

8-2022

Conservation of open-canopy-associated wildlife: multi-scale management impacts on imperiled herpetofauna

Ethan Joseph Royal
University of Arkansas, Fayetteville

Follow this and additional works at: <https://scholarworks.uark.edu/etd>



Part of the [Animal Studies Commons](#), [Natural Resources and Conservation Commons](#), [Terrestrial and Aquatic Ecology Commons](#), and the [Zoology Commons](#)

Citation

Royal, E. J. (2022). Conservation of open-canopy-associated wildlife: multi-scale management impacts on imperiled herpetofauna. *Graduate Theses and Dissertations* Retrieved from <https://scholarworks.uark.edu/etd/4659>

This Dissertation is brought to you for free and open access by ScholarWorks@UARK. It has been accepted for inclusion in Graduate Theses and Dissertations by an authorized administrator of ScholarWorks@UARK. For more information, please contact scholar@uark.edu, uarepos@uark.edu.

Conservation of open-canopy-associated wildlife:
multi-scale management impacts on imperiled herpetofauna

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in Biology

by

Ethan Joseph Royal
Stetson University
Bachelor of Science in Biology, 2015

August 2022
University of Arkansas

This dissertation is approved for recommendation to the Graduate Council.

John D. Willson, Ph.D.
Dissertation Director

Steven J. Beaupre, Ph.D.
Committee Member

Daniel U. Greene, Ph.D.
Committee Member

Adam M. Siepielski, Ph.D.
Committee Member

Abstract

The loss of open-canopy ecosystems throughout North America has precipitated declines in reptile and amphibian species associated with these habitat types. Current efforts to restore open-canopy ecosystems are underway in many areas, but the local distributions of, habitat characteristics required by and the effects of management actions on many herpetofauna species are poorly understood or entirely unknown. Research examining relationships among herpetofauna and their environments is often complicated by the extremely low detectability seen in many studies. We used landscape-scale, assemblage-level surveys to investigate the occupancy patterns and habitat associations of open-canopy-associated herpetofauna in two regions, as well as gain a broad understanding of the effects of management actions on these assemblages. We also used a long-term monitoring program to document the direct effects of prescribed burn management on a snake community in a restored prairie site. Finally, we used advanced statistical modeling techniques to examine spatial, methodological, and species-specific variation in the detection process that can skew our understanding of species' distributions and habitat associations when ignored. In Chapter 1, we conducted seven rounds of herpetofauna surveys at 81 open-canopy pine savanna sites under a wide range of management regimes, including working forests and conservation areas, and featuring a variety of landscape and vegetation characteristics in Northwest Louisiana. Open-canopy-pine-associated species richness and occupancy were positively related to open vegetation structure in the canopy and understory, as well as the presence of sandy soils, regardless of overstory tree species. These results suggest that working pine forests are capable of supporting open-canopy-pine-associated herpetofauna if certain structural and landscape conditions are present. In Chapter 2, we used a similar study design to examine the status and associations of prairie-associated herpetofauna at

34 remnant, restored, or degraded tallgrass prairie sites in Western Arkansas. Prairie mound density, suggesting a lack of intense anthropogenic disturbance in a site's land-use history, had a significant positive relationship with community and species-specific occupancy of prairie-association herpetofauna, while current vegetation conditions did not strongly influence occupancy. Our findings suggest that prairie-associated herpetofauna distributions in this fragmented landscape are driven more by historic land use than by current habitat conditions. In Chapter 3, we used a long-term monitoring program to track the direct effects of prescribed burn management on a tallgrass prairie snake community. We documented direct mortality from burns in six snake species over an eight-year period, but populations did not appear to suffer meaningful declines due to these mortalities in the long-term. Finally, we used data from Chapters 1 and 2 to investigate spatial and methodological sources of variation in species-specific detection probabilities of squamate reptiles in Chapter 4. We implemented occupancy models that produce method- and species-specific detection probabilities and highlighted variation in the detection process that should be accounted for in herpetofauna research in order to avoid inaccurate inference relating to occupancy, abundance, and habitat associations. In sum, this dissertation produced applicable management guidelines, tools for conservation work, and methodological insight that we believe will advance the state of herpetofauna research.

Acknowledgements

Thank you to Dr. J.D. Willson, my advisor, who provided invaluable opportunities and guided me through this dissertation with unmatched expertise in the world of reptile and amphibian research. His exceptional work ethic and scientific creativity acted as a template that I attempted to follow, making me a much better scientist in the process. His willingness to tolerate my occasionally uncouth provincial mannerisms allowed me to become comfortable in a formal academic setting that might otherwise have been overwhelming. My committee members were all incredibly supportive and were integral to my growth as a scientist. Dr. Steve Beaupre instilled in me the absolute importance of a thoroughly considered, technically rigorous research plan and encouraged me to consider every possible angle in a study design. Dr. Adam Siepielski provided much appreciated encouragement and a unique perspective that helped me consider my research from viewpoints outside the applied ecology bubble I typically inhabit. Dr. Dan Greene has been a great mentor and collaborator whose input was critical to my personal and professional development. I sincerely hope our professional collaboration continues beyond the completion of my dissertation.

I would not have completed this program without the support and help of my friends, lab mates, and colleagues in the department. Dr. Chelsea Kross was and is my closest collaborator, a great friend, and an important mentor. Thank you to Alan Rivero, who brought unrivaled field expertise and carried me on his broad, distinguished shoulders through my first field season. Thank you to Max Carnes-Mason, Larry Kamees, Jason Ortega, Dr. Jen Mortensen, and Ethan Hollender, who are irreplaceable friends and who challenged me to be a more thoughtful scientist. Thank you to Dr. Kyle Quinn; you know why. Thank you to all those who aided my research, including Dr. Darren Miller, Dr. Jessica Homyack, Dr. Casey Brewster, Dr. Jackie

Guzy, Dr. Meredith Swartwout, Elliot Lassiter, Alex Meinders, Annie Royal, Annemarie Saenger, Kory Roberts, Mitchell Pruitt, and many others, particularly those who were responsible for Willson Lab field work at Woolsey Wet Prairie Sanctuary before me. Thank you to the REU students and University of Arkansas undergraduates I collaborated with, particularly Gabriel Yerdon, Mary-Kate Shaver, and Elizabeth Hays. I hope y'all learned something from our work together, even if it was only to avoid the mistakes you watched me make. Thank you to the Department of Biological Sciences faculty and staff for making it a welcoming, productive workplace. Dr. Terry Farrell, Dr. Cindy Bennington, and Dr. Betsie Rothermel guided me early in my research career and put up with far too much nonsense while helping me grow into a real scientist.

Thank you to the Arkansas Natural Heritage Commission, the Northwest Arkansas Land Trust, the City of Fayetteville, the US Forest Service - Kisatchie National Forest, Hancock Forest Management, the Weyerhaeuser Company, Joe Woolbright, Jeff Hickie, Luke Walker, Al Brazzel, Matt Reynolds and many others for site access and logistical help during my research. Thank you to the organizations that funded parts of my work, including the Weyerhaeuser Company, the National Council for Air and Stream Improvement, Inc. (NCASI), Arkansas Game and Fish Commission, the University of Arkansas, and the UA Graduate School.

My family, particularly my parents, Kim and Richard Royal, supported me unconditionally. More than anyone else, they gave me the opportunity to pursue something I cared about, no matter how strange it seemed to them. Lauren Maynard supported me, challenged me, and, without fail, motivated me to continue forward when I felt stuck. I am deeply grateful for what she has done and I hope I can reciprocate. This work is dedicated to baby Annie.

Table of Contents

Introduction.....	1
Literature Cited	7
Chapter 1	11
Influence of landscape and vegetation characteristics on herpetofaunal assemblages in Gulf Coastal Plain pine forests.....	11
Abstract	12
Introduction.....	13
Methods.....	16
Study Area	16
Site Selection	17
Herpetofauna Surveys.....	19
Vegetation Sampling	21
Vegetation and Landscape Characteristics	21
Occupancy Analyses.....	23
Results.....	25
Vegetation Characteristics	25
Herpetofauna Surveys.....	26
Herpetofaunal Occupancy and Detection	27
Herpetofaunal Species Richness.....	29
Discussion	30
Management Implications	36
Acknowledgements.....	37
Literature Cited	37
Tables	43
Figures.....	52
IACUC Approval Documents.....	60
Chapter 2	62

Legacy Land Use Predicts Occupancy Patterns of Prairie-associated Herpetofauna in Western Arkansas.....	62
Abstract.....	63
Introduction.....	64
Methods.....	67
Site Selection	67
Herpetofaunal Surveys	68
Vegetation Surveys.....	70
Habitat Covariates	70
Landscape Covariates	71
Occupancy Modeling.....	72
Results.....	74
Herpetofaunal Surveys	74
Vegetation Surveys.....	74
Occupancy Results	75
Discussion.....	77
Acknowledgements.....	81
Literature Cited	82
Tables.....	86
Figures.....	89
IACUC Approval Forms.....	95
Chapter 3.....	98
Prescribed fire causes direct mortality, but not long-term population declines in a tallgrass prairie snake community	98
Abstract.....	99
Introduction.....	99
Methods.....	102
Study Site.....	102
Burn Mortality Surveys	103
Mark-recapture Surveys	103
Mark-Recapture Models	104
Results.....	105
Mortality Surveys	105

Mark-recapture Analyses.....	106
Discussion.....	107
Acknowledgements.....	111
Literature Cited	111
Tables.....	116
Figures.....	118
IACUC Approval Forms.....	123
Chapter 4.....	128
Quantifying detection probability to account for spatial and methodological variation: a case study of squamate reptiles.....	128
Abstract.....	129
Introduction.....	129
Methods.....	133
Herpetofaunal Surveys	133
Statistical Analysis	134
Results.....	136
Discussion.....	138
Acknowledgements.....	142
Literature Cited	142
Tables.....	145
Figures.....	147
Conclusions.....	149
Literature Cited	152

List of Published Papers

Chapter 1

Royal, E. J., D. Greene, D. Miller, and J. D. Willson. 2022. Influence of landscape and vegetation characteristics on herpetofaunal assemblages in Gulf Coastal Plain pine forests. *Journal of Wildlife Management*.

Introduction

Open-canopy Ecosystems

Open-canopy ecosystems have suffered severe losses throughout North America in the time since European colonization for reasons primarily due their potential for human development and suitable soils for agricultural production (Noss and Scott, 1995). Wetland systems are often described as the most imperiled ecosystem type in North America, but in many cases open-canopy systems have lost an even higher proportion of their historic range due to human development (Sampson and Knopf 1994; Noss and Scott, 1995). Conservation and restoration efforts in open-canopy systems face steep challenges due to extensive, long-standing anthropogenic development and disturbance that can erode pre-development underlying landscape conditions and obscure our understanding of the actual state of historic ecosystem conditions that restoration efforts should attempt to recreate (Peet and Allard 1993; Lauenroth et al. 1999; Horwath and Johnson 2006; Spies et al., 2006). Longleaf pine (*Pinus palustris*) savanna and tallgrass prairie are open-canopy ecosystems that have each seen losses of over 90% of their historic ranges following European colonization (Sampson and Knopf 1994; Landers et al. 1995). Both ecosystems support diverse groups of endemic species that rely on their unique ecological conditions, and the loss of pine savanna and tallgrass prairie has been a significant cause of biodiversity losses in North America (Risser 1988; Noss 1989). However, recent conservation and restoration initiatives have gained momentum for both ecosystem types, with longleaf pine savanna in the southeastern US and tallgrass prairie in the Central US. These efforts have often included the return of fire via prescribed burns after hundreds of years of fire suppression by humans (He et al. 2019). While prescribed fire has provided immense value to conservation and restoration efforts by maintaining appropriate structural and ecological

conditions for wildlife (Kaufman et al., 1988; Wilgers and Horne, 2006; Powell, 2008; Winder et al., 2017), the many effects of prescribed fire regimes remain understudied, including direct effects like burn mortality (Jolly et al. 2022).

Open-canopy pine management and herpetofauna

Longleaf pine savanna is characterized by sparse overstory and low midstory tree densities, with understory consisting of diverse herbaceous plant communities and bare, sandy soils (Peet and Allard 1993). The open-canopy conditions in longleaf pine savanna support a wide range of plant and wildlife species, including endemics that are of significant conservation concern because of land use change (Peet and Allard 1993; Means 2007), as much of the historic range of longleaf pine savanna has been converted to working pine forests used for wood production in the southeastern US coastal plain (Hedman et al. 2000). Conservation of remnant old growth longleaf stands and restoration of historic longleaf pine savanna are vital. However, it is also imperative that we understand how management efforts can facilitate the persistence of species associated with longleaf pine savanna in the working loblolly pine forests that now dominate the landscape.

Research has shown that working forests can provide viable habitat for wildlife, given that certain landscape and ecological conditions characteristic of open-canopy pine savannas are maintained (Loehle et al. 2005; Demerais et al. 2017). A disproportionate number of reptiles and amphibians within the SE US occur primarily in open-canopy pine forests, making these ecosystems important strongholds of diversity (Means 2007). Unfortunately, the loss of open-canopy pine ecosystems has resulted in significant declines for associated reptile and amphibian species (Gibbons et al. 2000). Some open-canopy-pine-associated reptile and amphibian species have been shown to persist in working forest landscapes, particularly in cases where the use of

prescribed fire, herbicide, and mechanical thinning management practices maintain open canopy conditions and facilitate diverse herbaceous understory plant communities (Jones and Chamberlain 2004; Greene et al. 2016; Howze and Smith 2021). As ectotherms reliant upon appropriate environmental and structural conditions for behavioral thermoregulation, reptiles and amphibians are particularly sensitive to management activities that influence physical vegetation structure (Garden et al. 2007; Brewster et al. 2018). Thus, research to assess what management characteristics, structural habitat conditions, and landscape characteristics most strongly influence open-canopy-pine-associated reptile and amphibian species is needed to best inform conservation management efforts.

Tallgrass prairie management and herpetofauna

The vast expanses of tallgrass prairie that historically covered much of the eastern Great Plains have been dramatically reduced and fragmented primarily due to conversion for agricultural production (Sampson and Knopf 1994; Lauenroth et al. 1999). These prairies featured rich vegetation communities and complex micro-topographical features that created structural and environmental heterogeneity (Risser 1988; Horwath and Johnson 2006). However, remnant tallgrass prairie patches are typically small and scattered within heavily developed landscapes, limiting the biodiversity they can support (Risser 1988). Additionally, degraded and restored prairies often lack pieces of their original structural or ecological conditions and are unable to support the full range of prairie-associated species once found in these ecosystems (Fitch 2006; Alford et al. 2012; Tack et al. 2017). The historic range of tallgrass prairie reaches its southeastern limit in Arkansas, with stretches extending into Northwest and Central portions of the state (Baskin et al. 1995). These peripheral sections of the ecosystem's extent currently

support patchy, isolated populations of many prairie-associated wildlife species nearing their eastern range limits (Trauth et al. 2004).

The current statuses of prairie-associated species in Arkansas are largely unknown, particularly for reptiles and amphibians, but research in other regions suggests that prairie-associated herpetofauna are declining due to habitat loss, fragmentation, and degradation (Fitch 2006; Cagle 2008). Being sensitive to changes in habitat structure, herpetofauna populations have suffered as human fire-suppression tactics have allowed woody encroachment in prairie systems (Fitch 1978; Fitch 2006). Prairie-associated herpetofauna face conservation challenges throughout their ranges, but these challenges are poorly understood at their range limits, including in Arkansas where these species might naturally have occurred only in patchy populations (Trauth et al. 2004; Lesbarrères et al. 2014). The need to assess species' statuses at their range limits and implement conservation action has only grown more urgent as human development continues to reduce available habitat (Steen and Barrett 2015), and this need is readily apparent for prairie-associated species in Arkansas.

Prescribed fire management effects on herpetofauna

The return of fire to pyrophilic landscapes has been an important step for conservation management in areas that have been managed with fire suppression tactics for much of the last four hundred years (Fuhlendorf et al. 2011). Fire has played an important role in the management of open-canopy pine savannas and prairies, encouraging biodiversity and habitat heterogeneity in both systems (Frost 1993; Brockway et al. 2002; Igley et al. 2004; Simmons et al. 2007). However, prescribed fire management regimes do not necessarily replicate the frequency, seasonality, or burn conditions of natural historic fire regimes (Bragg, 1982; Engle and Bidwell, 2001). Thus, species that were adapted to natural fire regimes might be poorly suited for aspects

of prescribed fire regimes, potentially leading to exacerbated negative effects like mortality (Whelan et al. 2002; Jolly et al. 2022). Anecdotal evidence and a handful of radiotracking studies show that reptile populations in fire-maintained landscapes can suffer significant mortality during burns (Komarek, 1969; Cross et al., 2015; Harris et al., 2020). While there is obvious potential for mortality from prescribed burns to negatively impact reptile populations, little is known about the long-term effects of consistent burn mortality and few studies place recorded mortalities into the population-contexts needed to be of use in management planning.

Herpetofaunal detection challenges to conservation research

While the conservation challenges facing reptiles are well documented, additional obstacles are presented for the many reptile species that lack sufficient data for conservation assessment (Gibbons et al. 2000; IUCN 2021). Reptiles are, for a variety of ecological, physiological, and behavioral reasons, notoriously difficult to detect even during targeted sampling efforts, and this prevents the collection of adequate data to assess their population statuses (Mazerolle et al. 2007). Low detectability may lead to the false acceptance of species absences, skewing our understanding of their distributions, conservation statuses, and habitat associations (Tyre et al. 2003; Gu and Swihart 2004; Ruiz-Gutiérrez and Zipkin 2011). Further complicating matters, detectability of squamate reptiles can vary due to spatial and temporal differences in environmental conditions, local abundances, survey method, size and latent behavioral characteristics of individuals, and host of other factors that decrease our ability to accurately assess population statuses across space and time (Kery 2002, Durso et al. 2011, Willson et al. 2011, Durso and Seigel 2015, Lardner et al. 2015; Nafus et al. 2015; Rodda et al. 2015). Thus, to improve inference related to species' distributions and habitat associations,

factors that impact detectability should be quantified and accounted for in studies attempting to monitor spatial and temporal population trends.

Dissertation Focus

This dissertation aimed to increase our understanding of how open-canopy-associated herpetofauna respond to human management actions in remnant, restored, and disturbed open-canopy systems. I conducted landscape-scale, assemblage-level studies in two regions, employed long-term monitoring surveys and population modeling at a single site under intense restoration management, and used statistical techniques to demonstrate the scale of variation in detection probability present within species in two different portions of their ranges. The four chapters of my dissertation addressed the following questions:

- 1) What management characteristics, structural conditions, and landscape features influenced the distribution and assemblage composition of herpetofauna in remnant open-canopy pine forests and the working pine forests that have replaced them?
- 2) How has the loss of tallgrass prairie affected prairie-associated herpetofauna at the periphery of their ranges? How do land use history, current management practices, current vegetation conditions, and topographic characteristics affect the regional distributions and habitat associations of these species?
- 3) What levels of burn mortality occur in a snake community subject to annual prescribed fire and do observed levels of mortality affect long-term population trends of species in this community? Are observed levels of burn mortality influenced by environmental factors that can be accounted for in management practices?

- 4) How does detection probability of common reptiles vary by species, within species in different portions of their ranges', and by survey method? How might differences in detectability affect our understanding of species conservation status?

Literature Cited

- Alford, A.L., E.C. Hellgren, R. Limb, D.M. Engle. 2012. Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecological Applications* 22(3):947–958.
- Baskin J.M., R.S. Stuckey, and C.C. Baskin. 1995. Variations in Transeau's maps of the Prairie Peninsula. In *Proceedings of the fourteenth North American prairie conference: Prairie diversity*. Kansas State University, Manhattan pp. 227–231
- Bragg, T. B. 1982. Seasonal Variations in Fuel and Fuel Consumption by Fires in a Bluestem Prairie. *Ecology* 63:7–11.
- Brewster, C. L., S. J. Beaupre, and J. D. Willson. 2018. Habitat loss and local extinction: linking population declines of eastern collared lizards (*Crotaphytus collaris*) to habitat degradation in Ozark glades. *Journal of Herpetology* 52(3):352-360.
- Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65:135–152.
- Cagle, N.L. 2008. Snake species distributions and temperate grasslands: A case study from the American tallgrass prairie. *Biol Cons* 141(3):744–755.
- Cross, M. D., K.V. Root, C. J. Mehne, J. McGowan-Stinski, D. Pearsall, and J. C. Gillingham. 2015. Multi-scale Responses of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) to Prescribed Fire. *American Midland Naturalist* 173:346–362.
- Demarais, S., J. P. Verschuyt, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the US. *Forest Ecology and Management* 385:308-330.
- Durso, A. M., and R. A. Seigel. 2015. A Snake in the Hand is Worth 10,000 in the Bush. *Journal of Herpetology* 49(4):503-506.
- Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515.

- Engle, D., and Bidwell TG. 2001. The response of central North American prairies to seasonal fire. *Rangeland Ecology and Management* 54:2–10.
- Fitch, H.S. 2006 Ecological succession on a natural area in northeastern Kansas from 1948 to 2006. *Herp Cons Bio* 1(1):1–5.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17-43 in *Proceedings of the Tall Timbers Fire Ecology Conference*. 1993 May Vol. 18.
- Fuhlendorf, S. D., R. F. Limb, D. M. Engle, and R. F. Miller. 2011. *Assessment of Prescribed Fire as a Conservation Practice*. Washington D.C.
- Garden, J. G., C. A. Mcalpine, H. P. Possingham, and D. N. Jones. 2007. Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane, Australia. *Australian Ecology* 32(6):669-685.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653-666.
- Greene, R. E., R. B. Iglay, K. O. Evans, D. A. Miller, T. B. Wigley, and S. K. Riffell. 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests opportunities for open pine conservation *Forest Ecology and Management* 360:30-39.
- Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation* 116:195–203.
- Harris, K. A., J. D. Clark, R. D. Elmore, and C. A. Harper. 2020. Direct and Indirect Effects of Fire on Eastern Box Turtles. *The Journal of Wildlife Management* 84:1384–1395.
- He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth’s biodiversity. *Biological Reviews* 94:1983–2010.
- Hedman, C., S. Grace, and S. King. 2000. Vegetation composition and structure of southern coastal plain pine forests: an ecological comparison. *Forest Ecology and Management* 134:233-247.
- Horwath, J.L., and D.L. Johnson. 2006. Mima-type mounds in southwest Missouri: Expressions of point-centered and locally thickened biomantles. *Geomorphology* 77: 308-319.
- Howze, J. M., and L. L. Smith. 2021. The influence of prescribed fire on site selection in snakes in the longleaf pine ecosystem. *Forest Ecology and Management* 481:118703.
- Iglay, R. B., B. D. Leopold, and D. A. Miller. 2014a. Vegetation responses to fire and herbicide in intensively managed, mid-rotation pine. *Forest Ecology and Management* 328:69-78.

- Jolly, C. J., C. R. Dickman, T. S. Doherty, L. M. van Eeden, W. L. Geary, S. M. Legge, J. C. Z. Woinarski, and D. G. Nimmo. 2022. Animal mortality during fire. *Global Change Biology* 28:2053–2065.
- Jones, J. D., and M. J. Chamberlain. 2004. Efficacy of herbicides and fire to improve vegetative conditions for northern bobwhites in mature pine forests. *Wildlife Society Bulletin* 32(4):1077-1084.
- Kery, M. 2002. Inferring the Absence of a Species: A Case Study of Snakes. *The Journal of Wildlife Management* 66:330.
- Komarek, E.V. 1969. Fire and Animal Behavior. Tall Timbers Fire Ecology Conference Proceedings 9:161:207.
- Lardner, B., G. H. Rodda, A. A. Y. Adams, J. A. Savidge, and R. N. Reed. 2015. Detection Rates of Geckos in Visual Surveys: Turning Confounding Variables into Useful Knowledge. *Journal of Herpetology* 49:522–532.
- Lauenroth W.K., I.C. Burke, M.P. Gutmann. 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 1999:223–259.
- Loehle, C., T. B. Wigley, S. Rutzmoser, J. A. Gerwin, P. D. Keyser, R. A. Lancia, C. J. Reynolds, R. E. Thill, R. Weih, D. White Jr., and P. B. Wood. 2005. Managed forest landscape structure and avian species richness in the southeastern US. *Forest Ecology and Management* 214(1-3):279-293.
- Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies. *Journal of Herpetology* 41:672–689.
- Means, B. D. 2007. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157-213 in S. Jose, E. Jokela, and D. Miller, editors. *The longleaf pine ecosystem*. Springer, New York, NY, USA.
- Nafus, Melia G, Amy A Yackel Adams, Page E Klug, Gordon H Rodda, M G Nafus, A A Yackel Adams, P E Klug, and G H Rodda. 2015. Habitat type and structure affect trap capture success of an invasive snake across variable densities. *Ecosphere* 9(8): e02339.
- Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal* 9:211-213.
- Noss, R. F., and J. M. Scott. 1995. *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degredation*. US Department of the Interior, National Biological Service.
- Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Pages 45-81 in *Proceedings of the Tall Timbers Fire Ecology Conference*. 1993 May Vol. 18.

