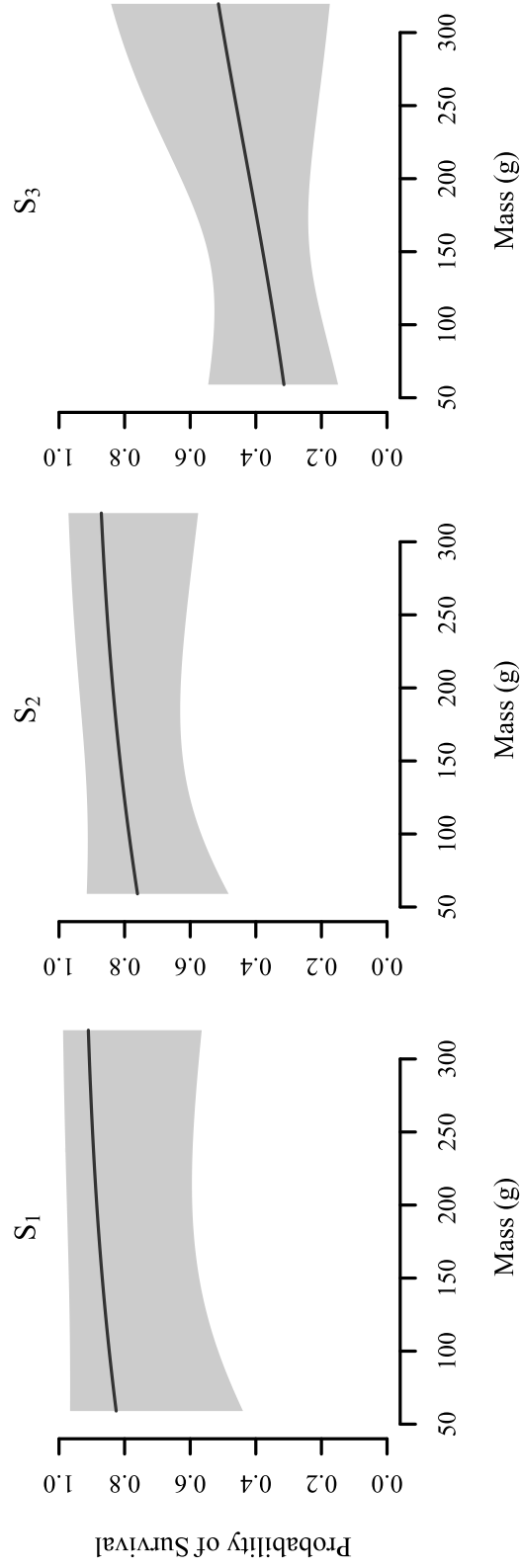


Figure 4. Model-averaged estimates of copperhead apparent survival as a function of mass for each sampling interval (S_x) for surveys conducted at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

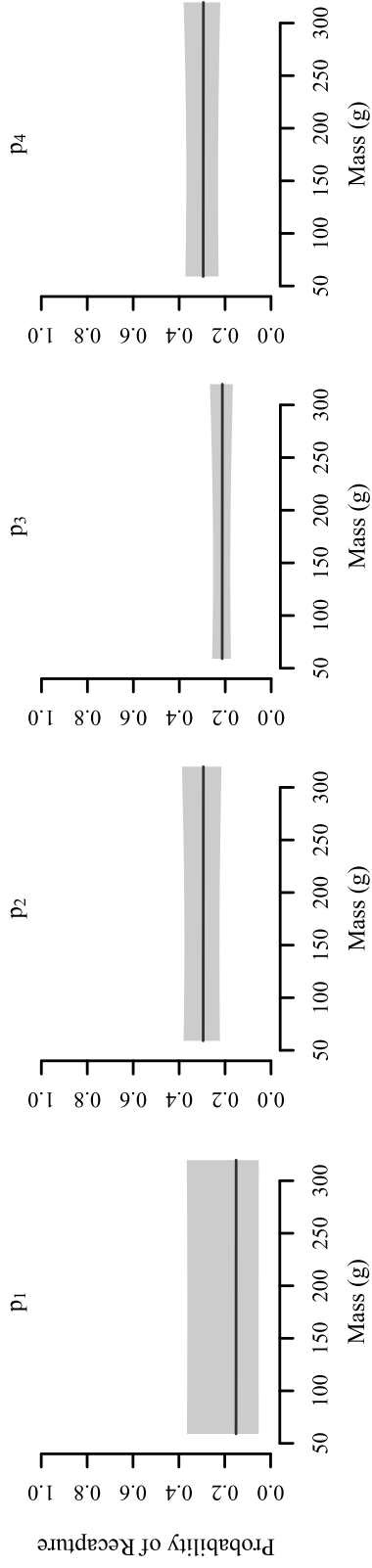


Figure 5. Model-averaged estimates of copperhead recapture as a function of mass for each sampling interval (px) for surveys conducted at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2018.

at the site ($21.8 \pm 0.3^\circ\text{C}$) was significantly higher than the forest ground temperature ($20.7 \pm 0.3^\circ\text{C}$) ($T_{85} = 2.81$; $p = 0.006$) (Table 4; Figure 6). The nightly soil temperature and relative humidity at the study site was $25.4 \pm 0.2^\circ\text{C}$ and $85.03 \pm 1.92\%$, respectively.

Table 4. Average temperatures (T) and relative humidity (%RH) of the study site and surrounding forest on nights that behavioral surveys were conducted at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2018.