- Risser, Paul G. Diversity in and among grasslands. 1988. Washington, DC: National Academy of Sciences. Eds. Wilson, E. O., and F.M. Peter. "Diversity in and Among Grasslands." Biodiversity. National Academies Press (US).
- Rodda, G. H., A. A. Y. Adams, E. W. Campbell, and T. H. Fritts. 2015*a*. General Herpetological Collecting is Size-Biased for Five Pacific Lizards. *Journal of Herpetology* 49:507–512.
- Rodda, G. H., K. Dean-Bradley, E. W. Campbell, T. H. Fritts, B. Lardner, A. A. Y. Adams, and R. N. Reed. 2015*b*. Stability of Detectability over 17 Years at a Single Site and other Lizard Detection Comparisons from Guam. *Journal of Herpetology* 49:513–521.
- Ruiz-Gutiérrez, V., and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. *Ecosphere* 2:1–14.
- Samson F.B. and F.L. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418–421.
- Simmons, M. T., S. Windhager, P. Power, J. Lott, R. K. Lyons, and C. Schwope. 2007. Selective and Non-Selective Control of Invasive Plants: The Short-Term Effects of Growing-Season Prescribed Fire, Herbicide, and Mowing in Two Texas Prairies. *Restoration Ecology* 15:662–669.
- Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummelt. 2006. Conserving Old-Growth Forest Diversity in Disturbance-Prone Landscapes. *Conservation Biology* 20:351–362.
- Steen, D.A., and K. Barrett. 2015. Should states in the USA value species at the edge of their geographic range?. *J Wild Manag* 79(6):872–876
- Tack, J.D., F.R. Quamen, K. Kelsey, and D.E. Naugle 2017. Doing more with less: removing trees in a prairie system improves value of grasslands for obligate bird species. *J Env Manag* 198:163–169.
- Tingley, R., S. Meiri, and D. G. Chapple. 2016. Addressing knowledge gaps in reptile conservation. *Biological Conservation* 204:1–5.
- Trauth, S.E., H.W. Robison, and M.V. Plummer. 2004. The Amphibians and Reptiles of Arkansas. The University of Arkansas Press, Fayetteville, AR.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving Precision and Reducing Bias in Biological Surveys: Estimating False-Negative Error Rates. *Ecological Applications* 13:1790–1801.
- Whelan, R.J., L. Rodgerson, and C.R. Dickman. 2002. Developing a process-based understanding of population changes in fire-prone landscapes. pp 94–124. In *Flammable Australia: the fire regimes and biodiversity of a continent*.
- Willson, J. D., C. T. Winne, and B. D. Todd. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. *The Journal of Wildlife Management* 75:36–45.

Chapter 1

Influence of landscape and vegetation characteristics on herpetofaunal assemblages in Gulf

Coastal Plain pine forests

Ethan J. Royal

and

Daniel U. Greene, Darren A. Miller, and John D. Willson

Abstract

Longleaf pine (*Pinus palustris*) savanna characterized by open-canopy, diverse herbaceous vegetation, and high amounts of bare soil once covered much of the southeastern United States Coastal Plain. The unique structural and vegetative conditions of this ecosystem support endemic reptiles and amphibians that have declined as longleaf pine forests have been lost or degraded. Private working pine (*Pinus* spp.) forests managed for timber production now occur throughout the southeastern United States and have replaced much of the historical longleaf pine savanna. The examination of herpetofaunal (reptile, amphibian) communities in private working loblolly pine (*P. taeda*) landscapes, particularly in the western Gulf Coastal Plain is lacking. Using repeated field surveys and hierarchical community occupancy models, we examined occupancy and species richness of herpetofauna across 81 sites spanning gradients of management practices, vegetative conditions, and soil composition in northwestern Louisiana, USA, 2017-2019. Young pine stands (<6 yr) exhibited structural characteristics most similar to mature longleaf pine reference sites (>30 yr), while mid-aged stands (13–26 yr) often featured closed canopy and dense midstory. Vegetation conditions varied widely depending on landscape characteristics and site-specific disturbance regimes. We documented 43 species of herpetofauna, including 9 open-pine-associated species. Occupancy of open-pine-associated herpetofauna was positively associated with open-canopy and understory conditions, and sandy soil area. Sites providing open-canopy conditions were often occupied by open-pine-associated species regardless of overstory type and disturbance method. Overall richness of herpetofauna was greatest at sites with moderate canopy cover outside of sandy soil regions. Working pine landscapes in the western Gulf Coastal Plain can support diverse herpetofaunal assemblages, including open-pine-associated species, when management practices maintain open-canopy conditions on sandy,

upland soils. More broadly, our results provide insight into how forest management practices affect herpetofauna and may guide practices that can contribute to conservation value of working pine forests.

Introduction

Longleaf pine (*Pinus palustris*) was historically the primary forest overstory species on sandy upland soils in Coastal Plain regions of the southeastern United States, with coverage of approximately 30 million ha from Virginia to eastern Texas (Frost 1993). Longleaf pine savannas were characterized by low tree densities, low canopy cover, and a dense and diverse understory plant community containing up to 40 herbaceous plant species/m² (Peet and Allard 1993). The diverse vegetation, sandy soils, and structural heterogeneity of longleaf pine savannas supported a wide variety of vertebrates, including several endemic species (Means 2007).

Following European colonization, coverage of longleaf-dominated forest decreased by >90%, with little old-growth forest remaining (Landers et al. 1995). Loss or conversion of forests dominated by native longleaf pine is a strong driver of biodiversity loss in the Coastal Plain (Noss 1989). Although recent initiatives have increased coverage of longleaf pine forests across the Coastal Plain, many longleaf-associated species are of conservation concern, including red-cockaded woodpecker (*Dryobates borealis*), gopher tortoise (*Gopherus polyphemus*), and Louisiana pine snake (*Pituophis ruthveni*; Rudolph et al. 2006, Kirkman and Jack 2017, Greene et al. 2019, Weiss et al. 2019). Understanding how requirements of these species can be met in other forest types is important for their conservation. Working loblolly pine (*P. taeda*) forests managed for wood production have become a dominant form of land cover across the historical range of longleaf pine savannas in the Coastal Plain (Hedman et al. 2000). The literature provides mixed evidence for the ability of working loblolly pine stands to support longleaf-

associated species specifically, with quality appearing to vary based on management (i.e., mechanical, chemical, prescribed fire, a combination of methods), the intensity and interval of management activities, and the focal taxa (Greene et al. 2016). Researchers have demonstrated that working forests can have considerable value as wildlife habitat, provided that important landscape, structural, and vegetative characteristics are maintained (Demarais et al. 2017). For example, Loehle et al. (2005) reported that across 3 mixed pine-hardwood landscapes in the southeastern United States, working pine forests harbored the greatest avian species richness. This difference may be attributable to greater heterogeneity in stand age and structure in working pine landscapes and presence of early-successional vegetation conditions with high vegetation species richness (Loehle et al. 2005; Jones et al. 2009, 2012).

Changes in vegetation composition, loss of important structural elements, or a change in intensity or frequency of disturbance can affect reptile and amphibian species' ability to thermoregulate, forage, and reproduce, and can entirely exclude species from portions of their geographic ranges (Jellinek et al. 2004). Within working forest landscapes, prescribed fire, herbicide, and thinning can increase herbaceous vegetation diversity (Verschuyl et al. 2011, Iglay et al. 2014a), and can provide understory conditions required by open-pine-associated species including northern bobwhite (*Colinus virginianus*) and some snakes (Jones and Chamberlain 2004, Greene et al. 2016, Howze and Smith 2021). Forest characteristics required by most species historically associated with longleaf pine savanna remain unknown (but see McIntyre et al. 2019 for a multi-taxa study addressing these knowledge gaps), and thus it remains largely unclear how management regimes (i.e., the method, intensity, and interval of management activities) within working forests might be tailored to provide the most benefit to the widest range of species.

In addition to the remaining knowledge gaps related to habitat requirements of open-pine-associated species, there are geographical research gaps. Most studies addressing wildlife conservation in longleaf pine forests have occurred in Florida, Georgia, and South Carolina, USA, while the western Gulf Coastal Plain remains understudied (Litt et al. 2001, Tuberville et al. 2005, Smith et al. 2006). Extensive loss of longleaf pine forest in parts of the western Gulf Coastal Plain, particularly in Louisiana, has resulted in an increasingly fragmented landscape that complicates conservation efforts for imperiled species in this region (Outcalt 1997, Rudolph and Burgdorf 1997). Understanding how species across the range of this threatened ecosystem vary in their habitat requirements and how they respond to habitat loss and alteration is important to successful conservation and restoration efforts.

Reptiles and amphibians are important components of the longleaf pine ecosystem and are recognized as diverse contributors to ecosystem function and as among the most rapidly declining vertebrate groups (Gibbons et al. 2000, Baillie et al. 2004). In the southeastern United States, a disproportionate number of reptile and amphibian species are associated with the longleaf pine ecosystem (Means 2007), many of which have declined precipitously in recent years (Gibbons et al. 2000). Because reptiles and amphibians are ectothermic and most have limited long-distance mobility, they exhibit strong dependencies on specific structural vegetation characteristics such as canopy, midstory, and groundcover to provide appropriate thermal conditions (Greenberg 2001, Garden et al. 2007). The relationship between vegetation structure and thermal conditions directly connects vegetation structure to every aspect of reptile and amphibian life history through its influence on available activity times and efficiency of physiological processes (Brewster et al. 2019). To effectively manage and conserve open-pine-associated herpetofauna, we must better understand relationships among management practices,

vegetation characteristics, and species' occupancy in pine stands with different overstory species and management regimes.

Few studies (Guzy et al. 2019, Jones et al. 2020) have rigorously assessed effects of vegetation structure on herpetofaunal assemblages and species distributions across heterogeneous landscapes with variable types and intensities of anthropogenic disturbance. Specifically, herpetofaunal communities in working loblolly pine forests and nearby longleaf forests remain understudied. Therefore, we addressed these knowledge gaps through a landscape-scale study evaluating relationships between site characteristics, vegetation, and herpetofauna assemblages in pine forests in the western Gulf Coastal Plain of northwestern Louisiana. By incorporating a variety of site- and landscape-level covariates affected by management practices and region, we aimed to determine which site characteristics most strongly influenced open-pine-associated herpetofauna assemblages. We predicted that regardless of overstory species (loblolly vs. longleaf), species richness of open-pine-associated herpetofauna and species-specific occupancy probabilities would be highest at sites with sandy upland soils and fire-maintained, open-canopy vegetation structure.

Methods

Study Area

We conducted herpetofauna and vegetation surveys in 3 parishes (Jackson, Bienville, and Winn; 212974 ha, 150219 ha, 247603 ha each, respectively) in northwestern Louisiana, from 2017–2019 (Figure 1). The study region represented a section of the western Gulf Coastal Plain containing sandy-soiled upland forest stands previously dominated by longleaf pine. During our study, this region was a mix of loblolly pine stands managed for timber production (i.e., working forest) and conservation land consisting either solely of longleaf pine forest or mixed forest

stands with both pine species and a variety of hardwood species. We targeted sites in each of these management groups across the region to capture the breadth of vegetation and landscape conditions available to open-pine-associated herpetofauna. Topography in the study region was characterized by rolling hills in upland and lowland areas at elevations ranging from 20–130 m above sea level and with intermittent and perennial streams and ephemeral wetlands interspersed throughout the landscape. The climate was characterized by mild winters (Dec–Feb) and hot, humid summers (Jun–Aug), with monthly average temperatures ranging from 1.6–13.9° C in January (average low-high) to 21.1–33.9° C in August and an annual average of 1,362 mm of precipitation (noaa.gov, accessed 14 Aug 2021).

Site Selection

We first established our study region using geographic information system (GIS; ArcMap 10.1; Esri, Redlands, CA, USA) soil layers from the Soil Survey Geographic Database (U.S. Department of Agriculture [USDA] 2016) relevant to available stand locations on private and public lands (Figure 1). We focused on a region in western Bienville and northern Winn parishes (Figure 1) that contained substantial representation of sandy upland soils (Hydrogroup A and B; USDA 2016), which influence distribution of open-pine-associated herpetofauna (Wagner et al. 2014). We designated a sampling site as a 20-ha area occurring within a single stand under uniform forest management where we completed all surveys and centered our remote sensing landscape analyses. We selected sites representing broad gradients of stand- and landscape-level characteristics that likely influence occupancy of herpetofauna of the western Gulf Coastal Plain, including vegetation structure and composition (Noss 1989), soil type (Wagner et al. 2014), stream presence, overstory tree species, and stand management regime (Lettow et al. 2014, Greene et al. 2016). Available study sites were embedded in largely homogenous land use

matrices, with stands managed for timber production or conservation primarily surrounded by similarly managed stands.

We began site selection by considering sites spanning a gradient of soil conditions, ranging from those located in higher elevations dominated by sandy upland soils (i.e., sandhills) to those at lower elevations with clay-dominated soils. Next, we established broad management categories defined based on stand age, overstory tree species (loblolly or longleaf), and management regime (mechanical management or prescribed fire; Table 1). Specifically, we filtered managed loblolly stands into young loblolly (<6 yr old) and mid-age, recently thinned loblolly (13–26 yr old) categories to capture vegetation conditions following high-intensity mechanical management events (clearcutting and thinning). Within the Winn District of the Kisatchie National Forest, we considered site locations within pine-dominated stands (most of which were managed with prescribed fire on variable 5–10-yr fire return intervals) consisting of mature loblolly and mature longleaf (>30 yr old), and young longleaf (<10 yr old; Figure 1). We also added sites within fire-maintained, privately owned longleaf stands located in sandy soil regions and managed for conservation, and fire-maintained, privately owned mature loblolly stands managed for conservation outside of sandy soil regions, with both groups on 2–5-year fire return intervals.

We visited an initial pool of >400 potential candidate sites in December 2016 to confirm GIS classifications and accessibility. From this pool, we selected our final sites by selecting for even distribution of sites across soil types, location within the largest stands (average stand size = 139.5 ha; range = 6.8–164.3 ha) to minimize edge effects, spatial interspersation to avoid clustering of sites with similar covariate values within management categories, and spatial separation of sites by ≥ 2 km, when possible. While we attempted to represent the range of available landscape

covariate conditions across sites within each management category, we encountered some limitations; particularly limiting was number of mature loblolly stands in sandy soil regions and the sizes of young stands, with some under the desired threshold of 20 ha. Although we included some sites within stands below the desired size threshold to increase representation of less common management categories, most stands were large enough to meet the home range minimums of this region's most vagile large-bodied snake species (Himes et al. 2006, Howze and Smith 2015).

For comparison of vegetation characteristics, we identified a subset of 4 reference sites from the pool of mature longleaf sites with high coverage of Hydrogroup A soils, based on the open canopy and high bare soil and herbaceous groundcover conditions that most closely matched those described as typical of mature longleaf savanna and sandhill conditions (Landers et al. 1995). These sites harbor populations of open-pine-associated herpetofauna of conservation concern (Rudolph et al. 2006).

Herpetofauna Surveys

We conducted herpetofauna surveys using 2 sampling techniques: coverboards and 1 person-hour diurnal visual encounter surveys. We set 5 $122 \times 81 \times 1.3$ -cm plywood coverboards 10 m apart in a transect located at least 30 m from any site boundary, streamside management zone, or wetland at each site in March 2017. Each visual encounter survey consisted of 2 observers opportunistically searching appropriate structures for herpetofauna (under litter and coarse woody debris [CWD], basking sites) for 30 minutes, while maintaining a >30-m buffer from edges (roads, site boundaries, streamside management zones) and water bodies, when possible. Each visual encounter survey included searching the area used for coverboard surveys and we attempted to thoroughly cover as much site area as possible. We attempted to capture all

reptiles and amphibians encountered. We identified individuals to species, photographed them, and released them at the end of the survey. We performed 7 herpetofauna surveys at each site, with each site surveyed 3 times from May–July 2017, 3 times from March–May 2018, and once during March 2019, with no site surveyed more than once every 2 weeks. Although survey timing varied among years, all surveys occurred within annual active periods for target species. For each survey, we also recorded date, time, and air temperature (°C) at the survey start (Kestrel™ 2500; Kestrel, Boothwyn, PA, USA) as potential predictors of detection probability.

Previous researchers demonstrated the importance of identifying target species most likely to be affected when studying large-scale land management strategies, including species associated with longleaf pine forests (Steen et al. 2010). Existing studies that have assigned reptile and amphibian species to longleaf-pine-associated guilds have primarily included the entire southeastern United States coastal plain and based guild designations on species' range overlap with longleaf pine forest coverage (Guyer and Bailey 1993, Means 2007). Given the variation in habitat associations that can exist across a species' range (Means 2007), we aimed to focus on a group of herpetofauna species most strongly influenced by open-canopy forest conditions in our specific study region. Thus, we used state field guides and the Southeast Partners in Amphibian and Reptile Conservation regional habitat management guidelines (Bailey et al. 2006) to identify a guild of open-pine-associated species a priori (Table 2). We limited this guild to species that had the potential to occur in northwestern Louisiana, were listed in the habitat management guidelines as having a suitable or optimal relationship with sandhill-scrub cover types, or were noted in field guides (Powell et al. 2016, Boundy and Carr 2017) as being strongly linked with open-canopy pine conditions in Louisiana. We used a similar process to identify a guild of mesic-forest-associated species (Table 2). This guild included species noted in

the state field guide as being associated with bottomland forest or having a suitable or optimal relationship with mesic hardwood forests in the habitat management guidelines.

Vegetation Sampling

We quantified vegetation structure at all 81 sites during May–June 2018 following a nested plot design based on Hedman et al. (2000). We intended these measures to capture general structural conditions influenced by management and landscape factors, rather than annual or seasonal vegetation growth patterns. Within each site, we randomly selected the location of a single large (20 × 50 m) overstory plot such that the entire plot fell within an area previously covered in our herpetofauna surveys and that each plot was ≥ 10 m from any edge. We used a GRS DensitometerTM (Geographic Resource Solutions, Arcata, CA, USA) to measure canopy cover along 4, 50-m parallel transects within each overstory plot, with each transect running the length of the overstory plot and separated from neighboring canopy cover transects by approximately 6.6 m (Paletto and Tosi 2009). We recorded a canopy cover measurement, and canopy tree species if present, every 10 m along each 50-m transect (24 points/site). Within each overstory plot, we systematically placed replicate sets of 3 nested plots to quantify midstory, understory, and herbaceous plant communities. In 2 midstory plots (circular, 100 m²), we identified and measured diameter at breast height (dbh) of all woody species < 2.5 cm dbh and ≥ 1.4 m tall. In 4 understory plots (circular, 10 m²), we identified and visually estimated percent cover of all woody species < 2.5 cm dbh and < 1.4 m tall, and total non-woody herbaceous, bare soil, litter, and CWD groundcover.

Vegetation and Landscape Characteristics

Because we measured many vegetation variables that were often inter-related, we performed a principal components analysis (PCA) without predictors and using correlation

coefficients in the vegan package in R (version 3.5.3; Dixon 2003, R Core Team 2019) to reduce potentially correlated variables to a lower number of uncorrelated components. We included average canopy cover, average density (trees/ha) of midstory trees, and understory plot measurements of average percent groundcover of herbaceous vegetation, bare soil, leaf litter, and CWD cover in the habitat PCA and used the first 2 principal components (PC) in occupancy analyses (see below). To isolate effects of overstory pine species (loblolly vs. longleaf) and soil composition, we did not include them in the PCA; exploratory analyses suggested that they were not significantly correlated with vegetation variables included in the PCA.

Lastly, we used management records and remote sensing data in ArcMap to produce landscape-level covariates for occupancy analyses. As a covariate representing soil composition, we determined upland soil area by calculating area (m²) of Hydrogroup A and B soils within a 1-km-diameter buffer around the center of each sampling site using the Spatial Analyst toolbox and the percent area of upland soils in site buffers ranged from 0% to 98%. Additionally, we calculated stream length in proximity to each site using regional stream shapefiles by measuring length of stream (m) clipped within a 1-km-diameter buffer for each site and stream length in site buffers ranged from 453 m to 4,401 m. We determined whether stand overstory composition was dominated by loblolly or longleaf using site management records and vegetation surveys. Finally, we determined if sites had been treated with a prescribed burn within the previous 10 years, the finest scale available for all sites in available management records, as previous research suggests fire management may be more beneficial for herpetofaunal assemblages than other management techniques (Steen et al. 2013).

Occupancy Analyses

We used hierarchical Bayesian occupancy models (Dorazio and Royle 2005) examining reptile and amphibian occupancy and detection (Ψ_{ij} and Θ_{ijk} , respectively) responses to site (vegetation PC1 and PC2, site overstory composition, upland soil area, recent fire management, and stream length) and sampling (linear and quadratic effect of temperature at survey) covariates. This modeling approach accounts for imperfect detection and improves precision of individual parameter estimates, particularly for rare species, by considering them in the context of the larger community (Dorazio et al. 2006). We used a model structure assuming static occupancy over the sampling period, given the short duration relative to the lifespans of our focal taxa, lack of intense management action within sites during the study, and the fact that the size of our sites exceeded the known home ranges of even the most wide-ranging of our target species (Bailey et al. 2014, Howze and Smith 2015). We built a binary encounter matrix representing detection (1) and non-detection (0) data for each species at each site during each survey occasion and used a variation of the model written and modified by Zipkin et al. (2009), Hunt et al. (2012), and Guzy et al. (2019). If species i occupies site j then the true occupancy state $z_{ij} = 1$, otherwise $z_{ij} = 0$. We assumed that occupancy status was constant across surveys during the study period. Occupancy state and species detection were each modeled as random Bernoulli variables. Occupancy state was $z_{ij} \sim \text{Bern}(\Psi_{i,j})$ and represents the probability that species i occupies site j . Species detection was represented by $y_{ijk} \sim \text{Bern}(p_{ijk} * z_{ij})$, where $y_{ijk} = 1$ if species i is detected at site j during survey k . We assumed species-specific occupancy probability ($\Psi_{i,j}$) followed a linear-logit function of the model covariates:

$$\begin{aligned} \text{logit}(\Psi_{ij}) = & u_i + \alpha_{1i} \text{VegPC1 } j + \alpha_{2i} \text{VegPC2 } j + \alpha_{3i} \text{OverstoryComposition } j \\ & + \alpha_{4i} \text{UplandSoil } j + \alpha_{5i} \text{RecentFire } j + \alpha_{6i} \text{StreamLength } j \end{aligned}$$

Species-specific detection probabilities (θ_{ijk}) also followed a linear-logit function of the model covariates:

$$\text{logit}(\theta_{ijk}) = v_i + \beta_{1i} \text{Temperature} + \beta_{2i} \text{QuadraticTemperature}$$

We included site overstory composition (0 = loblolly pine, 1 = longleaf pine) as a binary site covariate, indicating whether a site was dominated by loblolly or longleaf pine. We included recent fire (0 = no, 1 = yes) as a binary covariate indicating whether sites had been treated with a controlled burn within the previous 10 years, as determined by site management records. We included vegetation principal components (VegPCs) 1 and 2 using site scores for the 2 strongest PC axes from the PCA we performed on vegetation variables. We included upland soil area and stream length as continuous site covariates. We included temperature as a linear and quadratic sampling covariate to detect any non-linearity in species responses to survey temperature conditions. For example, species that prefer moderate temperatures might be less detectable at low or high survey temperatures, rather than exhibiting a linear (positive or negative) relationship between detectability and temperature. We standardized continuous covariates using z-scores where the mean site and sampling scores equal zero to allow us to compare model coefficients as effect sizes (Kéry and Royle 2015). We used separate models with the aforementioned site and sampling covariates for all herpetofauna species encountered (model 1), for species included in the open-pine-associated guild (Table 2; model 2), and for mesic-forest-associated reptile and amphibian species (Table 2; model 3).

We used R (3.5.3; R Core Team 2019) to organize data and performed a Bayesian analysis of the model using the program WinBUGS (Lunn et al. 2000) called through R2WinBUGS (Sturtz et al. 2005). We used uninformative priors for hyper-parameters, U (0,3) for σ parameters and U (-3,3) for all $\mu\alpha$ and $\mu\beta$ parameters, because of the lack of prior knowledge of the parameter's

actual value (Link et al. 2002). We ran each model with 3 Markov chain Monte Carlo chains of 200,000 iterations with the first 100,000 acting as a burn-in and a thinning rate of 3. We assessed model convergence by visual inspection of chains and using the Gelman-Rubin diagnostic test, for which all monitored parameters had values ≤ 1.02 (Gelman and Rubin 1992).

Results

Vegetation Characteristics

Vegetation data demonstrate that open-canopy cover conditions were most common in young loblolly (range = 0–0.87; average = 0.19) and young longleaf (range = 0–0.54; average = 0.15) sites. Mature fire-maintained loblolly and longleaf sites had similar closed canopy conditions (range = 0.29–1 and 0.16–0.95, respectively; average = 0.71 and 0.60, respectively) to thinned loblolly (range = 0.5–0.95; average = 0.63) sites. Groundcover conditions typical of open-pine longleaf forest, including bare soil and herbaceous groundcover, were also most common in young loblolly (ranges = 0–38% and 10–76%, respectively; averages = 20% and 46%, respectively) and young longleaf (ranges = 0–52% and 27–82%, respectively; averages = 24% and 47%, respectively) sites. Bare soil and herbaceous groundcover values were similar in mature loblolly (ranges = 0–42% and 3–48%, respectively; averages = 8% and 22%, respectively) and mature longleaf (ranges = 0–69% and 4–49%, respectively; averages = 14% and 26%, respectively) sites, with thinned loblolly sites featuring the least bare soil groundcover (range = 0–21%; average = 2%) but comparable herbaceous groundcover (range = 2–49%; average = 26%) to mature sites.