Location	T _{air}	T _{ground}	T _{soil}	% RH
Site	22.3 ± 0.3	21.8 ± 0.3	25.4 ± 0.2	85.0 ± 1.9
Forest	22.1 ± 0.3	20.7 ± 0.3		

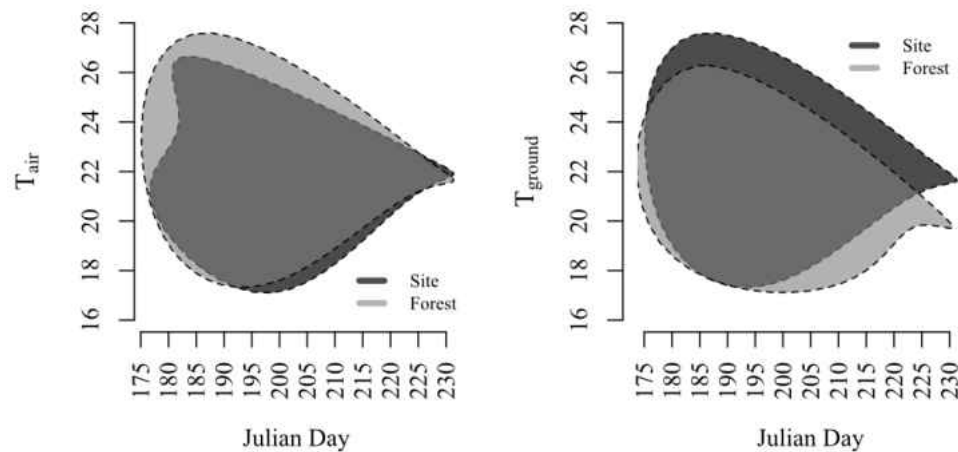


Figure 6. Average daily air (T_{air}) and ground (T_{ground}) temperature profiles during copperhead visual encounter surveys conducted at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2018.

The total amount of time copperheads were observed foraging in the field was 26.16 hours, which consisted of 20 observations of 13 individual copperheads (5 male; 6 female; 2 unknown). The total proportion of time individuals spent non-mobile (59%) was greater than the time spent mobile (41%) (Figure 7). On average, males were

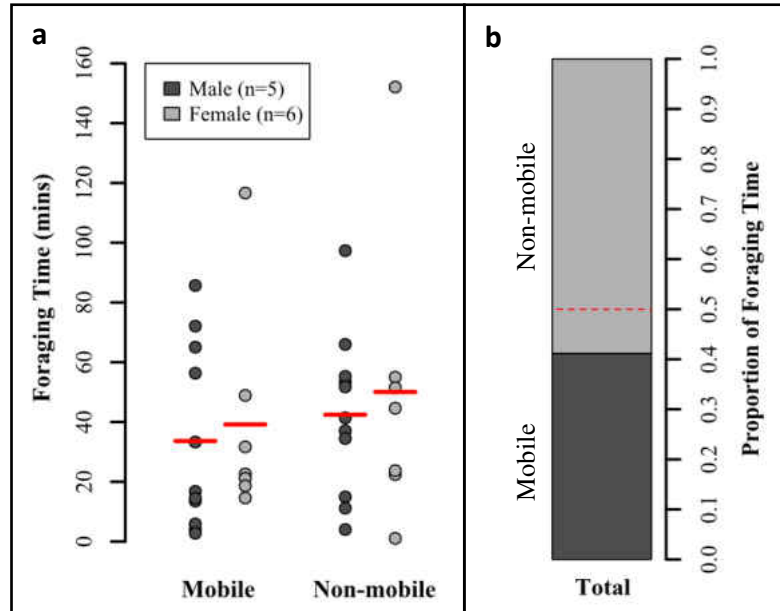


Figure 7. Averages (red lines) of mobile and non-mobile behavior during a single foraging event for male and female copperheads (a), and the total proportion of time observed mobile and non-mobile for all copperheads (b) surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

mobile for 33.63 ± 9.21 min and non-mobile for 42.40 ± 8.11 min; females were mobile for 39.17 ± 13.61 min and non-mobile for 50.04 ± 18.47 min (Table 5; Figure 7).

Although individuals spent more time non-mobile on average, this result is likely biased by an observation of a female individual that remained non-mobile for 152 min (Figure 7). Mass was not a good predictor of either distance traveled ($T_9 = 0.72$; $p = 0.488$; $r^2 = 0.055$) or amount of time spent moving ($T_9 = 0.497$; $p = 0.433$; $r^2 = 0.070$) (Figure 8).

To avoid pseudoreplication, observations of the same individual over time were averaged. The average distance traveled was 32.16 ± 10.27 m for males, 27.18 ± 8.76 m for females, and 30.20 ± 6.98 for all individuals (Figure 9). The average speed for all individuals was 0.40 ± 0.11 m/min. The number of directional changes during a

Table 5. Mean (\pm SE) of the total distance traveled, foraging speed, climbing duration, and foraging duration of a single foraging event for copperheads observed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Sex	Total Distance Traveled (m)	Foraging Speed (m/min)	Climbing Duration (mins)	Foraging Duration (mins)		
				Mobile	Non-mobile	Total
Male	32.16 \pm 10.27	0.40 \pm 0.11	13.1 \pm 4.8	33.60 \pm 9.2	42.43 \pm 8.1	76.06 \pm 12.8
Female	27.18 \pm 8.76			39.17 \pm 13.6	50.01 \pm 18.5	89.21 \pm 25.2

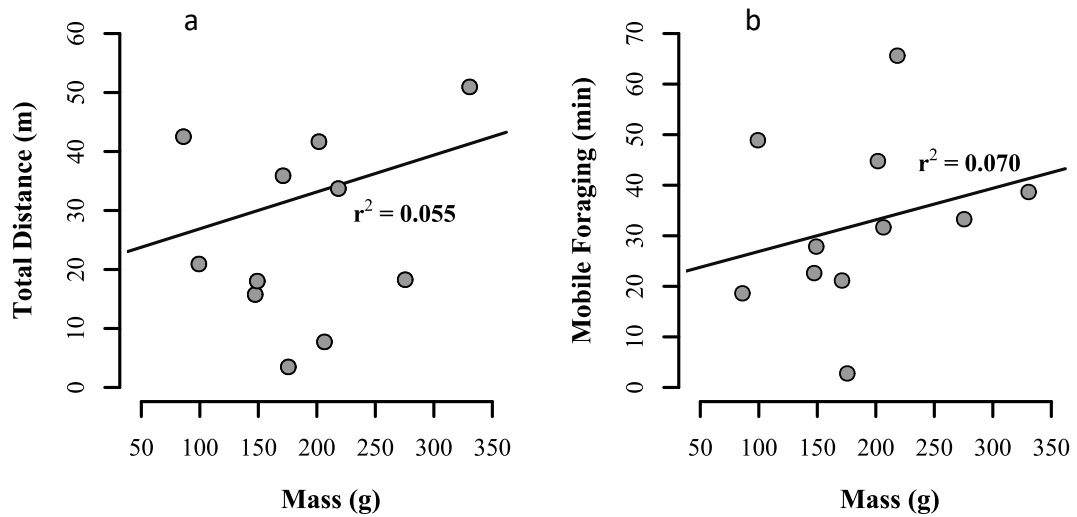


Figure 8. Simple linear regression models used to predict the effect of mass on (a) total distance traveled ($t_9 = 0.72$; $p = 0.488$) and (b) duration of mobile foraging ($t_9 = 0.82$; $p = 0.433$) by copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

foraging event ranged from 0 to 24 with a mean of 6 ± 1 changes. The average amount of time individuals spent climbing was 13.1 ± 4.8 min. Reproduction was not observed in the field. Active combat was not observed, although there was one instance of passive combat behavior, wherein a larger male made contact with a smaller male and the smaller male ‘writhed’ on the ground for ca. 20 seconds (see Schuett 1997). Cicadas were the only prey item observed to be eaten. The number of cicadas eaten per individual ranged from 0 to 3 and the average handling time was 3.17 ± 0.60 min.

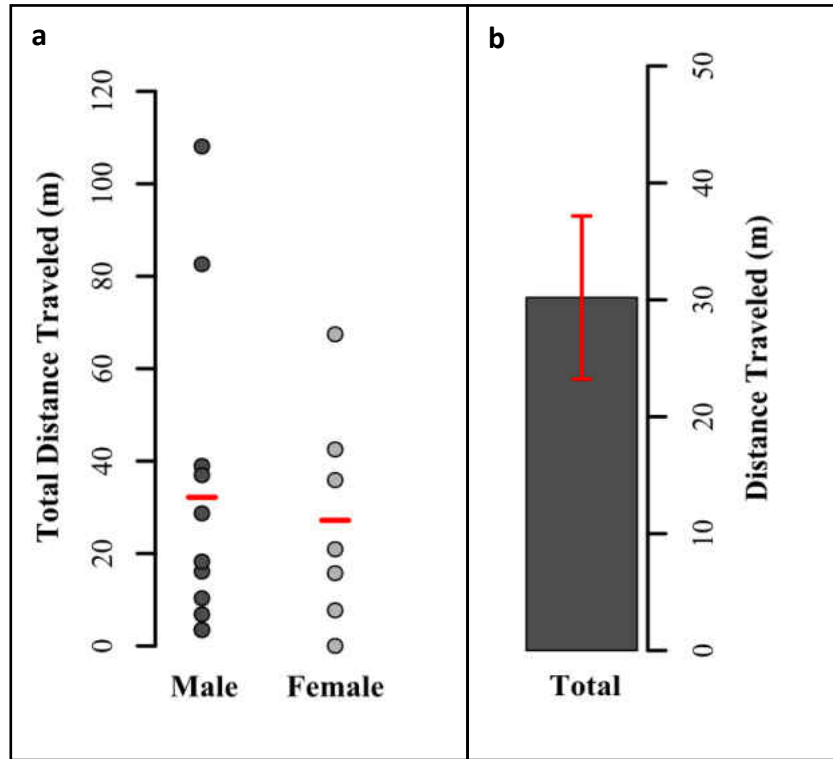


Figure 9. Individual observations and averages (red lines) of total distance traveled during a single foraging event for male and female copperheads (a), and the average total distance traveled for all individuals (b) surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