The first 2 PCA axes explained 44.8% and 23.4% of variance in vegetation data, respectively (cumulative 68.2%; Table 3). The remaining components accounted for substantially less variation, and we excluded these from further analyses. The strongest factor loading for PC1 was

a negative relationship with average canopy cover (Table 3), followed by strong loadings for percent litter (–), percent bare soil (+), percent herbaceous groundcover (+), midstory tree density (–), and percent CWD cover (+). Thus, PC1 captured differences between frequently disturbed sites with low canopy cover, high bare soil and herbaceous groundcover, and low leaf litter, and less frequently disturbed sites with higher canopy cover, higher midstory tree density, and high leaf litter groundcover. The former group was largely represented by young sites and some mature longleaf (reference) sites; thinned sites and mature sites comprised the latter (Figure 2A).

Principal component 2 was heavily weighted by midstory tree density (–), and percent woody (–), herbaceous (–), litter (+), and CWD (+) groundcover (Table 3). Although young sites and thinned sites had lower average PC2 scores than mature sites, these categories overlapped considerably on the PC2 axis (Figure 2A). Loblolly and longleaf overstory sites overlapped widely on PC1 and PC2 axes (Figure 2B).

Herpetofauna Surveys

We recorded 2,659 detections of 43 reptile and amphibian species across all replicate surveys and sites (Table 2). We captured 30 salamanders of 1 species, 471 anurans of 9 species, 25 turtles of 4 species, 1,971 lizards of 7 species, and 162 snakes of 22 species. Surface-active lizards (six-lined racerunner [*Aspidozelis sexlineatus*], prairie lizard [*Sceloporus consobrinus*], green anole [*Anolis carolinensis*], and ground skink [*Scincella lateralis*]) accounted for over half of all captures.

We detected 9 of 15 open-pine-associated species that potentially occurred in the study area, with 542 detections, again dominated by surface-active lizards and snakes (six-lined racerunner, North American racer [*Coluber constrictor*], coachwhip [*Masticophis flagellum*],

prairie lizard; Table 2). Several potentially occurring species associated with open-canopy pine forests and sandy soils were not detected in surveys, including Louisiana pinesnake (*Pituophis ruthveni*), scarletsnakes (*Cemophora coccinea*), flat-headed snake (*Tantilla gracilis*), western milksnake (*Lampropeltis gentilis*), slender glass lizard (*Ophisaurus attenuatus*), and Hurter's spadefoot (*Scaphiopus hurterii*).

Herpetofaunal Occupancy and Detection

Occupancy analysis of the full herpetofaunal assemblage (model 1) had weak community occupancy relationships to VegPC1 and stream length, notable but highly variable responses to overstory composition (–), VegPC2 (–), and recent fire (+), and a negative association with upland soil area (Figure 3). The negative response to upland soil area (higher occupancy at sites with lower area of sandy soils) and the slightly negative association with VegPC1 (higher occupancy with higher canopy cover) suggested that the full herpetofauna community was heavily influenced by mesic-associated species. Many of the species frequently encountered in our study (e.g., copperhead, cottonmouth, common five-lined skink, green anole, ground skink, most anuran species) are more common in forested or bottomland areas, or require aquatic areas associated with lowlands. Overall species richness showed a negligible decline in response to increasing VegPC1 values (Figure 4A) and decreased slightly with increasing upland soil area (Figure 5A). For all species, linear temperature did not influence detection probability and a negative response to quadratic temperature indicated higher detection at intermediate survey temperatures.

Species richness of open-pine-associated reptiles and amphibians increased with increasing VegPC1 values (Figure 4B) and with increasing upland soil area (Figure 5B). In contrast to the overall herpetofaunal community, occupancy of species in the open-pine-

associated guild were positively associated with VegPC1, overstory composition, and upland soil area (Figure 3), with considerably less interspecific variation within the guild (Figure 6). Open-pine-associated species showed positive species-specific occupancy relationships with increasing VegPC1 value (Figure 7) and increasing upland soil area (Figure 8), indicating higher species richness in sites with open-canopy, herbaceous groundcover, and sandy soils. These responses indicate higher occupancy probability of open-pine-associated species at sites with sandy, well-drained soils, longleaf pine overstory, lower canopy cover, and higher herbaceous understory and bare soil cover. Although all 9 open-pine-associated species exhibited generally positive occupancy relationships with VegPC1 and upland soil area, variation among species was evident (Figures 7, 8). North American racers and prairie lizards showed particularly positive responses to VegPC1 but relatively weak responses to upland soil area. Conversely, coachwhips displayed a positive association with sandy soils, with a 95% credible interval that did not overlap zero, but a more variable response to open-canopy conditions (VegPC1). Six-lined racerunners, Slowinski's cornsnake (*Pantherophis slowinskii*), and eastern narrow-mouthed toads (*Gastrophryne carolinensis*) all exhibited their highest occupancy at sites with sandy soil and open canopy. Some species were predicted to have high (>75%) occupancy probability under open-canopy, open-understory forest conditions (e.g., six-lined racerunners, North American racers, coachwhips, prairie lizards), whereas others had low (<40%) occupancy probability even under sandy soil or open-canopy, open-understory vegetation conditions typical of open-pine forest conditions (e.g., eastern narrowmouthed toads, prairie kingsnakes [*Lampropeltis calligaster*], Slowinski's cornsnakes; Figures 7, 8). Finally, some species thought to be associated with open-pine conditions exhibited low occupancy probabilities that remained

relatively unaffected by covariates we measured (e.g., eastern hognose snakes [*Heterodon platirhinos*] and pygmy rattlesnakes [*Sistrurus miliarius*]; Figures 7, 8).

As with the overall herpetofaunal community, open-pine-associated species showed weak occupancy responses to VegPC2, recent fire, and stream length, and weak detection responses to temperature and quadratic temperature (Figure 3). Examining species-specific responses to temperature revealed contrasting patterns of detectability that might have partially driven the weak overall response (Figure 6).

Grouping mesic forest-associated species as a guild produced notable community associations with overstory composition, upland soil area, and recent fire (Figure 3). The negative responses to soil type and overstory composition indicate higher occupancy of mesic-guild species at loblolly-dominated bottomland sites without sandy soils. The notable negative responses to VegPC1 and VegPC2 suggested higher occupancy of mesic forest species at sites with closed canopy conditions, prevalent midstory, and woody understory. Unlike the open-pine guild, mesic-forest-associated species exhibited a positive response to recent fire and a negative response to overstory composition (indicating a positive relationship with loblolly overstory).

Herpetofaunal Species Richness

The estimated median species richness was highest (16–18 species) at mature loblolly and longleaf sites compared to young sites, recently thinned loblolly sites (11–15 species), and conservation-managed longleaf reference sites (10–13). Young sites and reference sites supported the highest estimated median richness of open-pine-associated species (4–6 species). Recently thinned loblolly sites had the lowest estimated median richness of open-pine-associated (average 2.7 species) and all reptile and amphibian species (average 12.1 species).

Discussion

Although overall herpetofaunal species richness was highest in pine forests on mesic soils, occupancy of open-pine-associated species was highest in sandy, open-canopy, longleaf forests. We also identified heterogeneous responses within our open-pine-associated guild, with some species only requiring open canopy and understory structure, while others also appeared to be strongly tied to the presence of sandy soils. The absence of some potentially occurring open-pine-associated species suggested that these species have very low detectability, are extremely rare, or do not occur at the sites we surveyed. Areas managed for timber production in the western Gulf Coastal Plain can provide appropriate conditions for open-pine-associated species.

Forest management category was a poor predictor of vegetation conditions across our study region. Vegetation conditions varied widely within and among management categories, depending on the combined influence of landscape characteristics (e.g., soils, topography, hydrology) and ownership-specific disturbance method and frequency (i.e., mechanically disturbed intensively managed sites, infrequently burned sites, privately owned, frequently burned sites). Although many young sites exhibited canopy conditions like those seen in reference sites, PC2 scores varied widely among young sites, indicating inconsistent understory conditions within the age group. As predicted, overstory species (longleaf vs. loblolly pine) did not predict any of the vegetation variables we measured. Our findings agree with previous studies, which suggest that vegetation structure and diversity result from the confluence of multiple factors, including disturbance regime and various landscape characteristics, such as soil composition (Hedman et al. 2000, Mitchell et al. 2015).

Our occupancy analyses suggested that vegetative structural characteristics (canopy cover, midstory density, and understory composition) influence herpetofaunal assemblage

composition and species richness. Open-canopy conditions were positively associated with occupancy probability of most open-pine-associated species. While canopy cover conditions did range widely among sites, young loblolly and longleaf sites, along with designated reference longleaf sites, featured many of the lowest canopy cover values, highest vegetation PC1 values (indicating open canopy and herbaceous and bare soil groundcover), and highest observed and predicted species richness of open-pine-associated reptiles and amphibians. Canopy cover is an important characteristic for herpetofauna, particularly to species adapted to longleaf pine savanna ecosystems (Pringle et al. 2003, Greene et al. 2016). The direct link between canopy cover and thermoregulatory opportunities available to ectotherms highlights importance of these characteristics, independent of the disturbance or management regime that maintains them (Pike et al. 2011, Basson et al. 2017). Additionally, canopy cover is likely to indirectly affect herpetofauna by influencing herbaceous understory vegetation that serves as an important food source for small mammals and insects, the prey base for most reptile and amphibian species in this assemblage (Converse et al. 2006, Perry et al. 2018). Thus, the closed canopy conditions found at many of our sites may severely limit their potential suitability for open-pine-associated species through multiple mechanistic pathways (Brewster et al. 2018, Clifford et al. 2020). Even sites that receive some management activity may be inadequate if the management interval or intensity is not sufficient to create open-canopy conditions. For example, despite management with periodic controlled burns, most mature longleaf and loblolly sites in our study region had high canopy cover values and negative values for vegetation PC1, indicating closed canopy and high leaf litter (Figure 2). Nevertheless, these sites exhibited high overall herpetofaunal species richness and were important for species not restricted to open pine conditions.

Although the full community occupancy response to upland soil area suggested lower herpetofaunal occupancy and species richness at sites with sandy, upland soils, this effect was driven by bottomland-associated species. Many species can persist across a range of soil conditions, including some species in our open-pine-associated guild that occupied open-canopy sites regardless of soil composition (e.g., prairie lizards and North American racers). The positive response of the open-pine guild and of several individual species to upland soil area highlights the importance of specific soil conditions to some open-pine-associated species (Davis et al. 2010). While some sites lacking sandy soils exhibited open-canopy conditions (particularly some fire-maintained mature loblolly sites in the former Jackson-Bienville wildlife management area), few open-pine-associated species were documented there. Species such as the six-lined racerunner, eastern narrowmouthed toad, and coachwhip were uncommon outside of sandy soil sites and appeared to prefer the combination of sandy soils and open-canopy conditions. Regardless of management regime or overstory composition, these species are unlikely to occupy a given site unless sandy soil conditions are available. Thus, soil conditions should be carefully considered when selecting sites for targeting management of open-pine-associated species.

The structural characteristics of vegetation are clearly important to herpetofauna in our study and there were no consistent differences in structural characteristics between longleaf and loblolly overstory sites in our study. Open-pine-associated species showed a positive response to longleaf overstory, but it seems likely that this trend was an artifact of uneven distribution of other site characteristics among overstory categories, as mature loblolly sites were exclusively located away from extensive regions of sandy Hydrogroup A and B soils. Likewise, the positive association of mesic-forest-associated species with loblolly overstory was the primary driver of

the positive response to overstory by the full community. This was also likely influenced by imperfect interspersions of management regimes across soil types in our study region. Given the limitations of our study region, further research is needed to isolate the specific effects of overstory composition on open-pine-associated herpetofauna. There was similar vegetation structure between mature longleaf and loblolly sites (Figure 2). These structural similarities and the presence of many open-pine-associated species at these sites suggest that, when located on sandy, upland soils, managed loblolly forest can support open-pine-associated reptile and amphibian species. Further, the high overall herpetofaunal species richness found at loblolly sites indicates that overstory species is not a primary determinant for biodiversity and that managed loblolly sites had considerable value for regional species.

The lack of a notable response by open-pine-associated species to the recent fire covariate, along with the similarity in vegetation structure between mechanically managed young loblolly, fire-maintained young longleaf, and reference mature longleaf sites, suggests that current mechanical management techniques can replicate open-canopy conditions for open-pine-associated herpetofauna. Mechanical management alone, or when combined with prescribed fire, may generate the open, herbaceous understory conditions linked with higher open-pine-associated species occupancy. Burning helps eliminate thick leaf litter and debris layers, and the combined use of mechanical thinning and controlled burns promotes herbaceous groundcover and increases the amount of understory light available (Lettow et al. 2014, Vander Yacht et al. 2020). Decreasing canopy and midstory cover to increase light availability and opening groundcover space for herbaceous growth can improve thermoregulatory opportunities and increase abundance of prey taxa, including arthropods and small mammals, important to herpetofauna populations (Humphrey et al. 1999, Miller et al. 2004, Webb et al. 2005). Open-

canopy-associated snakes in other regions of the southeastern Coastal Plain select frequently burned areas, potentially because of favorable thermal conditions and foraging opportunities provided by the open structure (Howze and Smith 2021). The positive response of mesic-forest-associated species to recent fire was unexpected and suggests that fire might play an important role in maintaining the vegetation structure needed by these species, perhaps by maintaining structural heterogeneity at sites with high canopy cover where the groundcover may otherwise be dominated by leaf litter (Greene et al. 2016). Using prescribed burns or mechanical or chemical management to reduce midstory density, leaf litter, and woody groundcover could extend the period during which intensively managed sites are viable for open-pine-associated herpetofauna and for the entire herpetofaunal community (Iglay et al. 2014*b*). Previous research suggests that repeated chemical management can provide the desired herbaceous understory and open midstory conditions in recently planted loblolly pine stands for up to 5 years (Jones et al. 2012), and prescribed burn frequencies varying between 3–5 years appear to promote the highest diversity of reptiles and amphibians (Darracq et al. 2016).

The uniformly weak detection responses to linear temperature at the community level suggested that our surveys appropriately addressed differences in temperature preferences among species by surveying across a wide seasonal window (early spring to mid-summer). Nonetheless, we documented variability in detectability-temperature relationships among species, illustrating importance of varying seasonal and daily timing of sampling. For example, six-lined racerunners were most detectable at the highest survey temperatures ($\sim 33^{\circ}\text{C}$) as indicated by a positive response to survey temperature. This effect likely results from increased detectability of lizards via visual surveys during high temperatures when this heliothermic species is highly active. Conversely, the negative response to linear temperature by prairie lizards was indicative of

higher detectability at low to intermediate temperatures, highlighting the differences in thermoregulatory strategies between these 2 surface-active, open-canopy-associated species. Temperature-constrained surveys may maximize the probability that target species are active during surveys, but it is important to consider interspecific variability in responses to temperature when designing community-level occupancy studies of ectotherms such as herpetofauna.

Further work is needed to understand herpetofaunal population dynamics in working forests, as evidenced by the relatively low occupancy estimates we saw for many species and by the variation in responses shown by herpetofauna to specific effects of forest management activities in other studies (Rothermel and Luhring 2005, Todd and Andrews 2008, Haggerty et al. 2019). Low occupancy estimates are a common feature of many reptile and amphibian species (Guzy et al. 2019, Zipkin et al. 2020), but it can be difficult to discern if low estimates are due to sampling methodology, interspecific interactions, unincorporated landscape variables, or naturally sparse populations. While our results suggest that vegetation structure and soil characteristics are influential in determining species distributions, the broad scope of some of our covariates, like the long timeframe used to determine recent use of prescribed burns and the use of only a single season of vegetation data, might have dulled some inferences. Additionally, factors we did not incorporate, like long-term land use history, proximity to ephemeral wetlands, fine-scale topographic features, and specific management techniques, all are likely to influence occupancy in a variety of species-specific ways. Some open-pine-associated species in this region have small, patchy ranges (Rudolph et al. 2006), which likely played a role in producing low occupancy estimates for some species. Additionally, low detection estimates for many species, regardless of temperature conditions, suggest that our sampling methodologies, designed to best assess overall species richness, were inefficient for some species that require more

specialized survey techniques. The ecological and physiological mechanistic relationships linking occupancy of open-pine-associated species with specific vegetation and landscape characteristics must be identified and understood to inform specific conservation efforts. Differences in physiological traits and ecological interactions among species caused the stark differences in species-specific responses to the variables examined in this study, and a finer understanding of these responses will allow for more optimized management.

Management Implications

Our findings suggest that working forests in the western Gulf Coastal Plain can support diverse herpetofaunal communities and, in regions with sandy soil conditions, can provide suitable landscapes for species of conservation concern associated with open-canopy upland pine forests. Additionally, many sites outside of regions with sandy upland soil featuring closed canopy conditions supported high overall herpetofaunal species richness, highlighting their value for conserving regional biodiversity and the importance of variation in structural conditions. We recommend counteracting the ephemeral nature of open-canopy conditions within individual stands by maintaining a mosaic of stand ages across the landscape, particularly within sandy soil regions. Although structural associations and dispersal dynamics vary widely among our study species, providing a broad range of conditions may provide refuge for species that are adapted to longleaf pine savanna. This mosaic landscape would in turn help facilitate recolonization of adjacent stands by species with high vagility. Employing management actions such as prescribed fire, herbicide application, or mechanical management individually or in combination on 1–5-year intervals will likely increase the window of time during which stands provide open structural conditions (low canopy cover, bare soil and herbaceous groundcover, low leaf litter), extending their viability for open-pine-associated herpetofauna.

Acknowledgements

We thank J. A. Homyack and T. B. Wigley for support and valuable input on the project. Hancock Forest Management and the United States Forest Service - Kisatchie National Forest graciously provided access to study sites on their holdings. We thank L. Walker, A. L. Brazzel, B. M. Rudd, M. D. Reynolds, and others for providing on-the-ground support and advice. We also thank A. A. Rivero, A. M. Saenger, and A. J. Meinders for their work in the field, and J. C. Guzy and J. E. Thornton-Frost for statistical advice. We thank A. L. Larsen-Gray and C. S. Kross for comments on the manuscript. This research was funded by Weyerhaeuser Company, the National Council for Air and Stream Improvement, and the University of Arkansas. Additional support for EJRB and conference travel was provided by the University of Arkansas and the University of Arkansas Graduate School Doctoral Academy Fellowship.

Conflicts of Interest

The authors are employed by organizations that provided funding but declare no conflicts of interest that compromise the integrity of the research.

Literature Cited

- Bailey, L. L., D. I. MacKenzie, and J. D. Nichols. 2014. Advances and applications of occupancy models. *Methods in Ecology and Evolution* 5:1269–1279.
- Bailey, M. A., J. N. Holmes, K. A. Buhlmann, and J. C. Mitchell. 2006. Habitat management guidelines for amphibians and reptiles of the southeastern United States. *Partners in Amphibian and Reptile Conservation*, Technical Publication HMG-2, Montgomery, Alabama, USA.
- Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart. 2004. *IUCN Red List of Threatened Species: a global species assessment*. IUCN Publications Services, Cambridge, United Kingdom.
- Basson, C. H., O. Levy, M. J. Angilletta, and S. Clusella-Trullas. 2017. Lizards paid a greater opportunity cost to thermoregulate in a less heterogeneous environment. *Functional Ecology* 31:856–865.

- Boundy, J. and J. L. Carr. 2017. Amphibians and reptiles of Louisiana. Louisiana State University Press, Baton Rouge, USA.
- Brewster, C. L., and S. J. Beaupre. 2019. The effect of body posture on available habitat and activity-time in a lizard: implications for thermal ecology studies. *Journal of Thermal Biology* 82:10–17.
- Brewster, C. L., S. J. Beaupre, and J. D. Willson. 2018. Habitat loss and local extinction: linking population declines of eastern collared lizards (*Crotaphytus collaris*) to habitat degradation in Ozark glades. *Journal of Herpetology* 52:352–360.
- Clifford, B. J., J. M. Bauder, and M. N. Marchand. 2020. Tree removal likely improves thermal quality of basking sites for an imperiled timber rattlesnake population at the northern edge of its range. *Northeastern Naturalist* 27:746–762.
- Converse, S. J., W. M. Block, and G. C. White. 2006. Small mammal population and habitat responses to forest thinning and prescribed fire. *Forest Ecology and Management* 228(1–3):263–273.
- Darracq, A. K., W. W. Boone, IV, and R. A. McCleery. 2016. Burn regime matters: a review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. *Forest Ecology and Management* 378:214–221.
- Davis, J. C., S. B. Castleberry, and J. C. Kilgo. 2010. Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. *Forest Ecology and Management* 259:1111–1117.
- Demarais, S., J. P. Verschuyt, G. J. Roloff, D. A. Miller, and T. B. Wigley. 2017. Tamm review: terrestrial vertebrate biodiversity and intensive forest management in the US. *Forest Ecology and Management* 385:308–330.
- Dixon, P. 2003. VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science* 14:927–930.
- Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association* 100:389–398.
- Dorazio, R. M., J. A. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854.
- Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pages 17–43 in S. M. Hermann, editor. *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida, USA.

- Garden, J. G., C. A. Mcalpine, H. P. Possingham, and D. N. Jones. 2007. Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: a case study from Brisbane, Australia. *Australian Ecology* 32:669–685.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457– 472.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653–666.
- Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *Forest Ecology and Management* 148(1–3):135–144.
- Greene, R. E., R. B. Iglay, K. O. Evans, D. A. Miller, T. B. Wigley, and S. K. Riffell. 2016. A meta-analysis of biodiversity responses to management of southeastern pine forests opportunities for open pine conservation *Forest Ecology and Management* 360:30–39.
- Greene, R. E., R. B. Iglay, K. O. Evans, T. B. Wigley, and D. A. Miller. 2019. Estimating capacity of managed pine forests in the southeastern US to provide open pine woodland condition and gopher tortoise habitat. *Forest Ecology and Management* 432:200–208.
- Guyer, C., and M.A. Bailey. 1993. Amphibians and reptiles of longleaf pine communities. Pages 139–158 in S. M. Hermann, editor. *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Guzy, J., K. Halloran, J. Homyack, J. E. Thornton-Frost, and J. D. Willson. 2019. Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests. *Ecological Applications* 29(8):e01995.
- Haggerty, C. J., T. L. Crisman, and J. R. Rohr. 2019. Effects of forestry-driven changes to groundcover and soil moisture on amphibian desiccation, dispersal, and survival. *Ecological Applications* 29(3):e01870.
- Hedman, C., S. Grace, and S. King. 2000. Vegetation composition and structure of southern coastal plain pine forests: an ecological comparison. *Forest Ecology and Management* 134:233–247.
- Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2006. Movement patterns and habitat selection by native and repatriated Louisiana pine snakes (*Pituophis ruthveni*): implications for conservation. *Herpetological Natural History* 9(2):103–116.
- Howze, J. M., and L. L. Smith. 2015. Spatial ecology and habitat use of the coachwhip in a longleaf pine forest. *Southeastern Naturalist* 14:342–350.

- Howze, J. M., and L. L. Smith. 2021. The influence of prescribed fire on site selection in snakes in the longleaf pine ecosystem. *Forest Ecology and Management* 481:118703.
- Humphrey, J. W., C. Hawes, A. J. Peace, R. Ferris-Kaan, and M. R. Jukes. 1999. Relationships between insect diversity and habitat characteristics in plantation forests. *Forest Ecology and Management* 113:11–21.
- Hunt, J. W., F. W. Weckerly, and J. R. Ott. 2012. Reliability of occupancy and binomial mixture models for estimating abundance of golden-cheeked warblers (*Setophaga chrysoparia*). *Auk* 129:105–114.
- Igley, R. B., B. D. Leopold, and D. A. Miller. 2014a. Vegetation responses to fire and herbicide in intensively managed, mid-rotation pine. *Forest Ecology and Management* 328:69–78.
- Igley, R. B., B. D. Leopold, and D. A. Miller. 2014b. Summer herpetofaunal response to prescribed fire and herbicide in intensively managed, mid-rotation pine stands in Mississippi. *Wildlife Society Bulletin* 38:33–42.
- Jellinek, S., D. A. Driscoll, and J. B. Kirkpatrick. 2004. Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Australian Ecology* 29:294–304.
- Jones, J. D., and M. J. Chamberlain. 2004. Efficacy of herbicides and fire to improve vegetative conditions for northern bobwhites in mature pine forests. *Wildlife Society Bulletin* 32:1077–1084.
- Jones, P. D., S. Demarais, and A. W. Ezell. 2012. Successional trajectory of loblolly pine (*Pinus taeda*) plantations established using intensive management in Southern Mississippi, USA. *Forest Ecology and Management* 265:116–123.
- Jones, P. D., B. Hanberry, and S. Demarais. 2009. Stand-level wildlife habitat features and biodiversity in southern pine forests: a review. *Journal of Forestry* 107:398–404.
- Jones, G. M., L. Smith, I. G. Gottlieb, H. K. Ober, B. Brosi, and R. J. Fletcher. 2020. Herpetofaunal responses to intensification of woody bioenergy production in a global biodiversity hotspot. *Forest Ecology and Management* 477:118493.
- Kéry, M., and J. A. Royle. 2015. *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*. Academic Press, Cambridge, United Kingdom.
- Kirkman, L. K., and S. B. Jack. 2017. *Ecological restoration and management of longleaf pine forests*. CRC Press, Boca Raton, Florida, USA.

- Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the Southeast: requiem or renaissance? *Journal of Forestry* 93:39–44.
- Lettow, M. C., L. A. Brudvig, C. A. Bahlai, and D. A. Landis. 2014. Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management* 329:89–98.
- Link, W., E. Cam, J. Nichols, and E. Cooch. 2002. Of bugs and birds: Markov chain Monte Carlo for hierarchical modeling in wildlife research. *Journal of Wildlife Management* 66:277–291.
- Litt, A. R., L. Provencher, G. W. Tanner, and R. Franz. 2001. Herpetofaunal responses to restoration treatments of longleaf pine sandhills in Florida. *Restoration Ecology* 9:462–474.
- Loehle, C., T. B. Wigley, S. Rutzmoser, J. A. Gerwin, P. D. Keyser, R. A. Lancia, C. J. Reynolds, R. E. Thill, R. Weih, D. White, Jr., and P. B. Wood. 2005. Managed forest landscape structure and avian species richness in the southeastern US. *Forest Ecology and Management* 214(1–3):279–293.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* 10: 325– 337.
- McIntyre, R. K., L. M. Conner, S. B. Jack, E. M. Schlimm, and L. L. Smith. 2019. Wildlife habitat condition in open pine woodlands: field data to refine management targets. *Forest Ecology and Management* 437:282–294.
- Means, B. D. 2007. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157–213 *in* S. Jose, E. Jokela, and D. Miller, editors. *The longleaf pine ecosystem*. Springer, New York, New York, USA.
- Miller, D. A., R. E. Thill, M. A. Melchior, T. B. Wigley, and P. A. Tappe. 2004. Small mammal communities of streamside management zones in intensively managed pine forests of Arkansas. *Forest Ecology and Management* 203(1–3):381–393.
- Mitchell, S., K. Palmquist, S. Cohen, and N. L. Christensen. 2015. Patterns of vegetation composition and diversity in pine-dominated ecosystems of the Outer Coastal Plain of North Carolina: implications for ecosystem restoration. *Forest Ecology and Management*. 356:64–73.
- Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal* 9:211–213.
- Outcalt, K. W. 1997. Status of the longleaf pine forests of the West Gulf Coastal Plain. *Texas Journal of Science* 49 Supplement:5–12.

- Paletto, A. and V. Tosi. 2009. Forest canopy cover and canopy closure: comparison of assessment techniques. *European Journal of Forest Research* 128:265–272.
- Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Pages 45–81 *in* S. M. Hermann, editor. *Proceedings of the Tall Timbers Fire Ecology Conference*. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Perry, K. I., K. F. Wallin, J. W. Wenzel, and D. A. Herms. 2018. Forest disturbance and arthropods: small-scale canopy gaps drive invertebrate community structure and composition. *Ecosphere* 9:e02463.
- Pike, D. A., J. K. Webb, and R. Shine. 2011. Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21:274–280.
- Platt, D. R. 1969. Natural history of the hognose snakes *Heterodon platirhinos* and *Heterodon nasicus*. University of Kansas Publications. Museum of Natural History 18:253–420.
- Powell, R., R. Conant, and J. T. Collins. 2016. Peterson field guide to reptiles and amphibians of eastern and central North America. Fourth edition. Houghton Mifflin Harcourt, New York, New York, USA.
- Pringle, R. M., J. K. Webb, and R. Shine. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rothermel, B. B., and T. M. Luhring. 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. *Journal of Herpetology* 39:619–626.
- Rudolph, D. C., and S. J. Burgdorf. 1997. Timber rattlesnakes and Louisiana pine snakes of the west Gulf Coastal Plain: hypotheses of decline. *Texas Journal of Science* 49:111–122.
- Rudolph, D. C., S. J. Burgdorf, R. R. Schaefer, R. N. Conner, and R. W. Maxey. 2006. Status of *Pituophis ruthveni* (Louisiana pine snake). *Southeastern Naturalist* 5:463–472.
- Smith, L. L., D. A. Steen, J. M. Stober, M. C. Freeman, S. W. Golladay, L. M. Conner, and J. Cochrane. 2006. The vertebrate fauna of Ichauway, Baker County, Georgia. *Southeastern Naturalist* 4:599–620.
- Steen, D. A., A. E. Rall McGee, S. M. Hermann, J. A. Stiles, S. H. Stiles, and C. Guyer. 2010. Effects of forest management on amphibians and reptiles: generalist species obscure trends among native forest associates. *Open Environmental Sciences* 4:24–30.

- Steen, D. A., L. L. Smith, L. M. Conner, A. R. Litt, L. Provencher, J. K. Hiers, S. Pokswinski, and C. Guyer. 2013. Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecological Applications* 23:148–158.
- Sturtz, S., U. L. Sibylle, and A. E. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* 12(3):1–16.
- Todd, B. D., and K. M. Andrews. 2008. Response of a reptile guild to forest harvesting. *Conservation Biology* 22:753–761.
- Tuberville, T. D., J. D. Willson, M. E. Dorcas, and J. W. Gibbons. 2005. Herpetofaunal species richness of southeastern national parks. *Southeastern Naturalist* 4:537–569.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture [USDA]. Soil Survey Geographic (SSURGO). Available online. Accessed [12/14/2016].
- Vander Yacht, A. L., P. D. Keyser, S. A. Barrioz, C. Kwit, M. C. Stambaugh, W. K. Clatterbuck, and R. Jacobs. 2020. Litter to glitter: promoting herbaceous groundcover and diversity in mid-southern USA oak forests using canopy disturbance and fire. *Fire Ecology* 16(1):article 17.
- Verschuyf, J., S. Riffell, D. A. Miller, and T.B. Wigley. 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests—a meta-analysis. *Forest Ecology and Management* 261:221–232.
- Wagner, R. O., J. B. Pierce, D. C. Rudolph, R. R. Schaefer, and D. A. Hightower. 2014. Modeling Louisiana pine snake (*Pituophis ruthveni*) habitat use in relation to soils. *Southeastern Naturalist* 13:146–158.
- Webb, J. K., R. Shine, and R. M. Pringle. 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed landscape. *Copeia* 2005:894–900.
- Weiss, S. A., E. L. Toman, and R. G. Corace. 2019. Aligning endangered species management with fire-dependent ecosystem restoration: manager perspectives on red-cockaded woodpecker and longleaf pine management actions. *Fire Ecology* 15(1):article 19.
- Zipkin, E. F., A. DeWan, and J. A. Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology* 46:815–822.
- Zipkin, E. F., G. V. DiRenzo, J. M. Ray, S. Rossman, and K. R. Lips. 2020. Tropical snake diversity collapses after widespread amphibian loss. *Science* 367(6479):814–816.

Tables

Table 1. Sites selected by management category and method to investigate herpetofauna response to stand and landscape conditions in northwestern Louisiana, USA, 2017–2019. There were 81 pine sites selected; LB = loblolly pine, LL = longleaf pine.

Management Category	Age (years)	# of Sites	Management Method
Mature Fire-maintained LL	18-50+	19	
Mature Fire-maintained LB	18-50+	19	Prescribed fire and mechanical/chemical understory management
Thinned LB	14-26	15	Recent thinning and pruning, with some chemical understory management
Young LB	<6	15	Recently planted after intense mechanical site preparation
Young LL	<10	13	Recently planted, with some prescribed fire

Table 2. Summary of herpetofauna detected during visual encounter surveys and coverboard surveys of 81 pine sites in northwestern Louisiana, USA, 2017–2019. Species-specific occupancy and detection values were taken from the all species model. Species included in the open-pine-associated (O) or mesic-forest-associated (M) guilds are noted.

Amphibians				Occupancy		Detection	
Genus	Species			# Captures	# Sites	Mean (95% posterior interval)	Mean (95% posterior interval)
			Guild				
<i>Acris</i>	<i>blanchardi</i>	Blanchard's	M	81	21	0.44 (0.25 - 0.66)	0.12 (0.08 - 0.19)
		Cricket Frog					
<i>Anaxyrus</i>	<i>fowleri</i>	Fowler's Toad	M	17	10	0.27 (0.11 - 0.52)	0.08 (0.04 - 0.15)
<i>Gastrophryne</i>	<i>carolinensis</i>	Eastern	O	2	2	0.09 (0.02 - 0.29)	0.02 (0.01 - 0.06)
		Narrowmouthed					
		Toad					
<i>Lithobates</i>	<i>catesbeianus</i>	Bullfrog		1	1	0.08 (0.02 - 0.27)	0.02 (0.01 - 0.05)
<i>Lithobates</i>	<i>clamitans</i>	Bronze Frog	M	59	18	0.40 (0.20 - 0.63)	0.10 (0.06 - 0.16)
<i>Lithobates</i>	<i>palustris</i>	Pickerel Frog		1	1	0.07 (0.02 - 0.26)	0.02 (0.01 - 0.05)
<i>Lithobates</i>	<i>epencephala's</i>	Southern	M	137	37	0.63 (0.42 - 0.79)	0.22 (0.17 - 0.28)
		Leopard Frog					

Table 2 (Cont.)

Genus	Species		Guild	# Captures	# Sites	Occupancy	Detection
						Mean (95% posterior interval)	Mean (95% posterior interval)
<i>Psuedacris</i>	<i>crucifer</i>	Spring Peeper	M	34	15	0.33 (0.15 - 0.62)	0.06 (0.04 - 0.11)
<i>Psuedacris</i>	<i>fouquettei</i>	Cajun Chorus Frog	M	107	26	0.51 (0.30 - 0.75)	0.12 (0.08 - 0.17)
<i>Eurycea</i>	<i>paludicola</i>	Western Dwarf Salamander	M	30	16	0.37 (0.18 - 0.65)	0.08 (0.05 - 0.13)
Reptiles							
<i>Chelydra</i>	<i>serpentina</i>	Common Snapping Turtle		1	1	0.07 (0.02 - 0.26)	0.02 (0.01 - 0.05)
<i>Kinosternon</i>	<i>subrubrum</i>	Eastern Mud Turtle		2	2	0.11 (0.03 - 0.32)	0.02 (0.01 - 0.06)
<i>Terrapene</i>	<i>triunguis</i>	Three-Toed Box Turtle	M	12	11	0.33 (0.14 - 0.72)	0.04 (0.02 - 0.08)

47

<i>Trachemys</i>	<i>scripta</i>	Pond Slider		10	3	0.16 (0.05 - 0.37)	0.05 (0.02 - 0.17)
						Occupancy	Detection
Genus	Species			# Captures	# Sites	Mean (95% posterior interval)	Mean (95% posterior interval)
			Guild				
<i>Anolis</i>	<i>carolinensis</i>	Green Anole	M	127	57	0.83 (0.66 - 0.95)	0.24 (0.20 - 0.29)
<i>Aspidoscelis</i>	<i>sexlineatus</i>	Six-Lined Racerunner	O	186	34	0.60 (0.40 - 0.78)	0.20 (0.15 - 0.26)
<i>Plestiodon</i>	<i>anthracinus</i>	Coal Skink	M	1	1	0.07 (0.02 - 0.26)	0.02 (0.01 - 0.05)
<i>Plestiodon</i>	<i>fasciatus</i>	Common Five- Lined Skink	M	180	54	0.73 (0.53 - 0.87)	0.28 (0.23 - 0.33)
<i>Plestiodon</i>	<i>laticeps</i>	Broad-Headed Skink	M	58	36	0.55 (0.32 - 0.81)	0.11 (0.08 - 0.15)
<i>Sceloporus</i>	<i>consobrinus</i>	Prairie Lizard	O	289	63	0.81 (0.65 - 0.91)	0.36 (0.31 - 0.41)
<i>Scincella</i>	<i>lateralis</i>	Ground Skink	M	980	79	0.98 (0.93 - 0.99)	0.70 (0.66 - 0.73)
<i>Agkistrodon</i>	<i>contortrix</i>	Eastern Copperhead	M	8	5	0.15 (0.04 - 0.38)	0.04 (0.02 - 0.10)

Table 2 (Cont.)

Genus	Species		Guild	# Captures	# Sites	Occupancy	Detection
						Mean (95% posterior interval)	Mean (95% posterior interval)
<i>Agkistrodon</i>	<i>piscivorus</i>	Northern Cottonmouth	M	21	14	0.36 (0.17 - 0.63)	0.07 (0.04 - 0.13)
<i>Coluber</i>	<i>constrictor</i>	North American Racer	O	27	19	0.42 (0.22 - 0.69)	0.09 (0.05 - 0.14)
<i>Crotalus</i>	<i>horridus</i>	Timber Rattlesnake	M	3	3	0.13 (0.04 - 0.37)	0.02 (0.01 - 0.06)
<i>Diadophis</i>	<i>punctatus</i>	Ringneck Snake	M	1	1	0.08 (0.02 - 0.27)	0.02 (0.01 - 0.05)
<i>Haldea</i>	<i>striatula</i>	Rough Earth Snake	M	1	1	0.09 (0.02 - 0.29)	0.02 (0.01 - 0.06)
<i>Heterodon</i>	<i>platirhinos</i>	Eastern Hog- nosed Snake	O	1	1	0.08 (0.02 - 0.27)	0.02 (0.01 - 0.05)
<i>Lampropeltis</i>	<i>calligaster</i>	Prairie Kingsnake	O	3	3	0.14 (0.04 - 0.40)	0.03 (0.01 - 0.07)

Table 2 (Cont.)

						Occupancy	Detection
Genus	Species			# Captures	# Sites	Mean (95%	Mean (95%
		Guild				posterior interval)	posterior interval)
<i>Lampropeltis</i>	<i>holbrooki</i>	Speckled Kingsnake	M	2	2	0.10 (0.03 - 0.32)	0.02 (0.01 - 0.06)
<i>Masticophis</i>	<i>flagellum</i>	Coachwhip	O	27	17	0.43 (0.23 - 0.71)	0.08 (0.05 - 0.13)
<i>Micrurus</i>	<i>tener</i>	Texas Coralsnake	M	5	5	0.16 (0.05 - 0.44)	0.03 (0.01 - 0.07)
<i>Nerodia</i>	<i>erythrogaster</i>	Plain-bellied Watersnake	M	7	7	0.29 (0.12 - 0.63)	0.04 (0.02 - 0.09)
<i>Nerodia</i>	<i>fasciata</i>	Banded Watersnake		5	3	0.12 (0.03 - 0.33)	0.04 (0.01 - 0.10)
<i>Opheodrys</i>	<i>aestivus</i>	Rough Greensnake	M	4	4	0.16 (0.05 - 0.44)	0.03 (0.01 - 0.07)
<i>Pantherophis</i>	<i>obsoletus</i>	Western Ratsnake	M	14	11	0.30 (0.14 - 0.60)	0.06 (0.03 - 0.11)

Table 2 (Cont.)

Genus	Species	Guild	# Captures	# Sites	Occupancy		Detection	
						Mean (95% posterior interval)	Mean (95% posterior interval)	
<i>Pantherophis</i>	<i>slowinskii</i>	Slowinski's Cornsake	O	5	3	0.11 (0.03 - 0.33)	0.03 (0.01 - 0.07)	
<i>Sistrurus</i>	<i>miliarius</i>	Pygmy Rattlesnake	O	2	2	0.10 (0.02 - 0.30)	0.02 (0.01 - 0.06)	
<i>Storeria</i>	<i>dekayi</i>	Brown Snake	M	3	3	0.10 (0.02 - 0.32)	0.02 (0.01 - 0.06)	
<i>Storeria</i>	<i>occipitamaculata</i>	Red-bellied Snake	M	1	1	0.07 (0.02 - 0.26)	0.02 (0.01 - 0.05)	
<i>Thamnophis</i>	<i>proximus</i>	Western Ribbonsnake	M	8	8	0.29 (0.12 - 0.64)	0.04 (0.02 - 0.09)	
<i>Thamnophis</i>	<i>sirtalis</i>	Common Gartersnake	M	10	8	0.27 (0.12 - 0.54)	0.06 (0.03 - 0.11)	
<i>Virginia</i>	<i>valeriae</i>	Smooth Earthsake	M	2	2	0.11 (0.03 - 0.34)	0.02 (0.01 - 0.06)	

Table 3. Factor loadings for the first 4 principal components (PC) based on a principal components analysis (PCA) completed using nested-plot vegetation data collected in northwestern Louisiana, USA, 2018. We included 7 site-specific vegetation variables.

Vegetation Site Covariate				
Principal Components	PC1	PC2	PC3	PC4
Eigenvalues	3.137	1.640	0.803	0.707
% of Variation	0.448	0.234	0.114	0.101
Cum. Variation	0.448	0.682	0.797	0.898
Eigenvectors				
Avg. Canopy Cover	-1.632	0.316	-0.105	0.008
Avg. Midstory Tree Density	-1.086	-0.888	0.712	-0.243
% Woody Cover	-0.452	-1.474	0.627	0.289
% Herb Cover	1.232	-0.947	-0.824	0.270
% Bare Soil Cover	1.289	0.432	0.615	-1.046
% Litter Cover	-1.609	0.796	-0.229	0.013
% CWD Cover	0.886	0.873	0.832	1.037

Figures

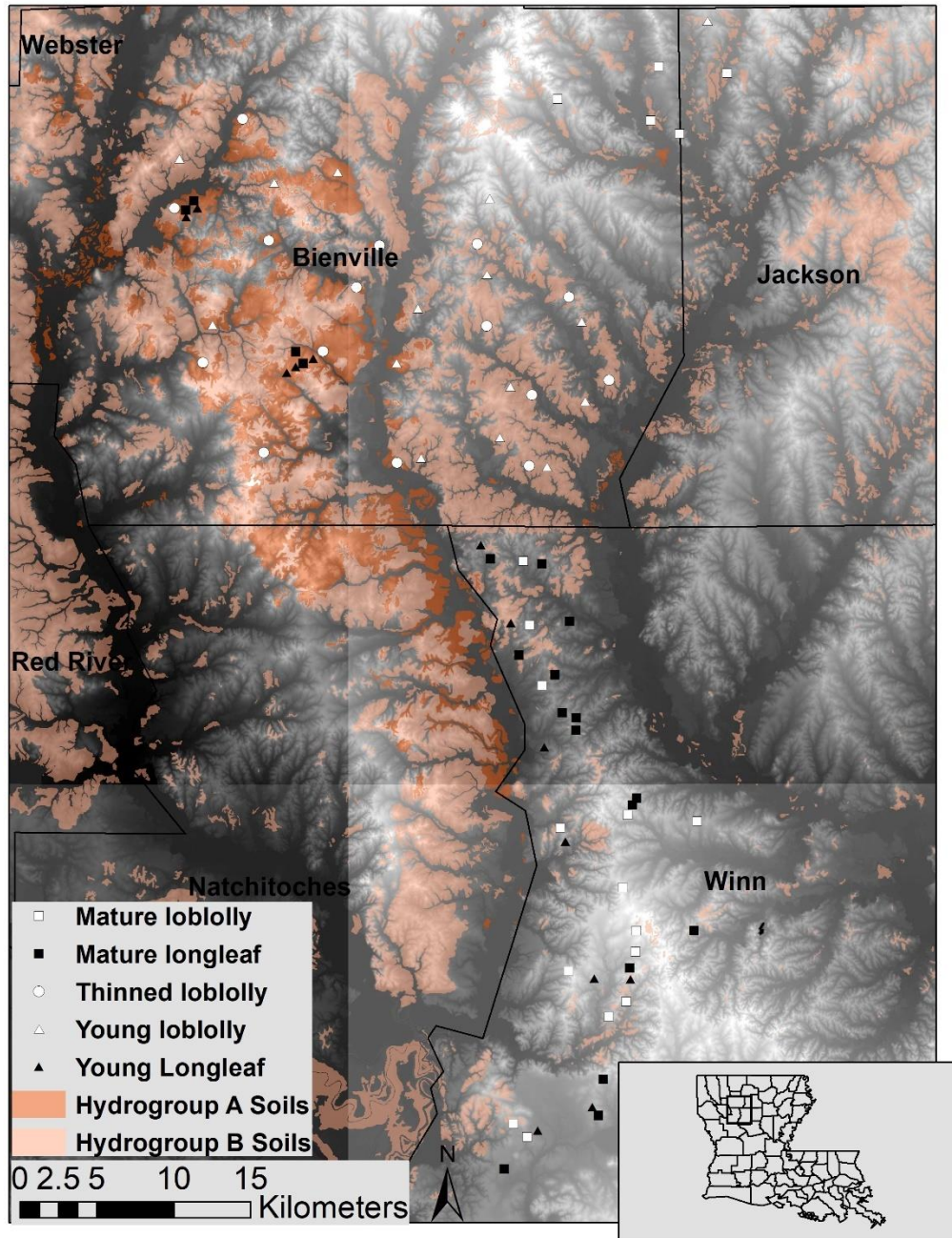


Figure 1. Distribution of study sites ($n = 81$) selected for herpetofaunal sampling in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. Map inset shows location within

Louisiana.

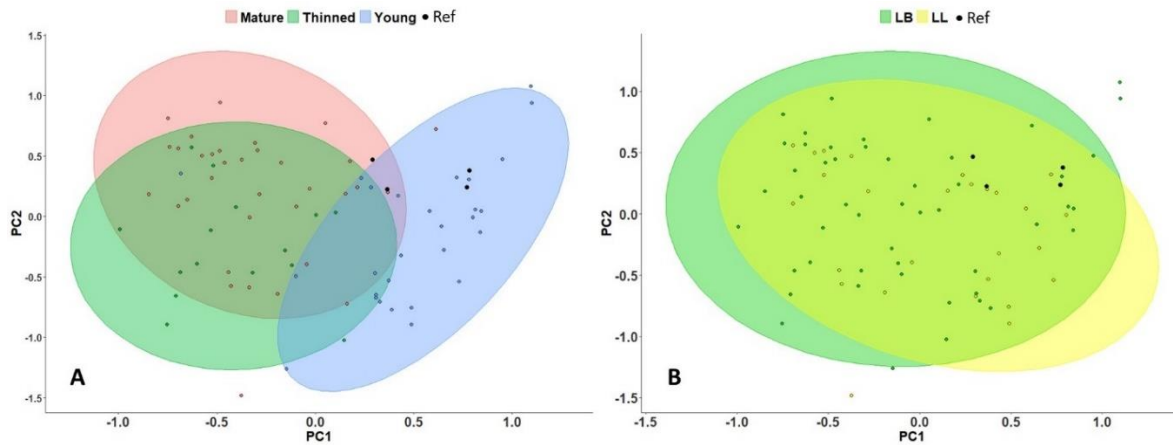


Figure 2. Site principal component (PC)1 and PC2 scores by A) management regime and B) overstory species, with associated 95% confidence interval ellipses. Mature longleaf and loblolly included >30-year-old sites managed with prescribed fire on the former Jackson-Bienville Wildlife Management Area, Louisiana, USA, and mature mixed age sites located in Winn District of the Kisatchie National Forest, Louisiana. Thinned sites included mid-aged, recently thinned, intensively managed loblolly sites. Young sites included <6-year-old intensively managed loblolly sites, and <10-year-old privately owned longleaf sites managed for conservation or those located with the National Forest. Reference (REF) points represent 4 mature longleaf sandhill sites, which have been managed for conservation and thus represent the closest approximation of historical longleaf pine savanna present in our study region. Higher PC1 values represent sites with lower canopy cover and leaf litter, and greater coverage of bare soil and herbaceous understory plants. Higher PC2 values represent sites with lower midstory tree density and understory woody plant cover, and greater leaf litter and coarse woody debris cover. Vegetation sampling occurred in 2018.