CHAPTER IV

DISCUSSION

During this study, copperheads were captured (2015–2018) and observed (2018) at a small recreational area in eastern Kentucky in order to investigate demographic structure and foraging behavior. Apparent survival was significantly lower for the last sampling interval and the probability of recapture differed between sampling occasions. Capture-recapture models show that mass predicts apparent survival, with a variable effect over time (Appendix E; Appendix F). Apparent survival varied as a function of mass by 8–11% during the first two sampling intervals and varied by 21% during the third sampling interval (Figure 4). Because true survival and site fidelity are confounded here, these differences could be attributable to variation in fitness (survival) or foraging mode (site fidelity). The greatest sex-specific difference in apparent survival as a function of mass was 3%, which is most likely not a biologically significant result. These results suggest that larger individuals may be more likely to survive overwintering and movement to summer foraging grounds. Additionally, the presence of relatively small individuals at the study site and the relatively lower probability of apparent survival for smaller individuals may be an interesting consequence of individual learning and conspecific trailing behavior (Ford 1986; Gibbons et al. 2005). Because copperheads utilized the study site strictly for foraging and individuals were only captured at the study site, estimates of recapture are directly related to foraging mode. Dependent upon survival and movement to foraging grounds, active foraging for cicadas does not seem to be a function of sex (Appendix D; Figure 3) or size (Appendix E; Appendix F; Figure 5).

Behavioral observations support these results by illustrating that mass may not be as important of a factor for active-foraging copperheads (Figure 8), and males and females displayed the same general foraging strategy (Figure 7; Figure 8). Copperheads in this study were observed using visual and vomeronasal cues to actively forage for emergent cicadas. Individuals spent a significant proportion of time (41%) moving between and within patches of small trees and vegetation. Due to their relatively small size, copperheads were generally not able to climb trees greater than 60 cm in circumference, although some smaller snakes were observed using the long ridges and furrows in the bark of large Eastern white pine (*Pinus strobus*) trees to climb vertically (Mullin and Cooper 2002). Because studies of snake behavior are mostly experimental (Mullin and Gutzke 1999), these results provide important insights into the dynamics of an active-foraging copperhead population and can serve as a model for joining elements of demographic structure and wild snake behavior.

Chemical trailing behavior is an important aspect of snake reproduction (Greene et al. 2001; Greenbaum 2004; Smith et al. 2008), defense (Miller and Gutzke 1999), and foraging (Ford 1986; Stiles et al. 2002). Although insects produce pheromones capable of rapid diffusion, signal reception is dependent upon the physiological, behavioral, and environmental state of the signaler and the receiver (Futrelle 1984). Many studies have experimentally examined snake responses to chemical signals from prey items such as fish (Teather 1991), amphibians (Mushinsky and Lots 1980), snakes and lizards (Cooper et al. 2000), mammals (Burger 1991), birds (Cooper et al. 2000), lepidopterans (Greenbaum 2004), and earthworms (Burghardt and Denny 1983; Zuri and Halpern 2003); but the reception of volatile chemical signals for locating prey in a natural setting

is not as well-studied (Cowles and Phelan 1958; Shivik and Clark 1997; Shine and Mason 2011). Mullin et al. (1998) observed a hierarchical foraging process where *Pantherophis spiloides* (gray rat snake) located active bird nests initially via volatile chemicals and subsequently from visual cues of avian nest. In this study, cicada breeding behavior and emergence at high local densities may facilitate the diffusion and strength of local pheromone signals for predators (Sueur and Aubin 2004). Additionally, some squamates are thought to have more vomeronasal specificity as a result of active foraging behavior (Cooper 1995; Baeckens et al. 2017), although vomeronasal specificity for cicadas has not been studied in snakes.

Visual cues play an important role in prey detection and location for actively-foraging snakes (Drummond 1985; Teather 1991; Shivik and Clark 1997; Cooper et al. 2000). Sparse ground vegetation at the study site may have allowed copperheads to better utilize their vision in order to locate and move between groves of small trees (Mullin and Cooper 2000). Periscoping behavior (Shine et al. 2005), wherein a non-mobile individual raises its head ca. 5–10 cm from the ground at a 45–90° angle, was almost always observed before a copperhead moved to a different vegetation patch. The frequency of periscoping behavior observed in this study suggests the importance of visual cues for patch location within a foraging site. Mullin and Gutzke (1999) found that habitat structural complexity did not affect the foraging ability of *P. spiloides*, which is adapted to foraging in a variety of habitat types. In contrast, a sit-and-wait forager like the copperhead is predicted to be better adapted to foraging in a complex forested habitat where there is a relatively decreased probability of predation due to sedentary behavior and cryptic morphology (Huey and Pianka 1981). Additionally,

physiological constraints such as lower metabolic rates and higher specific dynamic action support this behavioral prediction for sit-and-wait-foragers (Beaupre and Montgomery 2007).

Although copperheads are generally regarded as sit-and-wait predators (Fitch 1960), foraging mode is a dynamic process and can vary under certain conditions (Beaupre and Montgomery 2007). High local densities of annual cicadas, as well as their spatial and temporal predictability, make them a reliable food source that can yield high energy returns (Huey and Pianka 1981; Beaupre and Roberts 2001). Prey reliability can also lead to faster growth, earlier maturation, and higher fecundity in snakes (Bronikowski and Arnold 1999). Additionally, to maintain an active foraging mode, energy gain must be balanced with the associated increase in energy expenditure (Huey and Pianka 1981). Reptiles may manage these trade-offs by operating at levels of sub-optimal activity (Hertz et al. 1988). Although the ground temperature in the forest and the study site was only marginally different, higher site temperatures may help maintain the balance between optimal body temperature and energy expenditure associated with active foraging (Blouin-Demers and Weatherhead 2001). It should be noted that while foraging mode varies across a continuous spectrum, some snake behaviors, such as philopatry, may be less plastic (Reinert 1993). Burger and Zappalorti (1992) observed nesting site fidelity in female *Pituophis melanoleucus* (Pinesnake) even after the site was excavated. This idea seems to be supported by observations of copperhead site fidelity to hibernacula and summer foraging areas (Fitch 1960; Smith et al. 2009). Active foraging in an open area also increases the risk of predation by avian predators, which may be an important driver of foraging mode for diurnally foraging