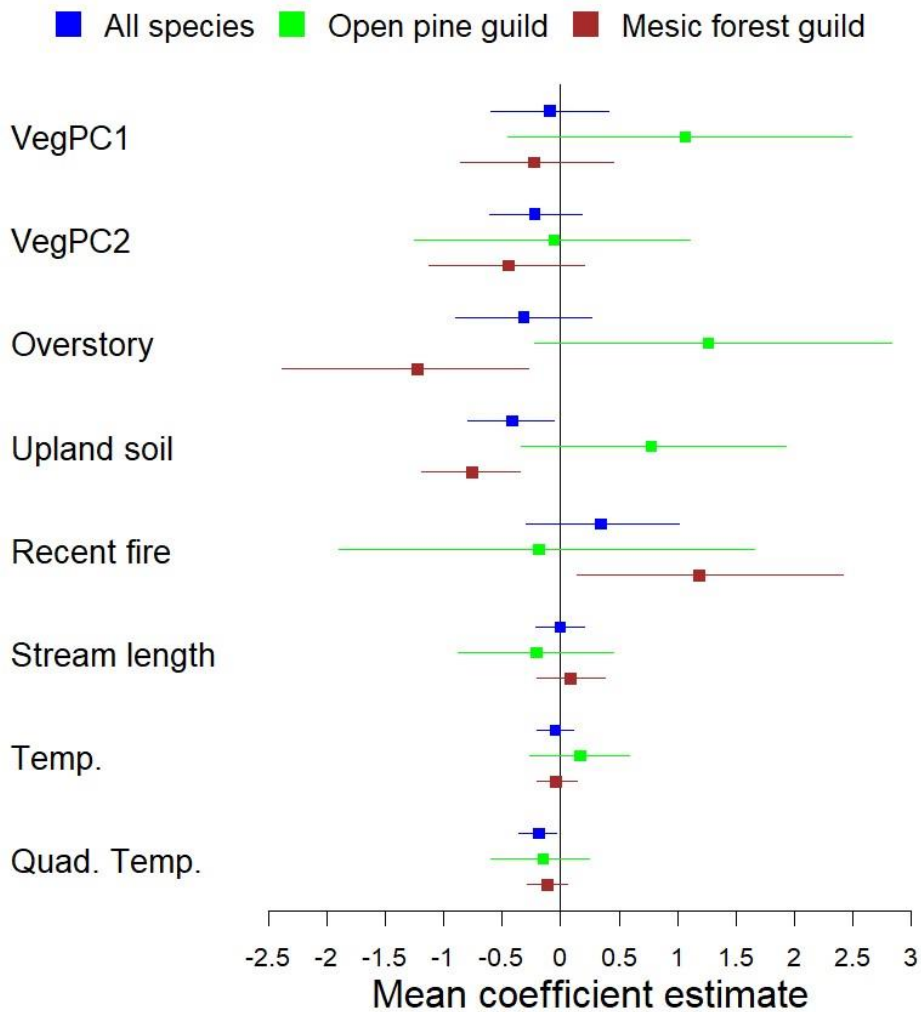


Figure 3. Summary of hyperparameters (mean assemblage response) for all species, open pine guild, and mesic forest guild models for site (vegetation principal components VegPCs 1 and VegPC2, overstory composition, upland soil area, recent fire, and stream length) and sampling (temperature [temp.] and quadratic temperature [quad. temp.]) covariates of herpetofauna occupancy and detection from all sites in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. Positive responses to VegPC1 indicate higher occupancy at sites with lower canopy cover, more bare soil, and understory herbaceous groundcover; positive responses to VegPC2 indicate higher occupancy at sites with greater coarse woody debris and leaf litter groundcover, and lower midstory density. Bars represent 95% credible intervals.

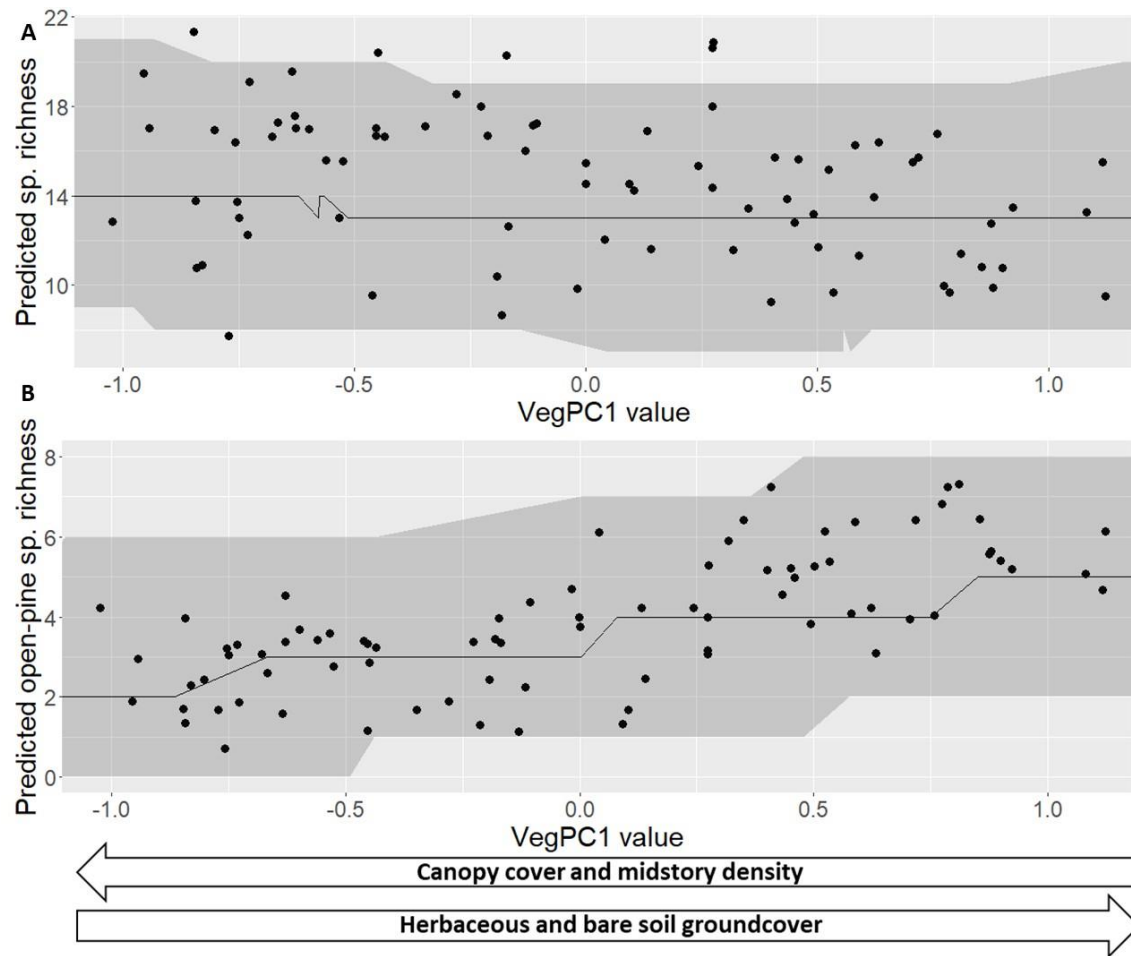


Figure 4. Median estimated species (sp.) richness in relation to vegetation principal component 1 (VegPC1) values for A) the full herpetofauna assemblage and B) open-pine-associated species at all sites in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. Lines represent the posterior means and shaded areas represent the 95% predictive intervals of species richness at hypothetical sites. Points are site-specific mean richness estimates.

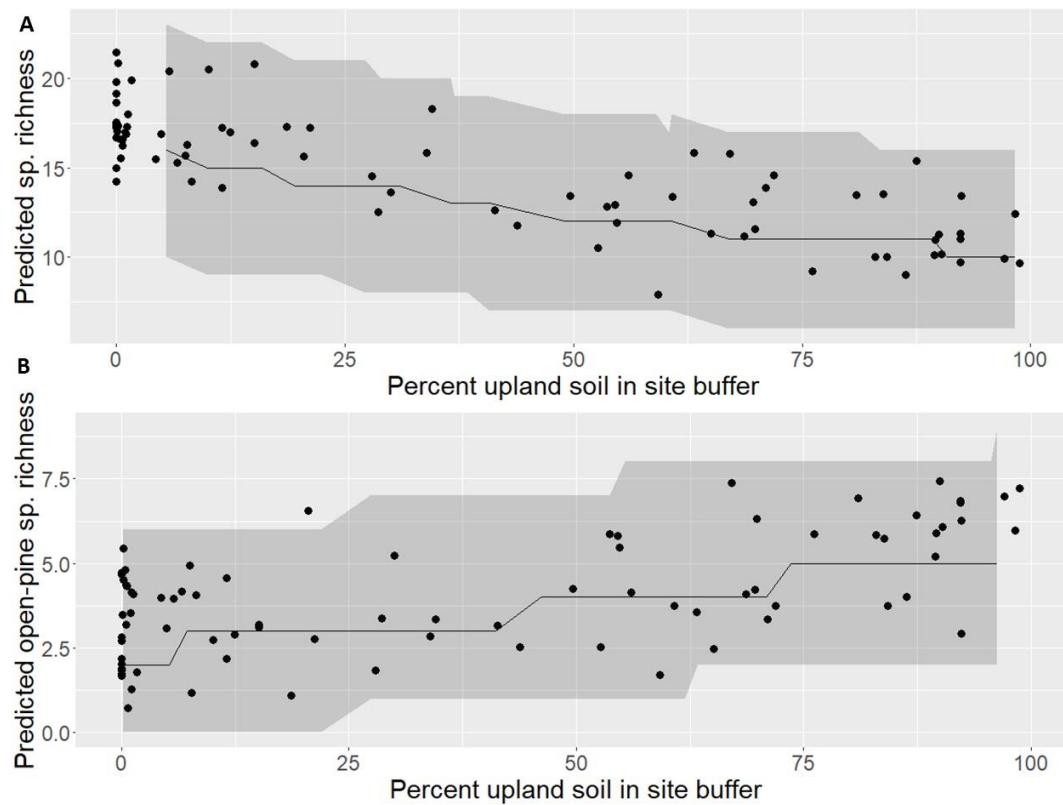


Figure 5. Median estimated species (sp.) richness in relation to upland soil area for A) the full herpetofauna assemblage and B) open-pine-associated species at all sites in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. Line represents the posterior means and shaded areas represent the 95% predictive interval of species richness at hypothetical sites. Points are site-specific mean richness estimates.

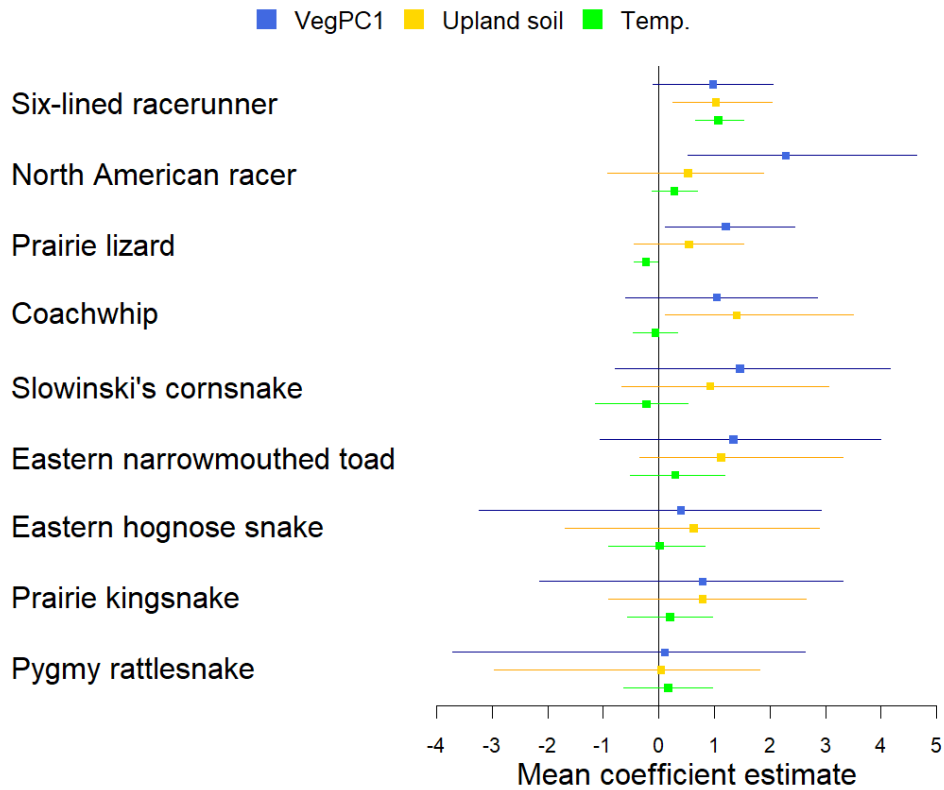


Figure 6. Species-specific occupancy responses of open pine guild species to vegetation principal component 1 (Veg PC1) and upland soil area, and detection response to survey temperature from sampling in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. Positive responses to VegPC1 indicate higher occupancy at sites with lower canopy cover, greater bare soil, and understory herbaceous groundcover. Bars represent 95% credible intervals.

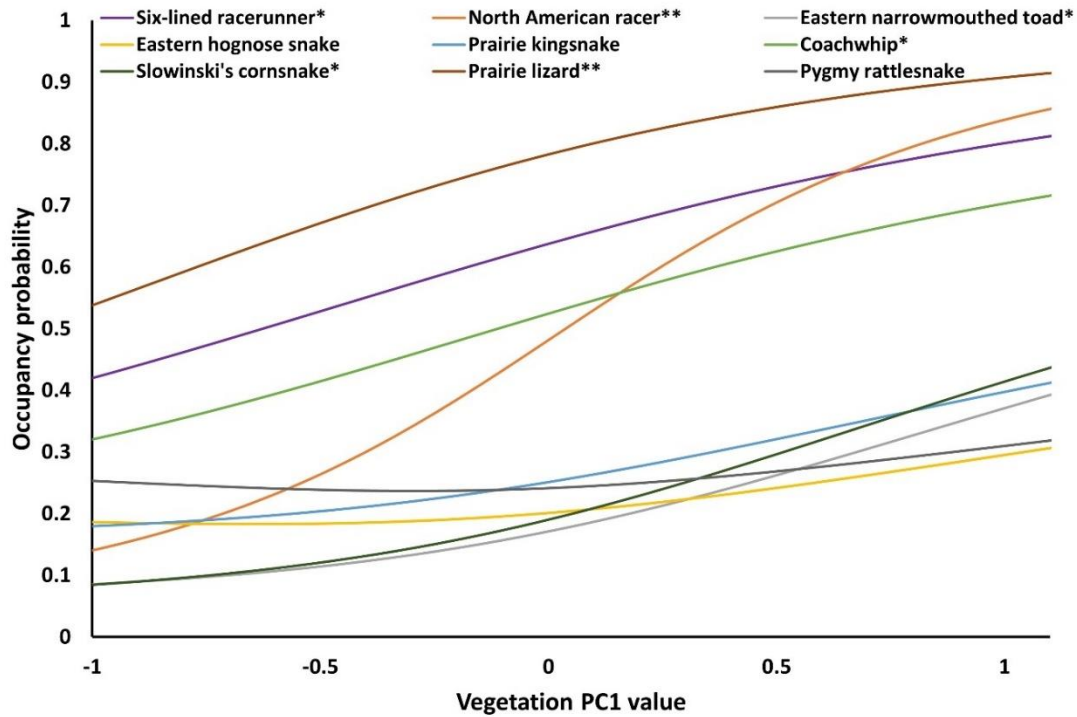


Figure 7. Species-specific responses of open pine guild species in model 2 to vegetation principal component 1 (PC1) values, with positive relationships indicating higher occupancy at sites with lower canopy cover and higher herbaceous and bare soil groundcover from sampling in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. ** indicates species for which >95% of the credible interval did not overlap zero; * indicates species for which >75% of the credible intervals did not overlap zero.

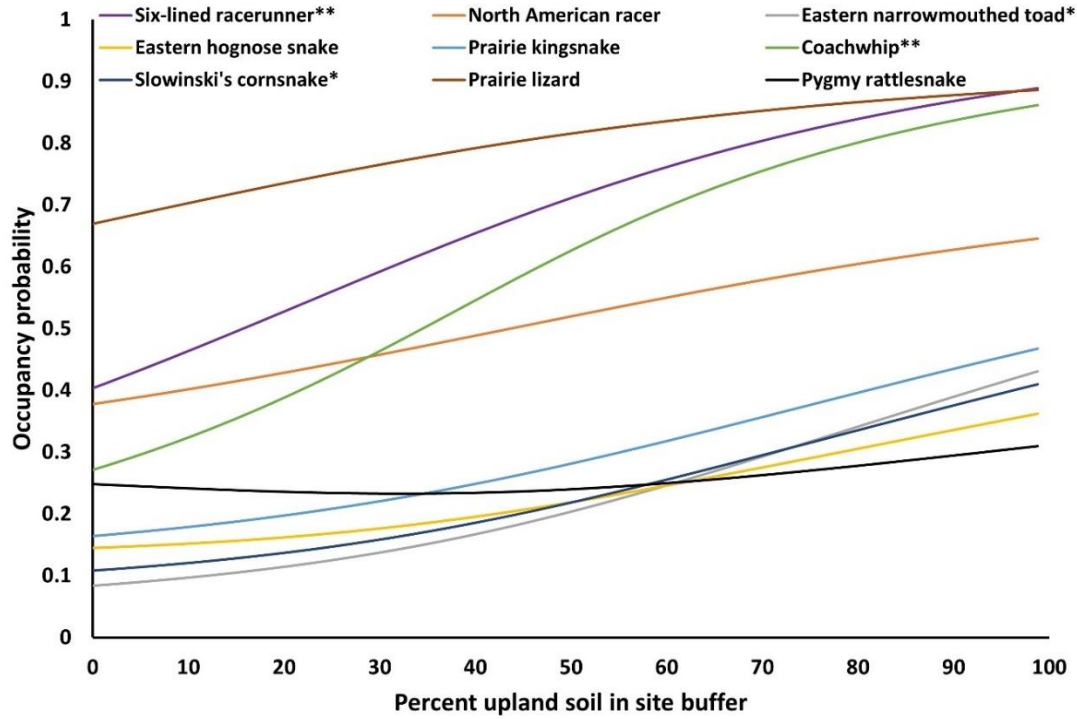


Figure 8. Species-specific responses of open pine guild species in model 2 to upland soil area, with positive relationships indicating higher occupancy probability at sites with more sandy soil area from sampling in Bienville, Jackson, and Winn parishes, Louisiana, USA from 2017-2019. ** indicates species for which >95% of the credible interval did not overlap zero; * indicates species for which >75% of the credible intervals did not overlap zero.

IACUC Approval Documents



Office of Research Compliance

To: John Willson
Fr: Craig Coon
Date: April 7th, 2017
Subject: IACUC Approval
Expiration Date: April 6th, 2020

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # 17069: Assessing the ability of managed loblolly pine forests to support longleaf pine-associated reptile and amphibian communities in the Western Gulf Coastal Plain .

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond April 6th, 2020 you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The following individuals are approved to work on this study: Ethan Royal and John Willson. Please submit personnel additions to this protocol via the modification form prior to their start of work.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

I, Dr. John D. Willson, certify that Ethan J. Royal completed the training as required by the Institutional Animal Care and Use Committee (IACUC) for work completed in Chapter 1.



7/21/2022

John D. Willson, Ph.D.
Associate Professor
Department of Biological Sciences

Date

Chapter 1, "Influence of landscape and vegetation characteristics on herpetofaunal assemblages in Gulf Coastal Plain pine forests" is published in the Journal of Wildlife Management with three coauthors, D.U. Greene, D.A. Miller, and J.D. Willson.

I, Dr. John D. Willson, advisor of Ethan J. Royal, confirm that Ethan J. Royal is first author and completed at least 51% of the work for this manuscript.



7/21/2022

John D. Willson, Ph.D.
Associate Professor
Department of Biological Sciences

Date

Chapter 2

Legacy Land Use Predicts Occupancy Patterns of Prairie-associated Herpetofauna in Western

Arkansas

Ethan J. Royal

and

Chelsea S. Kross and John D. Willson

Abstract

Prairies historically covered much of inland North America, and many species have adapted to the unique conditions found in prairie ecosystems. Less than 1% of prairies remain in Arkansas, with much historic prairie having been converted for urban and agricultural development, resulting in steep population declines for many prairie-associated species. Because many reptile and amphibian species are difficult to detect, the current distributions and habitat requirements of prairie-associated herpetofauna in fragmented landscapes are poorly understood. Thus, we assessed the state of prairie-associated herpetofauna communities in intact prairie, as well in degraded and developed historic prairie throughout Western Arkansas. Using repeated field surveys, remote sensing data, and hierarchical community occupancy models, we examined the influence of vegetation conditions, land use, and landscape characteristics on an assemblage of nine species of prairie-associated herpetofauna. Prairie mound density, representing prairie that has not been subject to intense anthropogenic disturbance, was the strongest positive predictor of occupancy by prairie-associated species. Historic prairie area also exhibited a positive relationship with occupancy for several species but not at the assemblage level. Current vegetation conditions did not strongly influence occupancy patterns. Our results suggest that long-term land use filters, rather than present site-level conditions, are the driving forces dictating current distributions of prairie-associated herpetofauna in Western Arkansas. Our findings provide insight into the present state of understudied populations in an increasingly fragmented region and present accessible tools for directing exploratory conservation and research efforts.

Introduction

Tallgrass prairie, supported by fertile soils and relatively moist conditions, historically dominated the eastern Great Plains (Risser 1988). Because of the fertile conditions, over 95% of tallgrass prairie has been degraded or lost in the last two centuries, largely due to agricultural conversion (Transeau 1935, Sampson and Knopf 1994, Lauenroth et al. 1999). Pristine tallgrass prairies boast immense vegetative diversity and a variety of topographical features that provide structural habitat heterogeneity, including prairie mounds, legacy micro-topographical features whose persistence indicate a lack of intense anthropogenic disturbance (Horwath and Johnson 2006). Remaining tallgrass prairie patches may retain vegetative diversity and original topographical features, but they are generally small and isolated within agricultural or urban landscapes, reducing their ability to support the historic diversity of prairie flora and fauna (Whitcomb et al. 1986, Risser 1988).

Degraded prairies show reduced capacity to support endemic vertebrate species as a result of fragmentation and changes to thermal and hydrologic regimes, ecological interactions, and habitat structure (Fitch 2006, Ceballos et al. 2010, Tack et al. 2017). Efforts to restore tallgrass prairie must contend with the consequences of agricultural land use that depress biodiversity, including the loss of topographic features (i.e., prairie mounds and ephemeral depression wetlands), the presence of exotic grasses and forbes, and isolation from other prairie fragments (Sampson 1980, Brotherson 1982, McLaughlin and Mineau 1995, Alford et al. 2012, van der Kamp et al. 2016). In addition to direct agricultural use, changes to grazing and fire regimes are the underlying drivers of structural changes in North American prairies via succession and encroachment of woody species that occurs in the absence of regular disturbance (Wright and Bailey 1982, Campbell et al. 1994). Declines of prairie-associated species have been extensively

documented in some cases, notably the greater prairie chicken (*Tympanachus cupido*; Svedarsky et al. 2000), black-footed ferret (*Mustela nigripes*; Clark 1978), and massasaugas (*Sistrurus catenatus*; Sovic et al. 2018). Yet, long-term and large-scale trends for many species, particularly reptiles and amphibians, are poorly understood (Corn and Peterson 1996, Cavitt 2000, Larson 2014).

Reptiles and amphibians (hereinafter herpetofauna) are particularly sensitive to changes in habitat structure and environmental conditions that compromise their abilities to thermoregulate and avoid desiccation (Jellinek et al. 2004, Voldseth 2007, Whisler et al. 2016, Haggerty et al. 2019). Much of the existing research on prairie-associated herpetofauna shows population declines in the hearts of the largest remaining contiguous tallgrass prairie tracts (Fitch 2006a, Wilgers et al. 2006, Cagle 2008). In rare long-term studies of tallgrass prairie herpetofaunal communities, Fitch (1978, 2006a, 2006b) documented the declines of prairie-associated species with encroachment of woody vegetation. Similar declines are suspected of many prairie-associated species at the outer limits of prairie habitat and species ranges, but a dearth of data in fringe areas limits our understanding of relevant conservation challenges (Lesbarrères et al. 2014).

Tallgrass prairie reaches its southeastern limit with patches in Arkansas (Transeau 1935, Baskin et al. 1995). Thus, many prairie-associated herpetofaunal species have patchy distributions within the state and Western Arkansas populations represent part of the eastern range limit for some species (Trauth et al. 2004). The value of conservation efforts for populations at the periphery of species' ranges is clear (Steen and Barrett 2015), yet there has been no systematic assessment of most prairie-associated species in Arkansas, and our understanding of these species relies primarily on haphazard and historic records that do not

reflect the current state of this rapidly urbanizing region. In Northwest Arkansas, Kross & Willson (2022) conducted wide-ranging surveys and found crawfish frog (*Lithobates aureolatus*) populations to be declining in areas with increasing urbanization, and the distribution of remaining populations was predicted by the presence of prairie mounds. However, for most prairie-associated species in this region much of our knowledge is based on scattered presence-only records that provide limited insight into historical distributions. Additionally, comprehensive community level assessments of herpetofaunal species are complicated by their low detectability (Mazerolle et al. 2007, Durso et al. 2011). Overcoming the challenges of low detectability requires specialized sampling and analytical methods, varied diel and seasonal survey timing, and intense survey effort to adequately assess herpetofaunal assemblages. When combined with adequate survey efforts, community occupancy modeling frameworks allow for partial pooling of multispecies data to inform species-specific estimates for species with few detections (Dorazio and Royle 2005). The community occupancy approach accounts for imperfect detection and produces community-level estimates of covariate relationships and species richness as well as species-specific estimates of covariate relationships and occupancy and detection (Dorazio et al. 2006). Joining community and species-specific processes provides an ideal framework for examining landscape-scale patterns in the distributions of difficult to detect herpetofauna.

We aimed to determine the ecological factors that drive the distribution of prairie-associated herpetofauna in Northwest Arkansas and the western Arkansas River Valley by conducting repeated, multi-method surveys and applying a community occupancy modeling approach. Our ultimate goal was to determine how land use history, current vegetation conditions, and landscape characteristics influence the occupancy patterns of nine prairie-associated

herpetofaunal species. We predicted the occupancy of these species to be positively associated with three primary characteristics related to land use: 1) historic prairie area, 2) the presence of prairie mounds, indicating a lack of intense anthropogenic disturbance, and 3) vegetation structure characterized by open canopy and herbaceous or shrubby groundcover. We also predicted that occupancy would be negatively associated with urban land cover in the surrounding landscape.

Methods

Site Selection

Our study focused on historic prairie regions in the Springfield Plateau of Northwest Arkansas and the Arkansas Valley Plains of the western Arkansas River Valley (Fig. 1). To begin site selection, we compiled a list of all publicly owned or managed properties in Northwest Arkansas and the Arkansas River Valley that were historically prairie based on historic records and geographic information system (GIS; ArcMap 10.1; Environmental Systems Research Institute, Redlands, California, USA) data or those that have been the focus of recent restoration initiatives. We also included sites on private land, most of which were former prairie currently managed as hay fields. We selected sites based on examination of aerial and GIS imagery, consultation with local land managers, and access permissions.

We selected 20 properties for systematic herpetofauna surveys across five counties in Arkansas: Benton, Boone, Franklin, Sebastian, and Washington (Fig. 1). The properties we selected were separated from neighboring sites by at least 1-km, covered a minimum of 3.5 ha (range 3.65 – 26000 ha), and represented a mix of private and public land in Northwest Arkansas and the Arkansas River Valley. Properties in Northwest Arkansas included publicly and privately owned hay fields located on historic prairie that are managed by private landowners, municipal

governments, the National Parks Service, or Arkansas State Parks, and small prairie preserves in urban or agricultural landscapes managed by the Northwest Arkansas Land Trust, the Arkansas Natural Heritage Commission, or contracted conservation managers. Properties in the Arkansas River Valley included Fort Chaffee, an Arkansas Army National Guard Training Facility and Wildlife Management Area covering over 26000 ha, and several large prairie conservation properties managed by the Arkansas Natural Heritage Commission or The Nature Conservancy. The substantial size of several protected areas greatly exceeded the effective sampling area of our surveys, and consequently we designated multiple survey sites within properties when they were sufficiently large to allow multiple sites to be separated by at least 1 km, resulting in a total of 34 survey sites for inclusion in analyses (Fig. 1).

Herpetofaunal Surveys

We completed 13 standardized effort-constrained herpetofaunal surveys at each of the 34 occupancy sampling sites, including six rounds of visual encounter surveys (VES) and seven rounds of amphibian auditory surveys. We completed six rounds of VES over two seasons, conducting three surveys each during April–June 2018 and March–May 2019. Each VES consisted of two observers opportunistically searching appropriate microhabitats for herpetofauna (e.g., under cover objects and basking locations) for 60 min (totaling two person-hours per survey). Visual encounter surveys also included coverboard checks, for which we placed ten 122x81x1.3-cm plywood coverboards approximately 10 m apart at each site in late April 2018. During VES, we checked each coverboard for herpetofauna sheltering underneath. At sites with wetlands or streams of adequate depth, we performed two overnight rounds of aquatic trapping concurrent with VES and coverboard surveys using 17 plastic minnow traps (model 700; manufactured by New Market Plastics, Inc., LaDoga, Indiana) and three larger mesh

turtle traps (15x10 mm mesh size; manufactured by American Maple, Inc., Gardena, CA) per site. We will subsequently refer to this combination of three survey methods as VES surveys, collectively, because we combine their captures in analyses. We identified all herpetofauna we encountered to species and released them at their capture location at the end of the survey.

We completed four early spring (March–April 2018 and 2019) and three late spring (May–June 2020) amphibian auditory surveys at each site. During auditory surveys, we listened for breeding anurans for a 5-min period, following national database methods (i.e., North American Amphibian Monitoring Program; Weir et al. 2014).

Finally, we have limited our analyses here to an assemblage of reptile and amphibian species identified *a priori* as being 1) species of greatest conservation concern (SGCN) associated with prairie ecosystems in the state of Arkansas by the Arkansas Game and Fish Commission (Fowler 2015), or 2) species noted as prairie-associated in state field guides (Trauth et al. 2004; Roberts 2020) for which there are clear knowledge gaps related to their local distributions and conservation status. The resulting assemblage consists of Small-mouthed salamander (*Ambystoma texanum*), Eastern tiger salamander (*Ambystoma tigrinum*; SGCN), Western narrow-mouth toad (*Gastrophyrne olivacea*; SGCN), Prairie kingsnake (*Lampropeltis calligaster*), Crawfish frog (*L. areolatus*; SGCN), Slender glass lizard (*Ophisaurus attenuates*; SGCN), Prairie skink (*Plestiodon septentrionalis*; SGCN), Graham’s crayfish snake (*Regina grahamii*; SGCN), and Ornate box turtle (*Terrapene ornata*; SGCN) While this species assemblage does not represent the entirety of our survey captures, they comprise the species most likely to experience consequences resulting from the loss or restoration of prairie ecosystems in Western Arkansas.

Vegetation Surveys

At each survey site we completed a single vegetation survey during the first half of July 2018. Each survey consisted of a single transect with six plots spaced 50 m apart. Each transect began at the center of the survey area (usually the coverboard array) and the direction of the transect was selected based on a randomly generated compass bearing. At each plot, we collected data on five vegetation variables to use in our analysis. Using the plot as the mid-point, we counted the number of trees with a diameter at breast height (dbh) ≥ 2.5 cm within a circular 100 m² area. We also counted the number of woody stems with dbh < 2.5 cm and the number of blackberry (*Rubus argutus*) and sumac stems (*Rhus sp.*) within a 10 m² circular area. Within a 1 m² circular area at the center of the plot, we estimated percent ground cover (i.e., herbaceous vegetation, grass, bare soil, etc.) and counted the number of flowering stems. We used the Robel pole method to estimate visual obstruction (VO) at the center of each plot (Robel et al. 1970). From the center of the plot, we took a measure of canopy cover using a GRS DensitometerTM (Geographic Resource Solutions Densitometer; Geographic Resource Solutions, Arcata, California, USA; Paletto and Tosi 2008). Vegetation sampling was repeated at each of the six plots along the transect. Vegetation variables were used as potential predictors of species occurrence (occupancy), richness, and community composition.

Habitat Covariates

Because many of the vegetation and habitat structural variables were interrelated, we performed a principal component analysis (PCA) to reduce potentially correlated variables to a lower number of uncorrelated components using the vegan package (Dixon 2003; 4.1.2) in R (R Development Core Team, 2021). We included visual obstruction, average canopy cover, average number of woody stems, average number of blackberry and sumac stems, understory plot

measurements of average number of flower stems, average percent cover of herbaceous vegetation, open ground, leaf litter, and woody debris cover in the habitat PCA and used the first principal component in occupancy analyses.

Landscape Covariates

We used geographic information system (GIS; ArcMap 10.1; Esri, Redlands, CA, USA) data to measure several landscape-level site covariates that we hypothesized would influence herpetofaunal occupancy, including historic prairie area, prairie mound density, developed area, topographic roughness, and latitude. Historic prairie area, prairie mound density, developed area, and latitude were calculated within 1-km diameter buffers created around the center of each sampling site. We calculated historic prairie area within each buffer using a historic prairie extent layer acquired from the Arkansas Natural Heritage Commission in ArcGIS. We calculated prairie mound density by manually counting visible mounds within each site buffer using a 1-meter Digital Elevation Model (1-m DEM; Arkansas GIS, 2018 <https://gis.arkansas.gov> [accessed 8 August 2019]) in ArcGIS that highlighted minor changes in elevation. Our intention in including Prairie Mound Density was for it to act as a proxy measure indicating historical land use, with sites that have undergone relatively minimal anthropogenic disturbance retaining prairie mounds and those that have experienced intense agricultural use (e.g., plowing and row-crop agriculture) or previous development having lost most prairie mound topography. We determined developed area using ArcGIS by calculating the area of each land cover type as designated by the 2016 USGS National Land Cover Database (NLCD, 2016. CONUS Landcover. <https://www.mrlc.gov/> [accessed 8 August 2019]) within each 1-km diameter buffer. Developed Area was the sum of the Developed – Open Space, Developed – Low Intensity, Developed – Medium Intensity, and Developed – High Intensity NLCD category areas. We

included topographic roughness to represent a landscape scale factor influencing habitat heterogeneity and calculated it using the 1-m DEM in ArcGIS by taking the standard deviation of elevation among DEM grid cells within a 1-km diameter buffer for each site. We included latitude to account for differences in species distributions between Northwest Arkansas and the Arkansas River Valley, which are different ecoregions separated by the Boston Mountains. While we considered site area as a covariate, the extremely large site size and loose delineation of site boundaries in the largest publicly owned properties prevented us from calculating meaningful site area values.

Occupancy Modeling

We used hierarchical Bayesian community occupancy models (Dorazio and Royle 2005; Zipkin et al. 2009) to examine reptile and amphibian occupancy and detection (Ψ_{ij} and Θ_{ijk} , respectively) responses to site (historic prairie area, prairie mound density, developed area, vegetation PC1, topographic roughness, and latitude), and sampling (survey type [VES vs. Auditory]) covariates, using data from 34 sites. Survey type was included as a binary sampling covariate to capture the effects of survey method on detection probability (VES = 0, call survey = 1). The community occupancy modeling approach accounts for imperfect detection and improves precision of individual parameter estimates, particularly for rare species, by considering them within the context of a larger assemblage of species (Dorazio et al. 2006). We built a binary encounter matrix representing detection/non-detection data for each species at each site during each survey occasion, including the six rounds of VES, and seven rounds of anuran call surveys. Because 7 of our 9 species are non-anurans that are not detectable by call survey, we filled the anuran call survey portion of those species' detection matrices with NAs to minimize the influence of an unsuitable survey method on their occupancy, detection, and

covariate relationship estimates. We used a variation of the model written and modified by Zipkin et al. (2009), Hunt et al. (2012), and Ribeiro et al. (2018). Our model assumed static occupancy during the three-year sampling period, due to the short duration of the study compared to the lifespans of our focal taxa and lack of significant land use change during the study. The true occupancy state for species i at site j , $z_{i,j}$, was treated as a binary latent state variable where $z_{i,j} = 1$ if occupied and 0 if not. We modelled occupancy state and detection probabilities as Bernoulli random variables. The occupancy probability of species i at site j ($\Psi_{i,j}$) was modeled as $z_{i,j} \sim \text{Bernoulli}(\Psi_{i,j})$. The probability of species i being detected at site j in the k th survey ($p_{i,j,k}$) was conditional upon occurrence, such that $z_{i,j} | y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} \times z_{i,j})$, where $y_{i,j,k} = 1$ if species i is detected at site j during survey k . We used the following equations to incorporate the effects of site and sampling covariates on species-specific occupancy and detection probabilities:

$$\begin{aligned} \text{logit}(\Psi_{i,j}) = & \alpha_{0i} + \alpha_{1i} * \text{Historic Prairie Area}_j + \alpha_{2i} * \text{Prairie Mound Density}_j \\ & + \alpha_{3i} * \text{Developed Land Area}_j + \alpha_{4i} * \text{VegPC1}_j + \alpha_{5i} \\ & * \text{Topographic Roughness}_j + \alpha_{6i} * \text{Latitude}_j \\ \text{logit}(p_{i,j,k}) = & \beta_{0i} + \beta_{1i} * \text{Survey Type}_{j,k} \end{aligned}$$

We standardized all non-binary covariates using z-scores to set the mean site values equal to zero to allow us to compare the model coefficients as effect sizes (Kéry and Royle 2015). Additionally, in order to most accurately inform occupancy estimates, we noted verified haphazard encounters of our target species made by surveyors or local naturalists that occurred at sites during the study period but outside of standardized surveys. We incorporated haphazard observations into the model through the latent z-state by declaring sites with haphazard records as known to be occupied ($z_{i,j} = 1$), regardless of detection within a survey. We recognize that the

inclusion of anuran call surveys, a method only suited for Western narrow-mouth toads and crawfish frogs in this assemblage, precludes in-depth inference related to the detection process. However, the inclusion of call surveys greatly improved our understanding of the distributions of the two prairie-associated anuran species targeted in this study. We report model results using the mean of the posterior distribution with 95% Bayesian credible intervals. We considered covariate effects to be statistically significant if the 95% credible interval did not overlap zero. Finally, we examined the relationships between estimated species richness and site covariates using post-hoc ordinary least squares regression (White et al. 2020). The posterior mean species richness estimated at each site was the response variable, with historic prairie area, prairie mound density, VegPC1, and latitude as predictor variables.

Results

Herpetofaunal Surveys

We documented the presence of at least one of our nine target species during our study period at 26 of 34 sites (Table 1). We documented small-mouthed salamanders at six sites, an Eastern tiger salamander at 1 site, Western narrow-mouth toads at 9 sites, prairie kingsnakes at 16 sites, crawfish frogs at 18 sites, slender glass lizards at 11 sites, prairie skinks at 1 site, Graham's crayfish snakes at 2 sites, and ornate box turtles at 9 sites.

Vegetation Surveys

The first PCA axis explained 31.5% of the variance in vegetation data. The strongest factor loading for Vegetation PC1 was a positive association with visual obstruction (VO), followed by strong loadings for average leaf litter ground cover (-), average herbaceous ground cover (+), canopy cover (-), average number of blackberry and sumac stems (+), and average

number of flower stems (+). Thus, PC1 captures the differences in vegetation structure among three rough site categories; restored prairies with high PC1 values reflecting brushy herbaceous growth and little canopy cover, partially forested sites and oak savanna with low PC1 values featuring higher canopy cover and open or leaf litter dominated ground cover, and degraded sites with moderate PC1 values characterized by moderate canopy cover and low, grass-dominated undergrowth (Fig. 2).

Our sites spanned a wide range of habitat conditions (Fig. 2). The more southern prairie sites located in the Arkansas River Valley were characterized by high PC1 scores, indicating high visual obstruction of forbs and blackberry/sumac and low canopy cover. Sites in Fort Chaffee, a mixed matrix of oak savanna, barrens, and prairie, were extremely variable in PC scores (Fig. 1 and Fig. 2), with some sites characterized by high visual obstruction and high herbaceous ground cover, while others were characterized by high canopy cover, high open ground cover, and high litter cover. Except for some sites managed for conservation, most of the Northwest Arkansas sites were characterized by high grass ground cover and low canopy cover. Although our habitat covariates roughly distinguish among degraded sites, intensively managed restored prairies, and forested areas, the differences are highlighted in very broad strokes and the overlap in conditions among sites under different management regimes limits our ability to make specific claims about strictly defined site categories.

Occupancy Results

The assemblage level response was strongly positive to prairie mound density and strongly negative to latitude (i.e., 95% credible intervals (CIs) did not overlap zero; Fig. 3). Although the positive community response to historic prairie had 95% CIs that overlapped zero, most values (90%) from the posterior distribution were positive, suggesting that the presence of

historic prairie is an influential predictor of the current distributions of our focal species. Developed area, VegPC1, and topographic roughness all elicited responses with 95% CIs that widely overlapped zero (Fig. 3). There was a notable negative relationship of the assemblage and most species to latitude (Fig. 3), suggesting higher occupancy rates in southern sites situated in the Arkansas River Valley.

Species detection probabilities were consistently low (range 0.04-0.11; Table 1). Conversely, species-specific estimates of occupancy probability varied widely among species, ranging from 0.13 to 0.90, and most had wide CIs (Table 1). All nine species exhibited positive species-specific occupancy relationships with prairie mound density and historic prairie area, although the low number of detections for some species limit inference due to wide CIs (Fig. 4).

Five of the nine species, the Western narrow-mouth toad, prairie kingsnake, crawfish frog, slender glass lizard, and ornate box turtle, exhibited strong positive relationships with Prairie Mound Density (95% CIs not overlapping zero; Fig. 4), indicating higher occupancy at sites that have retained prairie mounds due to a lack of intense anthropogenic land use. Predicted occupancy probability of the small-mouthed salamander, prairie kingsnake, crawfish frog, slender glass lizard, and ornate box turtle increased precipitously to nearly 100% at sites with the highest prairie mound densities (Fig. 5). As in the assemblage-level responses, developed area, VegPC1, and topographic roughness generally elicited neutral species-specific responses with wide CIs.

Naïve species richness estimates for each site ranged from 0 to 6 of the 9 prairie-associated species targeted in this study, and estimated species richness ranged from 0.45 (95% CI: 0.0, 2.0) to 8.3 (6.0, 9.0). Regression relationships between species richness and site covariates followed patterns seen in the occupancy results, with richness being positively related

to increasing prairie mound density (22.68 (16.36, 29.00)) and historic prairie area (12.55 (7.28, 17.82)), and negatively related to increasing site latitude (-0.14 (-0.28, 0.01)); Fig. 6). Regression relationships between species richness and developed land area, vegetation PC1, and topographic roughness were not significant.

Discussion

Our occupancy analyses suggest that land-use history, as indicated by the density of prairie mounds, is the strongest predictor of prairie-associated species presence at the periphery of their distributions. Prairie mound density (positive) and latitude (negative) elicited strong responses both at the assemblage and species-specific levels, and historic prairie also appears to have a positive relationship to species occupancy in this assemblage. Counter to our predictions, occupancy was not strongly influenced by current vegetation structure (VegPC1) or the nearby presence of developed areas. Topographic roughness also demonstrated little relationship to species occupancy at both levels. Our results provide insight into how conservation efforts might incorporate land-use histories to best inform the allocation of restoration resources.

We attempted to account for aspects of historical habitat conditions and anthropogenic land-use history using historic prairie boundaries and prairie mound density. We found positive relationships between prairie mound density and occupancy probabilities at the assemblage level (Fig 3) and at the species level for five of the nine target species (Fig 4). Our prairie mound density results support the findings of a targeted study of crawfish frog occupancy, which found prairie mound density to be the strongest predictor of occurrence within a smaller study area in extreme northwestern Arkansas (Kross and Willson 2022). For the four species where we did not

observe a clear relationship, there were few captures, resulting in wide credible intervals and limiting our ability to identify meaningful patterns with any covariates.

Historic prairie extent had a positive relationship with occupancy at the assemblage level. Yet, historic prairie was not a clear predictor for species-specific occupancy patterns. We believe this suggests that the available projections of historic prairie extent, based largely on historical reports, are broadly accurate and represent historically viable habitat for our focal species. However, current prairie-associated species distributions are depressed by the degraded state of most historic prairie. Urbanization and conversion of historic prairie for agriculture has undoubtedly diminished the distributions of prairie-associated species over much of their historic ranges in Arkansas, but the conservation of relict populations could be significantly aided by accounting for historical conditions. We have uncovered populations of prairie-associated species persisting in previously degraded sites, and historic prairie extent, along with prairie mound density, can serve as an indicator of where other relict populations persist. Additionally, the presence of many of our target species in large, conservation-managed oak–savanna sites located outside of historic prairie boundaries likely dampened species-specific effects of historic prairie in the model. While the stability and management of large sites located on an expansive military installation is not replicable for other sites in this study, they provide immense value to regional biodiversity as strongholds for species facing habitat loss throughout much of the region (Hayden 2014).

The consistent negative occupancy relationship with latitude reflects the regional range limits of some species within the state (e.g., Eastern tiger salamander, Western narrow-mouth toad, prairie skink; Trauth et al. 2004) and the importance of the large conservation properties in the southern portion of our study area to herpetofaunal conservation. The larger sites in our

study, namely the managed prairies and Fort Chaffee sites in the Arkansas River Valley, boasted the highest species richness of our target species. The Arkansas River Valley sites in our study are generally large and contiguous compared to many of the small, isolated prairies remnants and conservation areas in the urbanizing regions of the Springfield Plateau. Therefore, large, connected areas, such as those found in the Arkansas River Valley prairies and oak–savanna sites, are clearly vital for the persistence of many species and maintenance of overall regional diversity, regardless of historic prairie boundaries. Increasing conservation land area and connectivity between existing conservation properties in rapidly urbanizing areas of Northwest Arkansas should be a high priority in the future, particularly when considering species that make seasonal breeding migrations (Todd et al. 2009; Heemeyer and Lannoo 2012). However, non-significant assemblage and species-specific responses to developed area suggests that small, urban preserves can harbor viable populations of some prairie-associated species. Indeed, some species, including the Eastern tiger salamander, prairie kingsnake, and Graham’s crayfish snake, were found in small conservation properties in rapidly developing areas of Benton and Washington Counties. While not suitable for all species, the modest preserves used in our study can support some species with small home range requirements, providing pockets of diversity amongst increasing urban sprawl (Hodgkison et al. 2007, Delaney et al. 2021).

Intense site disturbance for agriculture or development alters soil structure, in turn destroying refugia such as crayfish burrows, changing local microtopography (i.e. removing prairie mounds), and depressing species that rely on underground refugia (Battigelli et al. 2004, Martinez-Estévez et al. 2013, Swab et al. 2020). Changes in soil structure, particularly soil compaction and the loss of burrows, severely reduce habitat quality and can drive population declines in herpetofauna species that rely on underground refugia (Shiple and Reading 2006,

Garden et al. 2007). Many prairie-associated herpetofauna are obligate burrow users and rely on the availability of underground structure for foraging, thermoregulation, and hibernacula (Heemeyer et al. 2012, Galan and Light 2017, Johnson et al. 2022). Thus, the loss of micro-topographical and underground structures resulting from anthropogenic land use could drive local extirpation of prairie-associated species. Furthermore, most herpetofauna have limited long-range dispersal ability (Greenberg et al. 1996), and thus may be unable to recolonize patches degraded by anthropogenic disturbance, even after restoration efforts have reestablished native vegetation. The inability of species to recolonize isolated restored areas is supported in our study by the non-significant assemblage and species-specific responses to VegPC1. The neutral response to current vegetation conditions, along with the strong responses to land use covariates, suggest that species in this highly fragmented landscape rely on long-term persistence in stable land use rather than recolonization of previously degraded, isolated sites. Thus, presence of intact prairie mounds, features destroyed by intense disturbance, might be useful as a proxy for long-term habitat stability and quality that can be used to identify areas where prairie-associated species are most likely to persist (Horwath and Johnson 2006, Kross and Willson 2022).

Our findings suggest that landscape-level filters, determined by current and historical land use, drive distribution patterns of prairie-associated herpetofauna across Northwest Arkansas and the Arkansas River Valley. Our results show that the density of remnant prairie mounds, and to a lesser extent, historic prairie area are strong predictors of prairie-associated herpetofauna occupancy. As a topographic feature that is easily detected using widely available remote sensing data, prairie mound density could be a useful metric for rapid, large-scale assessment of conservation value for prairie-associated species by uncovering remnant

populations. Conservation efforts targeting the areas that are most likely to harbor relict populations will most efficiently promote the persistence of prairie-associated species in the region without relying on extensive reintroduction efforts or natural recolonization in an increasingly fragmented landscape. Future research to determine what functional significance prairie mounds might have for wildlife, rather than simply serving as indicators of site suitability, and if that functionality could be restored to sites that have lost prairie mounds would greatly aid prairie conservation efforts moving forward. Additionally, as prairie restoration in western Arkansas continues and suitable sites are identified, research should explore the viability of reintroducing locally extirpated species to historic locales to increase local biodiversity and increase connectivity between what are currently patchily distributed populations.

Acknowledgements

We thank Max Carnes-Mason, Alex Meinders, Matt Gideon, Dr. Jennifer Mortensen, Kory Roberts, Bailey Singleton, Dr. Meredith Swartwout, and Gabriel Yerdon for their work in the field. We thank the Marley, Stokenbury, and Thraillkill families, Terry Stanfill, and Polly Canez and the Horses for Healing staff for access to their properties. We are extremely grateful for the support of Elizabeth Phillips, SGT. Jobe, and the Fort Chaffee range control staff for their assistance in accessing sites at Fort Chaffee. We thank Joe Woolbright, Kelly Irwin, Dustin Lynch, Theo Witsell and the Arkansas Natural Heritage Commission, Bruce Shackleford, Seth Pickens, Jeff Hickie and the City of Fayetteville, Alan Edmundson, Marson Nance and the Northwest Arkansas Land Trust, and Joe Adams and the Charlie F. Craig Fish Hatchery for information and property access. We thank Matthijs Hollanders for input on occupancy model structure. We thank Dr. Steve Beaupre, Dr. Dan Greene, and Dr. Lauren Maynard for

constructive comments on the manuscript. We thank Kory Roberts for his work in the field and on the Arkansas Herpetological Atlas, and for his willingness to share his extensive knowledge of herpetofauna in Arkansas.