snakes (Sparkman et al. 2013). Kingsnakes can regulate copperhead populations through predation (Steen et al. 2014), although the dynamics of this relationship are unknown. By foraging at night, individuals not only avoid high daytime temperatures in the summer (Sanders and Jacob 1981; Smith et al. 2009; Putman and Clark 2017; DeGregorio et al. 2018), but may also lower their risk of predation (DeGregorio et al. 2015; Gaynor et al. 2018). Because body pigmentation is strongly correlated to foraging mode and predator avoidance in reptiles (Halperin et al. 2017), active-foraging at a visually homogeneous site may be a result of low predation risk. The risk of predation may be even lower in a human-use area where visually-oriented avian predators are less likely to forage (Potier et al. 2018).

There was no observable difference in copperhead apparent survival attributable to sex or mass, but small sample size ($n = 20$) and temporary emigration are likely to have affected these estimates. Although the data were insufficient to model temporary movement on and off the study site, temporary emigration was probable during the breeding season as a potential result of decreased female foraging activity (Brown and Weatherhead 1997; Smith et al. 2009) and increased male reproductive activity (Smith et al. 2009). The proportion of recaptures in this study declined over time, suggesting that many copperheads did not return to the study site over the course of the project. Because several individuals were only caught once during the study, estimation of transient individual recapture probabilities may help to decrease recapture biases (Pradel et al. 2005). Low survival estimates are commonly a result of low detection in cryptic species (Willson et al. 2008; Durso et al. 2011); however, low detection in this study is unlikely, due to the active nature of copperhead foraging and favorable

observation conditions due to habitat structure. Variable sampling effort among years can contribute to negatively biased survival estimates (Barbour et al. 2013; Kordjazi et al. 2016). Therefore, the probability of apparent survival may be higher merely as a result of increased effort and relatively fewer marked individuals from the previous year. Decreased seasonal rainfall resulting in low cicada abundance (Moriyama and Numata 2006) and decreased foraging at the study site likely affected estimates of apparent survival (Sperry and Weatherhead 2008). Environmental factors may be significant drivers of population structure and function, yet are generally underestimated compared to demographic factors (Kalyuzhny et al. 2014). Therefore, time-dependent environmental covariates should be included in models of copperhead population structure and function when possible. Because opportunistic data collection is often necessary in studies of rare or cryptic species, researchers should aim to decrease overall parameter bias by using ‘joint’ model structures that incorporate all available data (Sandercock 2006). Models that incorporate estimates of immigration and emigration can be even more useful, especially when managers are interested in predicting the effect of covariates on site use dynamics over time.

Integrating ecological and human concerns is an important aspect of a successful management strategy (Kellert et al. 1996). It is important that foraging behavior is considered when developing a management strategy to reduce human-wildlife conflict and promote copperhead conservation. Within this project’s study area, management activities should include decreasing the number of accessible cicadas by removing climbable saplings and small trees and filling in any natural or created cavities or holes that can be used as retreat sites. Because tree removal can facilitate the growth of

understory shrubs and create habitat for snakes (Bonnet et al. 2015), the study site should be consistently mowed and weeded. A simple drift fence could act as an effective barrier between copperheads and humans, as well as an effective tool for continual site monitoring (Greenberg et al. 1994; Todd et al. 2007). Although snake translocation often results in high mortality, short-distance translocation to suitable habitat may be a viable strategy (Nowak et al. 2002) for decreasing human-copperhead interactions. If possible, survival of translocated snakes should be monitored via radio telemetry (Nowak et al. 2002). Artificial canopy gaps (Carter et al. 2014; Sutton et al. 2017) could also be used to ‘intercept’ snakes on their way from overwintering sites to the summer foraging ground at the study site. The effectiveness of forest gaps could be improved by providing coarse woody debris cover (Cross and Peterson 2001; Sutton et al. 2017), leaf litter cover with a depth of 6–10 cm (Sutton et al. 2017), and rock cover (Reinert 1984). It may be an effective strategy to combine short-distance translocation with artificial forest gaps, although continual monitoring would be needed to assess the success of this strategy over time (see Reinert et al. 2011). In this case, a multi-state capture-recapture model would be a useful method for monitoring survival, recapture, and site transition probabilities over time (Sandercock 2006).