Literature Cited

- Alford AL, Hellgren EC, Limb R, Engle DM (2012) Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecological Applications* 22(3):947–958
- Arkansas Natural Heritage Commission (ANHC) (2016) Natural Communities of Arkansas No. 2: Tallgrass Prairies. Poster. <http://www.naturalheritage.com/Education/natural-communities-poster-series>
- Baskin JM, Stuckey RS, Baskin CC (1995) Variations in Transeau's maps of the Prairie Peninsula. In *Proceedings of the fourteenth North American prairie conference: Prairie diversity*. Kansas State University, Manhattan (pp. 227–231)
- Battigelli JP, Spence JR, David WL, Berch SM (2004) Short-term impact of forest soil compaction and organic matter removal on soil mesofauna density and oribatid mite diversity. *Can J of For Res* 34(5):1136–1149
- Brotherson JD (1982) Vegetation of the mima mounds of Kalsow Prairie, Iowa. *The Great Basin Naturalist* 246–261
- Cagle NL (2008) Snake species distributions and temperate grasslands: A case study from the American tallgrass prairie. *Biol Cons* 141(3):744–755
- Campbell C, Campbell ID, Blyth CB, McAndrews JH (1994) Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17:360–362
- Cavitt JF (2000) Fire and a tallgrass prairie reptile community: effects on relative abundance and seasonal activity. *J Herp* 12–20
- Ceballos G, Davidson A, List R, Pacheco J, Manzano-Fischer P, Santos-Barrera G, Cruzado J (2010) Rapid decline of a grassland system and its ecological and conservation implications. *PloS one* 5(1):e8562
- Clark TW (1978) Current status of the black-footed ferret in Wyoming. *J Wildl Man* 128–134
- Dorazio RM, Royle JA (2005) Estimating size and composition of biological communities by modeling the occurrence of species. *J Amer Stat Ass* 100:389–398

- Dorazio RM, Royle JA, Soderstrom B, Glimskar A (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854
- Delaney KS, Busteed G, Fisher RN, Riley SP (2021). Reptile and amphibian diversity and abundance in an urban landscape: impacts of fragmentation and the conservation value of small patches. *Ichthyology & Herpetology* 109(2):424–435
- Dixon P (2003) VEGAN, a package of R functions for community ecology. *J Veg Sci* 14:927–930
- Fitch HS, Hall ER (1978) A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller Experimental Tract. Natural History Museum, University of Kansas
- Fitch HS (2006a) Ecological succession on a natural area in northeastern Kansas from 1948 to 2006. *Herp Cons Bio* 1(1):1–5
- Fitch HS (2006b) Collapse of a fauna: Reptiles and turtles of the University of Kansas Natural History Reservation. *Journal of Kansas Herpetology* 17:10–13
- Fowler A (Ed) (2015) Arkansas Wildlife Action Plan (AWAP). Arkansas Game and Fish Commission, Little Rock, Arkansas. 1678 pp
- Galán AP, Light JE (2017) Reptiles and Amphibians Associated with Texas Pocket Gopher (*Geomys personatus*) Burrow Systems Across the Texas Sand Sheet. *Herp Rev* 48(3):517–521
- Garden JG, McAlpine CA, Possingham HP, Jones DN (2007) Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane, Australia. *Austral Ecology* 32(6):669–685
- Guzy JC, Halloran KM, Homyack JA, Thronton-Frost JE, Willson JD (2019) Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests. *Ecological Applications* e01995
- Haggerty CJ, Crisman TL, Rohr JR (2019) Effects of forestry-driven changes to groundcover and soil moisture on amphibian desiccation, dispersal, and survival. *Ecol Apps* 29(3):e01870
- Hayden TJ (2014) US military installations as bioreserves: a case study from Fort Hood, Texas. *Military Geosciences in the Twenty First Century*. Geological Society of America, North Carolina 215pp 101–108

- Heemeyer JL, Lannoo MJ (2012) Breeding migrations in Crawfish Frogs (*Lithobates areolatus*): long-distance movements, burrow philopatry, and mortality in a near-threatened species. *Copeia* 2012(3):440–450
- Heemeyer JL, Williams PJ, Lannoo MJ (2012) Obligate crayfish burrow use and core habitat requirements of Crawfish Frogs. *J Wildl Man* 76(5):1081–1091
- Hodgkison S, Hero JM, Warnken J (2007) The efficacy of small-scale conservation efforts, as assessed on Australian golf courses. *Biol Cons* 135(4):576–586
- Hunt JW, Weckerly FW, Ott JR (2012) Reliability of occupancy and binomial mixture models for estimating abundance of Golden-cheeked Warblers (*Setophaga chrysoparia*). *The Auk* 129:105–114
- Jellinek S, Driscoll DA, Kirkpatrick JB (2004) Environmental and vegetation variables have a greater influence than habitat fragmentation in structuring lizard communities in remnant urban bushland. *Austral Ecology* 29(3):294–304
- Johnson NB, Poulin, RG, Somers CM (2022) Thermoregulation by bullsnakes (*Pituophis catenifer sayi*): do burrows make life easier on the prairies?. *Can J Zoo* 100(999):303–314
- Larson DM (2014) Grassland fire and cattle grazing regulate reptile and amphibian assembly among patches. *Env Manag* 54(6):1434–1444
- Lauenroth WK, Burke IC, Gutmann MP (1999) The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 223–259
- Lesbarrères D, Ashpole SL, Bishop CA, Blouin-Demers G, Brooks RJ, Echaubard P, Govindarajulu P, Green DM, Hecnar SJ, Herman T, Houlahan J, Litzgus JD, Mazerolle MJ, Paszkowski CA, Rutherford P, Schock DM, Storey KM, Loughheed SC (2014) Conservation of herpetofauna in northern landscapes: Threats and challenges from a Canadian perspective. *Biol Cons.* 170:48–55
- Martínez-Estévez L, Balvanera P, Pacheco J, Ceballos G (2013) Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. *PLoS One* 8(10):e75229
- Paletto A, Tosi V (2009) Forest canopy cover and canopy closure: comparison of assessment techniques. *Euro J of For Res* 128:265–272
- R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>
- Risser PG (1988) Diversity in and among grasslands. In: Wilson EO (ed) *Biodiversity*, National Academy Press, Washington DC, pp 176–180

- Risser PG, Birney EC, Blocker HD, May SW, Parton JW, Wiens JA (1981) The True Prairie Ecosystem. Hutchinson Ross, Stroudsburg, Penn
- Roberts KG (2020) Arkansas Herpetological Atlas 2019: Distributions of Amphibians and Reptiles (<http://www.herps of arkansas.com/Herp/Atlas>; Accessed November 2020)
- Samson FB, Knopf FL (1994) Prairie conservation in North America. *BioScience* 44:418–421.
- Shipley BK, Reading RP (2006) A comparison of herpetofauna and small mammal diversity on black-tailed prairie dog (*Cynomys ludovicianus*) colonies and non-colonized grasslands in Colorado. *Journal of Arid Environments* 66(1):27–41
- Sovic M, Fries A, Martin SA, Gibbs LH (2019) Genetic signatures of small effective population sizes and demographic declines in an endangered rattlesnake, *Sistrurus catenatus*. *Evol Apps* 12(4):664–678
- Steen DA, Barrett K (2015) Should states in the USA value species at the edge of their geographic range?. *J Wild Manag*, 79(6), 872–876
- Svedarsky WD, Westemeier RL, Robel RJ, Gough S, Toepfer JE (2000) Status and management of the Greater Prairie-Chicken *Tympanuchus cupido pinnatus* in North America. *Wild Biol* 6(4):277–284
- Swab RM, Lorenz N, Lee NR, Culman SW, Dick RP (2020) From the Ground Up: Prairies on Reclaimed Mine Land—Impacts on Soil and Vegetation. *Land* 9(11):455
- Tack JD, Quamen FR, Kelsey K, Naugle DE (2017) Doing more with less: removing trees in a prairie system improves value of grasslands for obligate bird species. *J Env Manag* 198:163–169
- Todd BD, Luhring TM, Rothermel BB, Gibbons JW (2009) Effects of forest removal on amphibian migrations: implications for habitat and landscape connectivity. *Journal of Applied Ecology* 554–561
- Transeau ED (1935) The prairie peninsula. *Ecology* 16:423–437
- Trauth SE, Robison HW, Plummer MV (2004) The Amphibians and Reptiles of Arkansas. The University of Arkansas Press, Fayetteville, AR
- van der Kamp G, Hayashi M, Bedard-Haughn A, Pennock D (2016) Prairie pothole wetlands— suggestions for practical and objective definitions and terminology. *Wetlands* 36(2):229–235
- Voldseth RA, Johnson WC, Gilmanov T, Guntenspergen GR, Millett BV (2007) Model estimation of land-use effects on water levels of northern prairie wetlands. *Ecol Apps* 17(2):527–540

- Weir LA, Royle JA, Gazenski KD, Villena O (2014) Northeast regional and state trends in anuran occupancy from calling survey data (2001-2011) from the North American Amphibian Monitoring Program. *Herp Cons Biol* 9:223–245
- Whisler KM, Rowe HI, Dukes JS (2016) Relationships among land use, soil texture, species richness, and soil carbon in Midwestern tallgrass prairie, CRP and crop lands. *Agriculture, Ecosystems & Environment* 216:237–246
- White SE, Faulk E, Tzilkowski C, Weber A, Marshall M, Wagner T (2020) Predicting fish species richness and habitat relationships using Bayesian hierarchical multispecies occupancy models. *Canadian Journal of Fisheries and Aquatic Sciences* 77(3):602–610
- Wilgers DJ, Horne EA, Sandercock BK, Volkmann AW (2006) Effects of rangeland management on community dynamics of the herpetofauna of the tallgrass prairie. *Herpetologica* 62(4):378–388
- Wright HA, Bailey W (1982) *Fire ecology: United States and southern Canada*. John Wiley and Sons, New York City, New York
- Zipkin EF, DeWan A, Royle JA (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology* 46:815–822

Tables

Table 1. Summary of prairie-associated herpetofauna detected during surveys of 34 sites in Arkansas from 2018-2020.

Genus	Species		# Captures	# Sites	Occupancy	Detection
					Mean (95% posterior interval)	Mean (95% posterior interval)
<i>Ambystoma</i>	<i>texanum</i>	Small-mouthed salamander	8	6	0.51 (0.13 - 0.89)	0.05 (0.04 - 0.07)
<i>Ambystoma</i>	<i>tigrinum</i>	Tiger salamander	1	1	0.27 (0.03 - 0.86)	0.04 (0.03 - 0.07)
<i>Gastrophryne</i>	<i>olivacea</i>	Western Narrow-mouthed Toad	9	14	0.13 (0.05 - 0.56)	0.05 (0.04 - 0.12)
<i>Lampropeltis</i>	<i>calligaster</i>	Prairie kingsnake	23	16	0.90 (0.72 - 0.95)	0.11 (0.05 - 0.18)
<i>Lithobates</i>	<i>areolatus</i>	Crawfish Frog	40	18	0.68 (0.40 - 0.90)	0.05 (0.04 - 0.07)
<i>Ophisaurus</i>	<i>attenuatus</i>	Slender glass lizard	11	11	0.69 (0.29 - 0.93)	0.05 (0.03 - 0.07)
<i>Plestiodon</i>	<i>septentrionalis</i>	Prairie skink	2	1	0.26 (0.04 - 0.82)	0.05 (0.04 - 0.08)

Table 1 (Cont.)

<i>Regina</i>	<i>grahamii</i>	Graham's crayfish snake	3	2	0.28 (0.05 - 0.82)	0.06 (0.04 - 0.09)
<i>Terrapene</i>	<i>ornata</i>	Ornate box turtle	9	9	0.48 (0.09 - 0.89)	0.04 (0.03 - 0.08)

Figures

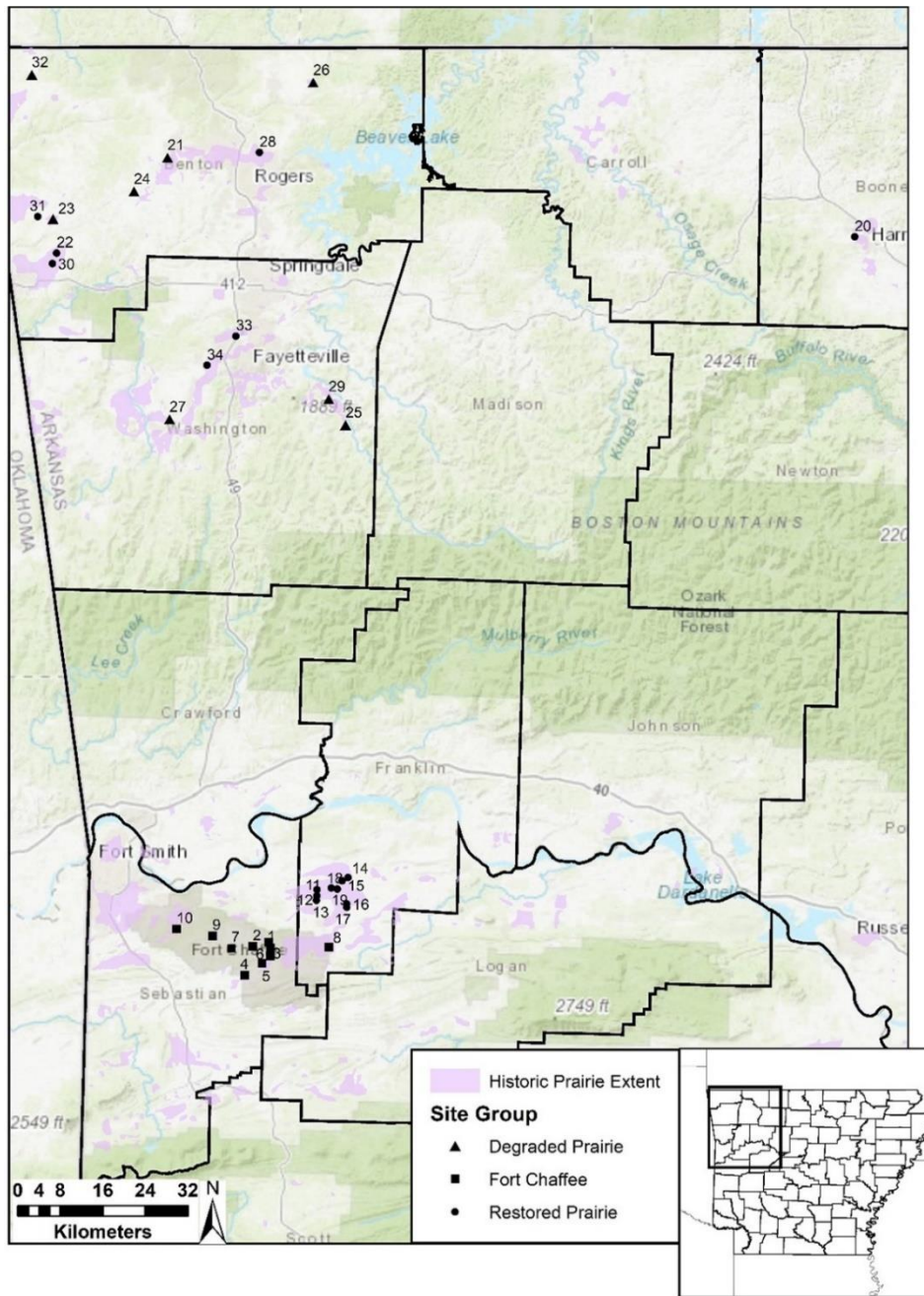


Figure 1. Distribution of study sites ($n = 34$) selected for herpetofaunal surveys across Benton, Boone, Franklin, Sebastian, and Washington counties Arkansas, USA from 2018-2020. Sites 1-10 are within Fort Chaffee, sites 11-19 represent Arkansas River Valley restored prairie sites, and sites 20-34 are in Northwest Arkansas. Map inset shows location within Arkansas.

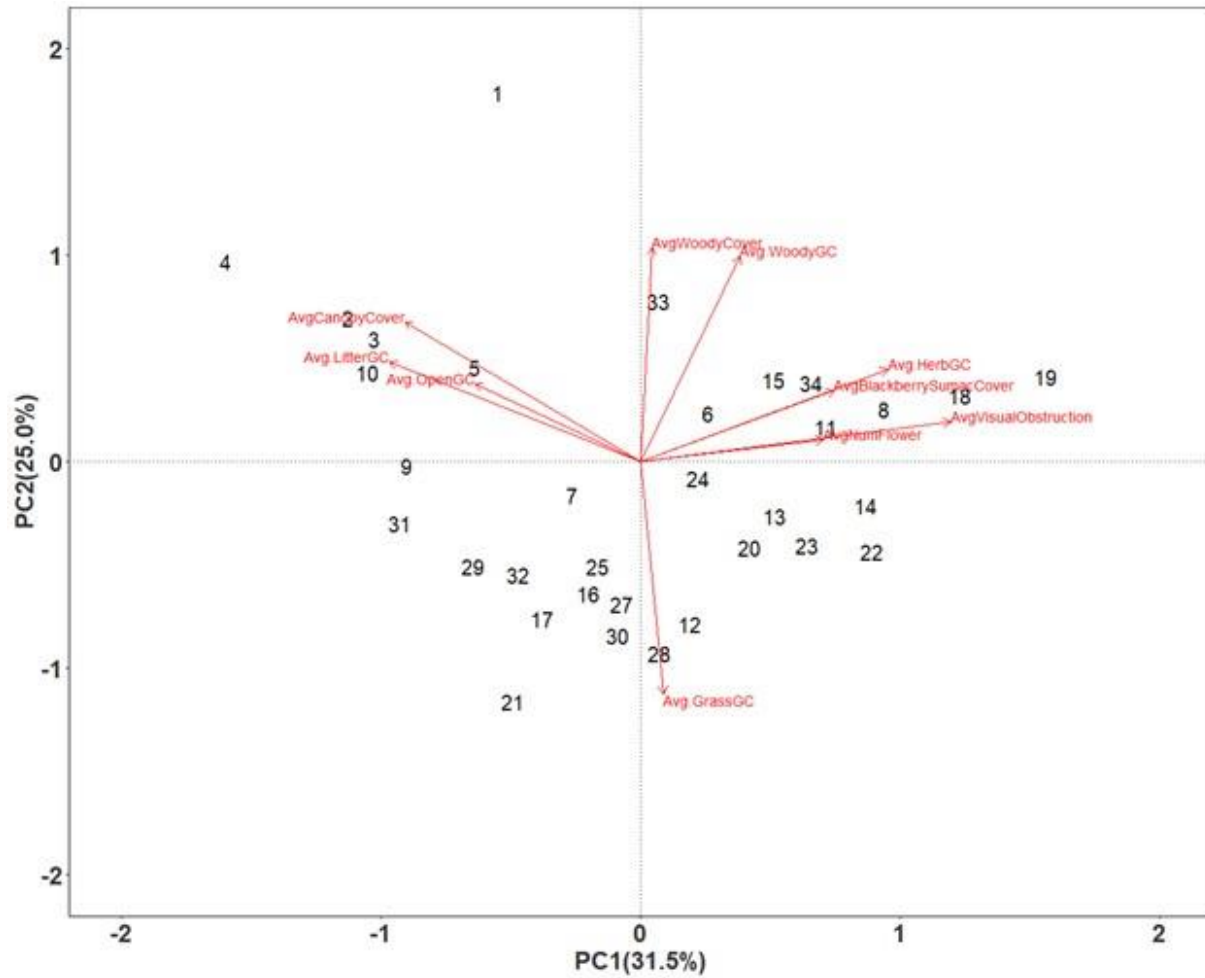


Figure 2. Biplot illustrating relative weights of each vegetation metric on Principal Components (PC) 1 and 2 and site-specific PC1 and PC2 scores designated with numbers corresponding to Fig. 1 site markers. Sites 1-10 are within Fort Chaffee, sites 11-19 represent Arkansas River Valley restored prairie sites, and sites 20-34 are in Northwest Arkansas.

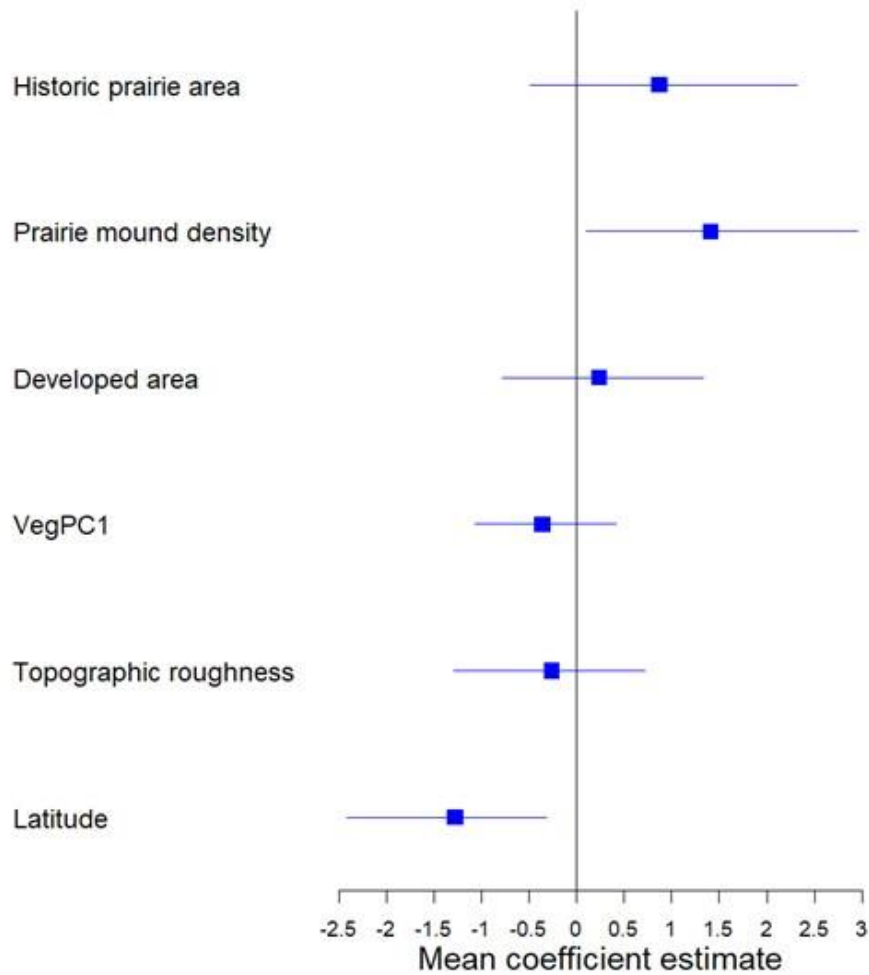


Figure 3. Summary of hyperparameters (mean assemblage response) for all species for site (historic prairie area, prairie mound density, developed area, vegetation principal component 1 [VegPC1], topographic roughness, and latitude) covariates of herpetofauna occupancy and detection from all sites in Northwest Arkansas and the Arkansas River Valley, USA from 2018-2019. Positive responses to VegPC1 indicate higher occupancy at sites with higher visual obstruction and herbaceous groundcover, and lower canopy cover and leaf litter groundcover. Bars represent 95% credible intervals.

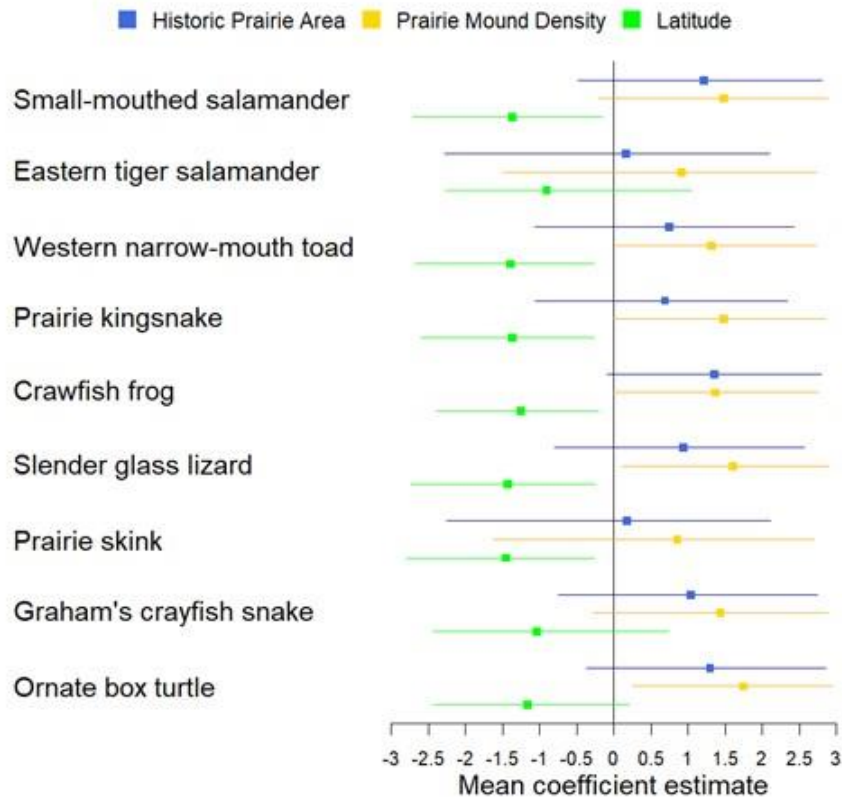


Figure 4. Species-specific occupancy responses of prairie-associated species to historic prairie area, prairie mound density, and latitude from sampling in Northwest, Arkansas, USA from 2018-2019. Bars represent 95% credible intervals.