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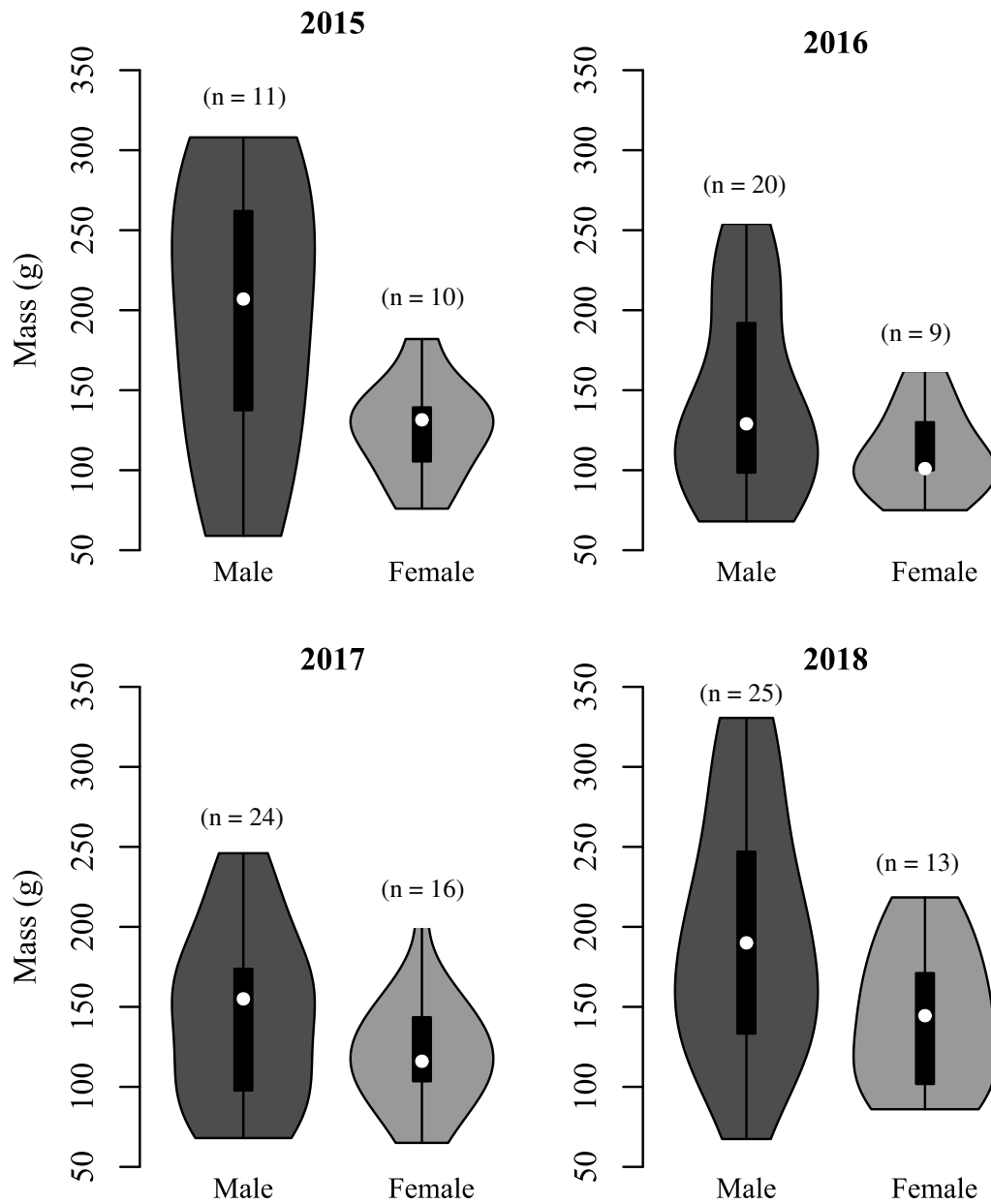
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APPENDICES

APPENDIX A:

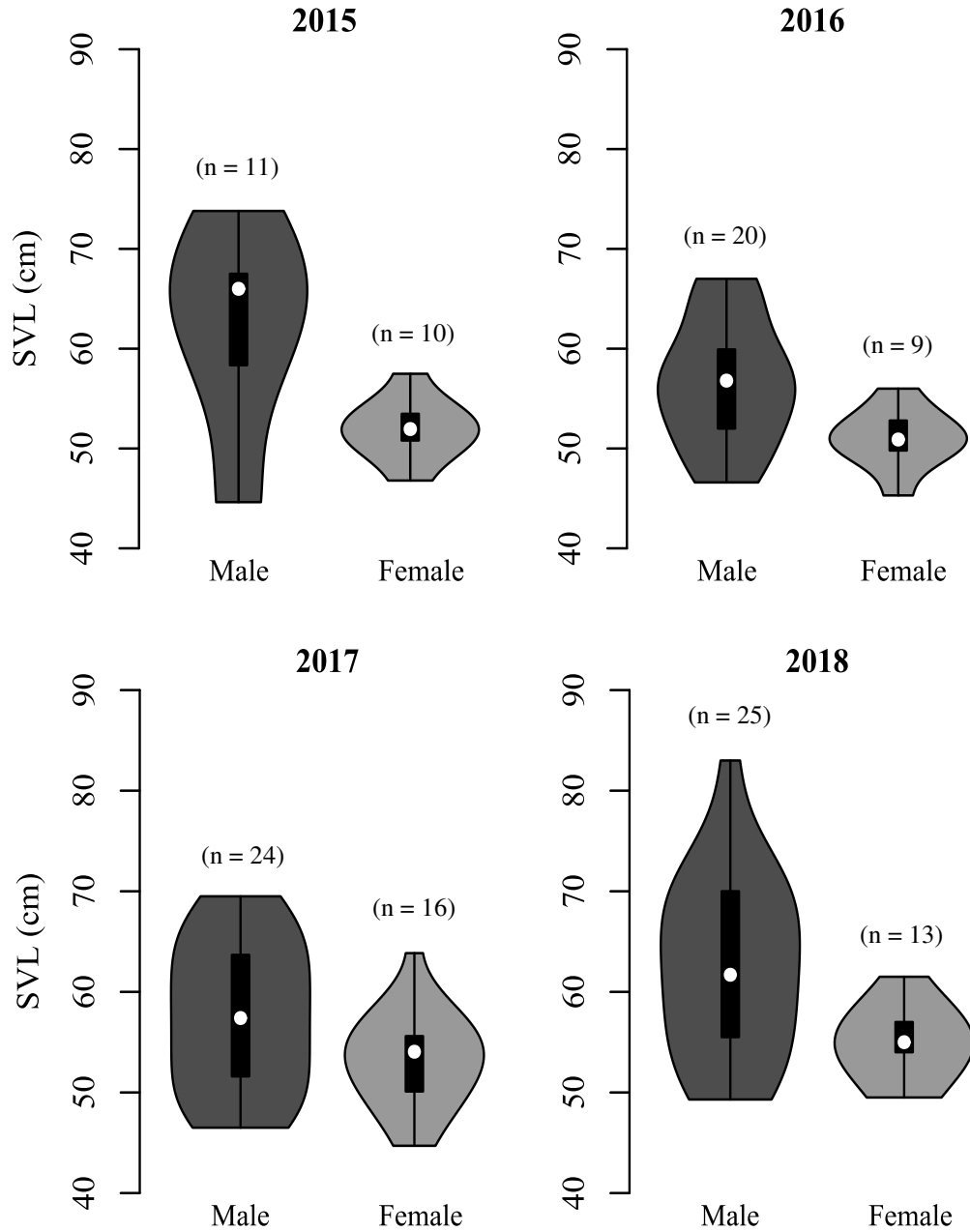
Weight distribution of copperheads captured at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018. Sex-specific sample sizes for each year are specified below the year.



Length (SVL) distribution of copperheads captured at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018. Sample sizes for each year are specified below the year.

APPENDIX B:

Length (SVL) distribution of copperheads captured at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018. Sample sizes for each year are specified below the year.



Length (SVL) distribution of copperheads captured at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018. Sample sizes for each year are specified below the year.

APPENDIX C:

List of a priori capture-recapture models for copperheads surveyed at the Cumberland
Ranger District, Daniel Boone National Forest, KY, 2015–2018.

List of a priori capture-recapture models for copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Model	k	AICc	Δ AICc	w_i	$-2\log(\mathbf{L})$
S(t+mass), $G'' = 0, G' = 1, p(t)$	8	1190.00	0.00	0.210	1173.43
S(t), $G'' = 0, G' = 1, p(t)$	7	1190.50	0.50	0.163	1176.06
S(t+mass), $G'' = 0, G' = 1, p(t+sex)$	9	1191.10	1.10	0.121	1172.39
S(t), $G'' = 0, G' = 1, p(t+sex)$	8	1191.48	1.47	0.101	1174.90
S(t+sex), $G'' = 0, G' = 1, p(t)$	8	1191.58	1.58	0.095	1175.01
S(t+sex+mass), $G'' = 0, G' = 1, p(t)$	9	1191.93	1.93	0.080	1173.22
S(t+mass), $G'' = 0, G' = 1, p(t+mass)$	9	1192.14	2.13	0.072	1173.42
S(t), $G'' = 0, G' = 1, p(t+mass)$	8	1192.63	2.63	0.056	1176.06
S(t+sex), $G'' = 0, G' = 1, p(t+sex)$	9	1192.79	2.79	0.052	1174.07
S(t+mass), $G'' = 0, G' = 1, p(t+mass)$	9	1193.73	3.73	0.033	1175.01
S(t+mass+sex), $G'' = 0, G' = 1, p(t+mass+sex)$	11	1195.06	5.06	0.017	1172.00

APPENDIX D:

Sex-specific model averaged estimates of survival and recapture for copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Sex-specific model averaged estimates of survival and recapture for copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Parameter	Male		Female	
	Estimate	SE	Estimate	SE
S ₁	0.8684	0.0948	0.8569	0.1011
S ₂	0.8147	0.0771	0.7988	0.0872
S ₃	0.3804	0.0866	0.3577	0.0905
p ₁	0.1534	0.0777	0.1467	0.0752
p ₂	0.2995	0.0407	0.2885	0.0419
p ₃	0.2167	0.0208	0.2079	0.0229
p ₄	0.2994	0.0367	0.2885	0.0391

APPENDIX E:
Model averaged estimates of survival and recapture for small, average, and large† male
copperheads surveyed at the Cumberland Ranger District, Daniel Boone National
Forest, KY, 2015–2018.

Model averaged estimates of survival and recapture for small, average, and large† male copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Parameter	Small	SE	Average	SE	Large	SE
S ₁	0.8309	0.1329	0.8862	0.0855	0.9147	0.0826
S ₂	0.7679	0.1164	0.8381	0.0743	0.8770	0.0882
S ₃	0.3249	0.1154	0.4211	0.1006	0.5250	0.2011
p ₁	0.1536	0.0782	0.1533	0.0777	0.1530	0.0784
p ₂	0.2997	0.0423	0.2993	0.0409	0.2989	0.0455
p ₃	0.2169	0.0227	0.2165	0.0212	0.2162	0.0266
p ₄	0.2996	0.0384	0.2992	0.0369	0.2988	0.0418

† Small = 59g; Average = 189g; Large = 320

APPENDIX F:
Model averaged estimates of survival and recapture for small, average, and large† male
copperheads surveyed at the Cumberland Ranger District, Daniel Boone National
Forest, KY, 2015–2018.

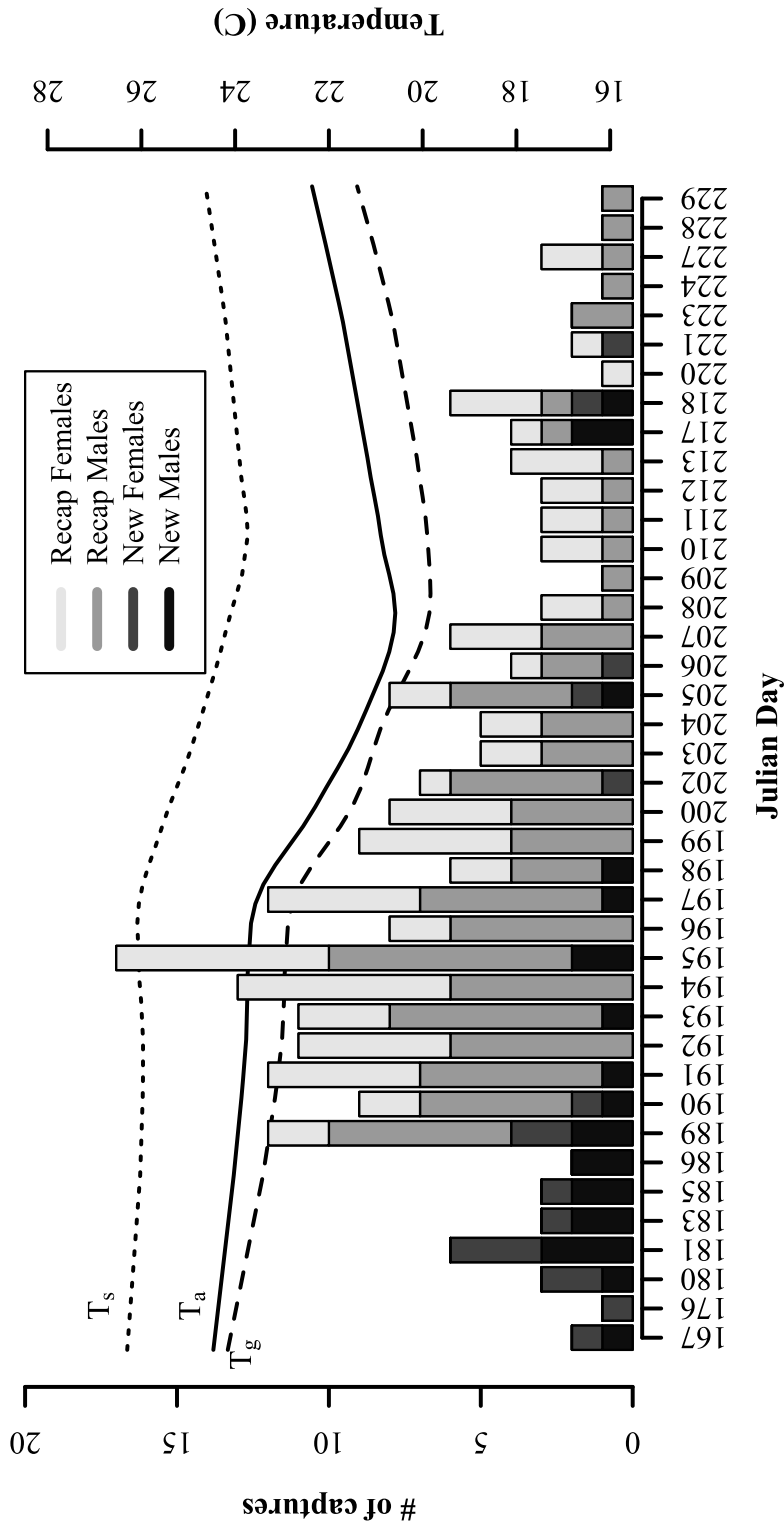
Model averaged estimates of survival and recapture for small, average, and large† male copperheads surveyed at the Cumberland Ranger District, Daniel Boone National Forest, KY, 2015–2018.

Parameter	Small	SE	Average	SE	Large	SE
S ₁	0.8163	0.1356	0.8733	0.0952	0.9029	0.0953
S ₂	0.7482	0.1190	0.8201	0.0898	0.8604	0.1064
S ₃	0.2992	0.1066	0.3941	0.1128	0.4983	0.2197
p ₁	0.1468	0.0756	0.1466	0.0751	0.1464	0.0759
p ₂	0.2888	0.0431	0.2884	0.0423	0.2880	0.0469
p ₃	0.2081	0.0242	0.2078	0.0234	0.2075	0.0286
p ₄	0.2887	0.0404	0.2883	0.0394	0.2879	0.0443

† Small = 59g; Average = 189g; Large = 320g

APPENDIX G:

History of copperhead captures for each sampling day in 2018 at the Cumberland Ranger District, Daniel Boone National Forest, KY. Captures are classified by sex and whether the individual was a new capture or a recapture for the year. The air (T_a), ground (T_g), and soil (T_s) temperature for each survey day is also shown.



History of copperhead captures for each sampling day in 2018 at the Cumberland Ranger District, Daniel Boone National Forest, KY. Captures are classified by sex and whether the individual was a new capture or a recapture for the year. The air (T_a), ground (T_g), and soil (T_s) temperature for each survey day is also shown.