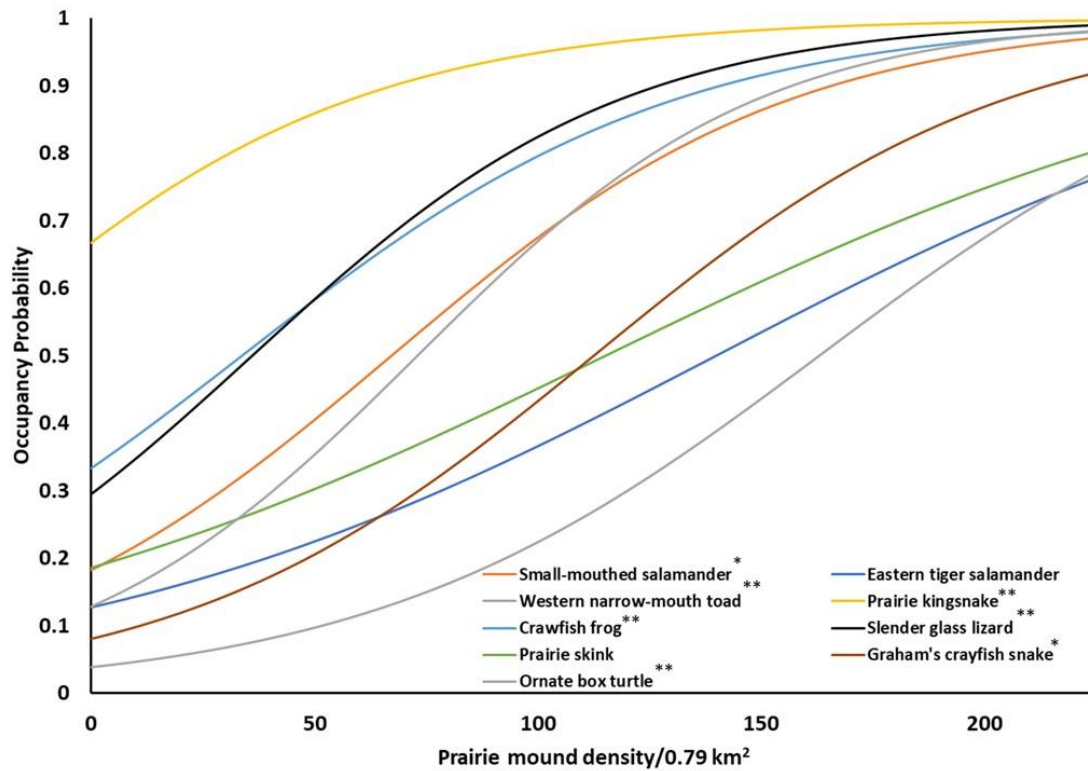


Figure 5. Species-specific responses to prairie mound density, with positive relationships indicating higher occupancy at sites with higher counts of prairie mounds. ** indicates species for which greater than 95% of the credible interval did not overlap zero; * indicates species for which greater than 75% of the credible intervals did not overlap zero.

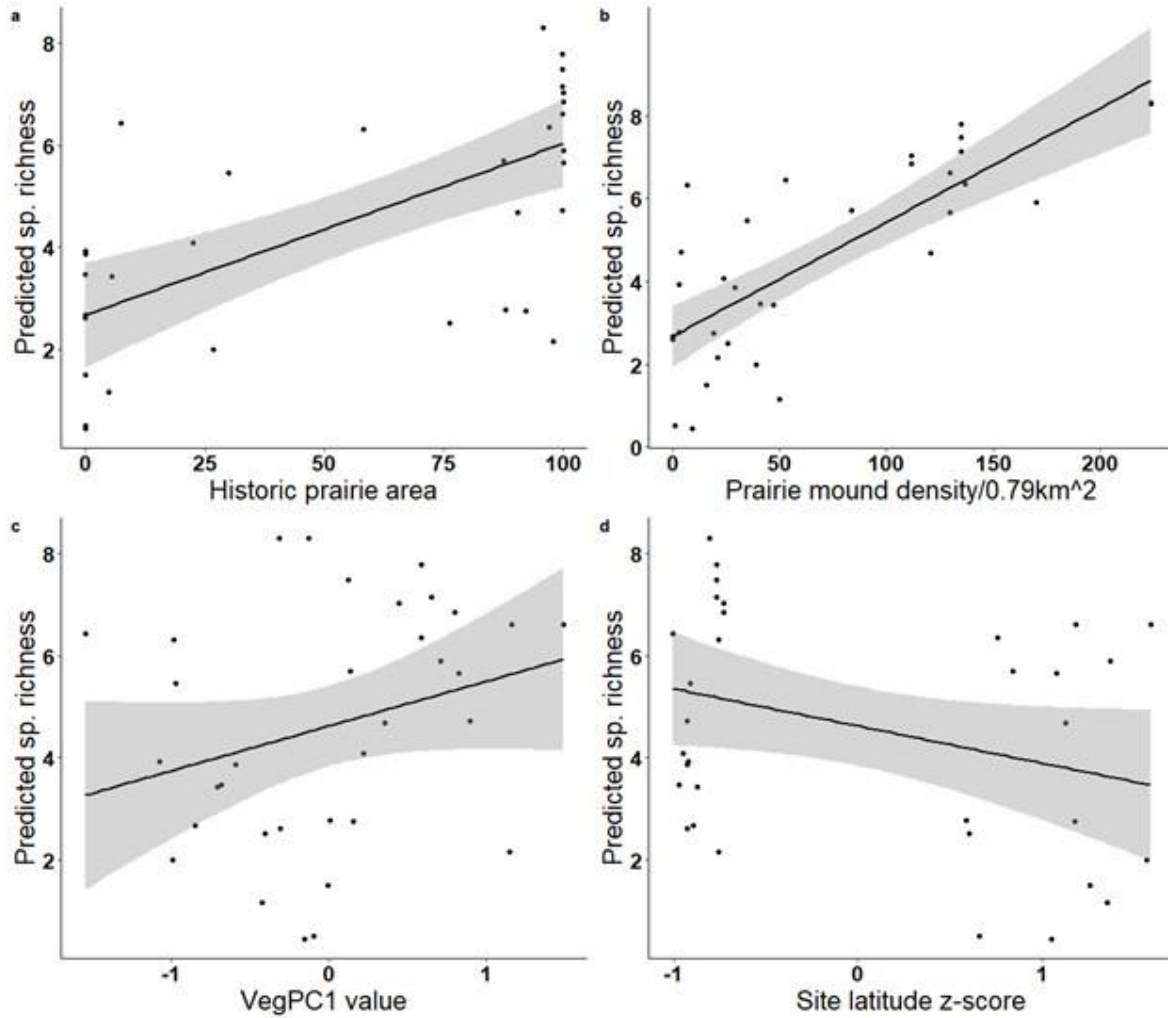


Figure 6. Relationships between species richness at each site and four habitat covariates used in the community occupancy model. The solid lines are fitted regression lines and shaded areas are 95% confidence intervals. In the occupancy model, the positive effect of prairie mound density (b) and negative effect of latitude (d) had 95% credible intervals that did not overlap zero, the positive effect of historic prairie area (a) had 90% credible intervals that did not overlap zero, and vegetation PC1 (c) had 95% credible intervals that widely overlapped zero.

IACUC Approval Forms



Office of Research Compliance

MEMORANDUM

TO: John David Willson
FROM: Craig N. Coon, Chairman
DATE: May 6, 2016
SUBJECT: IACUC Approval
Expiration Date: May 5, 2019

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # 16067 "Anthropogenic Impacts on Herpetofaunal Biodiversity in Arkansas"

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond May 5, 2019 you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian



UNIVERSITY OF
ARKANSAS

Office of Research Compliance

To: John David Willson
Fr: Craig Coon
Date: April 8th, 2019
Subject: IACUC Approval
Expiration Date: April 4th, 2022

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # **19074: *Anthropogenic Impacts on Herpetofaunal Biodiversity in Arkansas***.

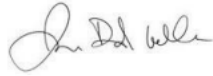
In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond April 4th, 2022, you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The following individuals are approved to work on this study: JD Willson, Chelsea Kross, Ethan Royal, Meredith Swartwout, Mitchell Pruitt, Jennifer Mortensen, Brian Becker, Brett DeGregorio, Brett DeGregorio, and Bailey Singleton. Please submit personnel additions to this protocol via the modification form prior to their start of work.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/tmp

I, Dr. John D. Willson, certify that Ethan J. Royal completed the training as required by the Institutional Animal Care and Use Committee (IACUC) for work completed in Chapter 2.



7/21/2022

John D. Willson, Ph.D.

Date

Associate Professor

Department of Biological Sciences

Chapter 2, "Legacy Land Use Predicts Occupancy Patterns of Prairie-associated Herpetofauna in Western Arkansas" is in review in the journal Landscape Ecology with two coauthors, C.S. Kross and J.D. Willson.

I, Dr. John D. Willson, advisor of Ethan J. Royal, confirm that Ethan J. Royal is first author and completed at least 51% of the work for this manuscript.



7/21/2022

John D. Willson, Ph.D.

Date

Associate Professor

Department of Biological Sciences

Chapter 3

Prescribed fire causes direct mortality, but not long-term population declines in a tallgrass prairie

snake community

Ethan J. Royal

and

John D. Willson

Abstract

As prescribed fire is restored to landscapes that have been managed under fire-suppression tactics for several hundred years, there is an urgent need for research documenting its effects on local wildlife. Much of the existing prescribed fire-wildlife research focuses on indirect effects of fire related to habitat use. Direct effects like mortality are primarily documented in anecdotal records featuring raw counts with little context about potential population-level effects. Using repeated field surveys and mark-recapture efforts, we documented direct mortality following annual prescribed burns and monitored long-term population trends in a tallgrass prairie snake community. We aimed to place burn mortalities in population-level contexts and determine if regular burn mortalities constitute a threat to population stability. We documented burn mortalities in six snake species over an eight-year period, with considerable temporal and interspecific variation in mortality. Mark-recapture analyses suggest that populations did not suffer serious declines due to burn mortality, but we do note decreases in some population estimates following burns with high species-specific mortality. We also explore issues hampering our monitoring efforts, as detection of burn mortalities appears to be extremely low, even with experienced observers. Our study represents the first long-term study pairing consistent burn mortality records with population monitoring in a snake community, and we highlight persistent knowledge gaps and future research directions of conservation and management value.

Introduction

Fire plays a vital role in fostering biodiversity at local and regional scales (Burkle et al., 2015; He et al., 2019). At the local scale, nutrient cycling and structural heterogeneity driven by fire can encourage plant diversity and maintain requisite habitat conditions for species adapted to

fire-dependent landscapes, particularly open-canopy savannas and grasslands (Brockway et al., 2002; Russell et al., 2009; Grant et al., 2010; Howze and Smith, 2021). As the value of fire in maintaining biodiversity has become clear, fire-suppression tactics employed in North America for much of the last 300 years are being phased out in favor of prescribed burns (Fuhlendorf et al., 2011; He et al., 2019). Tallgrass prairies in central North America were historically shaped by wildfires, and prescribed burns are now the primary tool used during restoration and maintenance to curb woody encroachment, combat invasive species, recycle soil nutrients, and encourage native plant diversity (Brockway et al., 2002, Courtwright, 2007; Simmons et al., 2007; Twidwell et al., 2016; Nippert et al., 2021). Accompanying the rise of prescribed fire as a management tool, considerable research has been done to assess the effects of fire on prairie biota.

Prescribed fire can help maintain suitable structural and foraging conditions for wildlife, including keystone species, such as bison, as well as a range of prairie-associated small mammals, invertebrates, birds, reptiles, and amphibians (Kaufman et al., 1988; Coppedge and Shaw, 1998; Collins, 2000; Panzer, 2002; Callahan et al., 2003; Wilgers and Horne, 2006; Powell, 2008; Winder et al., 2017). However, most studies of wildlife–prescribed fire relationships are framed as comparisons of occupancy, abundance, or habitat use by taxa between burned and unburned sites (Cavitt, 2000; Darracq et al., 2016; Russell et al., 2009; Steen et al., 2013). Indeed, most of these studies focus entirely on the indirect effects that result from altered habitat conditions and overlook direct effects, such as mortality or injury resulting from burns (Engstrom, 2010; Jolly et al., 2022; Whelan et al. 2002). Evidence from anecdotal reports and a growing number of radiotelemetry studies suggests that direct mortality from fire does occur, creating the potential for negative population-level effects (Cross et al., 2015; Engstrom,

2010; Griffiths and Christian, 1996; Harris et al., 1920; Hingtgen, 2000; Jolly et al., 2022; Webb and Shine, 2008). The negative impacts of prescribed burns on wildlife could be exacerbated if the management plan deviates from the natural fire regimes to which species are adapted, including differences in burn frequency and/or seasonality (Bragg, 1982; Engle and Bidwell, 2001).

Existing research on reptiles demonstrates that burn regimes can spur short-term, species-specific changes in habitat use (Cavitt, 2000; Wilgers and Horne, 2006). There are ample anecdotal reports of reptiles experiencing direct mortality during burns. Yet nearly all these reports lack population-level context (Komarek, 1969; Means and Campbell 1981), so they offer limited use for conservation and management (Russell et al., 1999). The few studies that document the proportion of radio-tracked reptiles that died in burns suggest that populations may experience high rates of mortality under certain burn regimes or conditions (Griffiths and Christian, 1996; Harris et al., 2020). Unfortunately, studies of this kind are few and generally limited to short-term monitoring, and the taxa and ecosystems represented in them are extremely limited. The potential for high rates of direct mortality during burns is particularly concerning in light of research suggesting that ancillary sources of mortality can drastically increase extinction probabilities in reptiles (Gibbs and Shriver, 2002; Row et al., 2007; Webb et al., 2002; Winton et al., 2020). Studies assessing direct mortality of snakes during prescribed burns in prairie ecosystems are limited to a single species, the eastern massasauga (*Sistrurus catenatus*). Two studies have observed direct mortalities of radio-tracked massasaugas in prescribed burns (Durbian, 2006; Cross et al., 2015), and one study projected that population extinction probabilities increase dramatically under the most severe prescribed burn mortality scenarios (Hileman et al., 2018). There is clear potential for prescribed burns to significantly alter snake

population dynamics if they result in repeated instances of direct mortality. Yet, to date, no studies have tracked direct mortality in conjunction with long-term snake population trends.

Here, we used a prairie restoration site that is subjected to annual prescribed burns and has been used to conduct a long-term monitoring study of the snake community (see Baecher et al. 2018) to achieve the following objectives: 1) Quantify direct mortality from prescribed burns in a snake community, 2) Identify seasonal and/or environmental factors that may influence snake mortality during burns, and 3) Generate long-term population estimates for each common species in this snake community to provide population-level context to observed mortality. To accomplish these goals, we first performed post-burn mortality surveys covering the entirety of the prairie site immediately following annual prescribed burns from 2015–2021 to quantify observable direct mortality. Second, we conducted mark-recapture sampling for seven snake species from 2015–2021 to generate population estimates over that period. Post-burn mortality surveys allowed us to contextualize direct burn mortality within the long-term population trends of the snake community.

Methods

Study Site

We conducted our long-term study at Woolsey Wet Prairie Sanctuary (WWPS; 36.067100°N, -94.233810°W), a 16.6-ha wetland mitigation prairie restoration site that has been burned every spring since restoration work began in 2007. Baecher et al. (2018) describe the site conditions and the reptile and amphibian communities of the site in 2014, at the start of the mark-recapture sampling used in this study. Annual prescribed burns occurred at WWPS between February 10 and March 25 each year and covered the entirety of the restoration area described in Baecher et al. (2018).

Burn Mortality Surveys

We performed systematic visual surveys to detect burn mortality of snakes within 24 h of the prescribed burn at WWPS each year from 2015–2022. These surveys consisted of 2–6 experienced observers walking in a grid (spaced approximately 5 m apart) over the entirety of the restoration site and visually searching for any snakes, live or dead. Although the number and composition of observers varied across years, the area surveyed and survey methods remained consistent. We collected each snake discovered during post-burn mortality surveys and recorded location, species, individual ID (if marked), and a qualitative description of burn damage. While we recognize the possibility that some snakes we discovered may have perished before the burn due to unrelated causes, most snakes we found were intact enough to infer that they had been in good body condition and lacked any major injuries other than clear burn wounds.

Mark-recapture Surveys

We performed approximately weekly coverboard and visual-encounter surveys for snakes at WWPS between early-mid March to late October each year during 2015–2021. We placed approximately 60 coverboards throughout the restored section of WWPS in 2014, checked all boards each week during the active season, captured all snakes found during coverboard checks, and replaced degraded coverboards as necessary during the study period. We also opportunistically checked natural cover and visually searched for snakes during the coverboard checks, with survey effort typically consisting of 1.5–2 h of searching per week by 2–3 experienced observers. We captured all snakes encountered, recorded their capture locations, and returned them to the University of Arkansas for processing. Following capture, we recorded snout-vent length, body mass, and sex. We marked each new capture with a unique identification

code by branding ventral scales (Winne et al. 2006), and we subsequently recorded identification codes at each recapture to create individual capture histories for all marked snakes.

As a highly aquatic species with seasonally variable activity, *Regina grahamii* (Graham's crayfish snake) is not effectively sampled using coverboards checks or visual encounter surveys. Thus, we conducted closed-design aquatic trapping sessions at two wetlands in WWPS in order to generate mark-recapture data for *R. grahamii*. In 2015, 2016, and 2022, we deployed minnow traps in WWPS wetlands (wetland sections: Regina Pond (0.11 ha) and E5 (0.24 ha); see Baecher et al. 2018 for site details), checked traps, processed and marked snakes as previously described, and released snakes on the day of capture for trapping periods ranging from 13–16 nights. Our capture and processing protocols for live animals were reviewed and approved by the University of Arkansas Institutional Animal Care and Review Committee (AUPs 13041, 16067, 19074, 22019).

Mark-Recapture Models

The goal of our capture-mark-recapture (CMR) modeling process was to generate population estimates for snake species in WWPS to provide context for the number of observed burn mortalities, as well as to examine population trends over time. For simplicity, we excluded young-of-year snakes from CMR models, as they would not have been available for capture for much of the year and are known to be difficult to detect (Pike et al., 2008). Additionally, due to our limited dataset, we restricted our model structures to time-varying models, with no demographic, individual, or environmental covariates included. Because species varied considerably in terms of sampling efficiency, overall capture numbers, recapture probability, and sampling methodology, the model structures we used differed from species to species (Table 1). We constructed robust models for *N. erythrogaster* (Plain-bellied watersnake), *T. proximus*

(western ribbon snake), and *T. sirtalis* (common garter snake) using year as the primary period, with secondary periods of months (active season Apr–Nov). We used the POPAN formulation of open mark-recapture model to estimate abundance for *C. constrictor* (eastern racer), *L. calligaster* (prairie kingsnake), and *L. holbrooki* (speckled kingsnake), using year as the sampling unit. We completed mark-recapture analyses using program MARK (White and Burnham 1999) via package RMark (Laake 2013) in program R v4.1.2 (R Core Team 2021). We then extracted annual population estimates from each model. This produced population estimates for each species during 2015–2021, except for *R. grahamii*, for which we ran three separate closed models for trapping efforts in 2015, 2016, and 2022. To account for unsampled wetland areas, we then took *R. grahamii* population estimates from the wetland sections (described above), converted them to a density estimate of snakes/wetland ha, and multiplied that by the total wetland surface area at WWPS (1.54 ha) to obtain a rough extrapolation of the total number of adult *R. grahamii* at WWPS in 2015, 2016, and 2022.

Results

Mortality Surveys

We documented a total of 60 snake mortalities resulting from prescribed burns at WWPS during 2015–2022 (range=0–35; average=7.5/yr; Table 2; Fig. 1). Observed mortalities varied considerably across years and species, and certain species seemed to experience clustered mortality in specific years (Table 2). Mortalities varied depending on the timing of prescribed burns, as minimal mortalities occurred during burns in February, which is before the start of the typical active season (Fig. 2). The highest number of documented mortalities occurred in 2016 with a total of 35 dead snakes of five different species, representing over half of the direct mortalities we observed from 2015–2022. Annual species composition of mortalities varied, as

some years were dominated by one species and others had more even species composition (Table 2; Fig. 3). For example, in 2019, all seven burn mortalities we observed were *L. calligaster*, and in 2015 *L. calligaster* constituted three of the four documented mortalities. During both years, the burn occurred in mid-March. *Lampropeltis calligaster* and *T. sirtalis* were the two species with the highest total number of mortalities over the study period (15 and 21 mortalities, respectively) and were found in more years than other species (five and four years, respectively, out of eight years of surveys). Alternatively, some species known from the site were rarely or never found in burn mortality surveys, with a single *L. holbrooki* found in 2015 and no *C. constrictor* mortalities found during 2015–2022.

Mark-recapture Analyses

During 2015–2021 we captured 76 individual *C. constrictor*, 102 individual *L. calligaster*, 41 individual *L. holbrooki*, 495 individual *N. erythrogaster*, 1531 individual *T. proximus*, and 535 individual *T. sirtalis*. We captured a combined total of 212 individual *R. grahamii* during the 2015, 2016, and 2022 trapping periods. Population estimates for the two most common species, *T. proximus* (annual mean = 373; range = 172–526) and *T. sirtalis* (annual mean = 235; range = 117–374), were highly variable across years but estimates featured wide intra-annual confidence intervals and did not exhibit clear long-term trends towards decline or growth (Figs. 4 and 5). Population estimates for *C. constrictor* (annual mean = 10; range = 4–20), *L. calligaster* (annual mean = 98; range: 71–156), *L. holbrooki* (annual mean = 9; range = 5–13), and *R. grahamii* (area-adjusted annual mean = 472; range = 280–551) remained stable over the study period, although estimates for *R. grahamii* are limited to 2015, 2016, and 2022 (Figs. 4 and 5). One species, *N. erythrogaster* (annual mean = 305; range = 112–583), exhibited a consistent decline in estimated population size 2016–2021.

Discussion

In this study, we present the first long-term data quantifying regular burn mortality within a snake community. Our surveys revealed that direct mortality occurred in six snake species over the eight-year study period, with a great deal of inter-specific and inter-annual variation. Mortality records in the existing literature are largely haphazard and suggest that mortality rates are low and unlikely to affect population dynamics (Means and Campbell, 1981). The annual number of mortalities we documented are low and generally align with mortality ranges seen in anecdotal reports (Russell et al. 1999). During our eight-year burn-mortality study, only one species, *T. sirtalis*, averaged more than two mortalities per year. Previous reports lack population-level context needed to assess the potential for long-term effects on populations. For example, Means and Campbell (1981) found two of 68 marked *Crotalus adamanteus* (Eastern diamondback rattlesnake) killed across five prescribed fires, but the fates of the other snakes were not always known. Cross et al. (2015) found two of five radio-tracked *S. catenatus* killed in a single burn, but the suggestion of a high population-level mortality rate is neutered by the small number of snakes tracked. In this study, we place observed burn mortalities in a larger context of annual population estimates, provide evidence that, in some cases, prescribed burns can kill a meaningful portion of a population, and highlight additional knowledge gaps and research directions.

Although we did not detect any mass mortality events likely to cause immediate population collapses in the WWPS snake community, the levels of mortality we observed may represent only a fraction of the actual deaths. Our ability, and the abilities of other researchers not using tracked animals, to detect burn mortalities may not provide a complete picture of actual mortality rates. Imperfect detection during mortality surveys, common instances of delayed

mortality of animals injured during the burn (Royal, pers. obs.; Harris et al., 2020), and our inability to detect animals that may perish in refugia due to smoke inhalation, asphyxiation, and heat exposure (Jolly et al. 2022) suggests actual mortality could be higher than what we observed. Our underestimation of true burn mortality rates highlights the importance of long-term population monitoring efforts, which provide the ability to determine when population declines occur even in the absence of clearly identifiable causes.

We did not observe severe population declines for most species over the course of the study, suggesting that the current burn regime is sustainable for long-term conservation management goals at WWPS. The one exception, *N. erythrogaster*, has largely disappeared from sections of WWPS, where it was once abundant, but this decline is likely unrelated to prescribed burn mortality and is instead driven by invasion of fish in WWPS wetlands (unpublished data). However, we did document significant mortality relative to estimated population sizes in several cases, as well as rough trends suggesting that some populations were depleted in years that featured high species-specific mortality in the spring prescribed burn. For example, we documented 15 burn mortalities of *T. sirtalis* following the 2016 burn, representing roughly 4% of the estimated adult population from 2015. Furthermore, mark-recapture analyses showed *T. sirtalis* population estimates declined from 374 to 122 adults (a 67% decrease) between 2015 and 2016 (Fig. 5). We also recorded 7 burn mortalities of *L. calligaster* following the 2019 burn, representing 8% of the estimated population from 2018, and the population estimates dropped from 87 to 70 individuals (a 20% decrease) between 2018 and 2019 (Fig. 5). While our population estimates do have wide confidence intervals, and we hesitate to directly attribute downward population shifts to burn mortality, the number of mortalities observed in some years relative to the estimated population sizes suggests that mortality events of this magnitude could

affect long-term population viability if they occur too frequently to allow for recovery between events. It seems likely that the annual fire-return interval employed at WWPS represents an extreme and places greater strain on populations than the 4–6-year fire return interval evidenced to have been the norm in this region before European settlement (Frost, 1998).

We observed substantial annual variation in the number of burn mortalities that appeared to be linked to the seasonal timing and weather conditions during the burn. Specifically, we detected no snake mortalities after the two prescribed burns that occurred before February 21, suggesting that snake mortality is minimal if burns are completed before snake activity increases in late winter/early spring. However, this pattern appears complex and likely contingent on local temperature conditions at the time of the burn. For example, we observed some mortalities after the 2017 and 2021 burns that occurred on February 23 and 24 when local temperatures were unseasonably warm, 17–19°C, during the time of the burns. Our data also suggest that burns that coincide with snake emergence from winter hibernacula, when snakes are in poorer body condition and thermoregulation is more difficult, may be more damaging than burns that occur before or well into the active season. The 2017 burn (Feb 23) appeared to coincide with emergence for several species, based on captures from mark-recapture surveys, which resulted in the highest number of observed mortalities by far. Burns that occurred later in the season (2015, 2018, and 2019) did not result in comparable mortality. Thus, the relationship among seasonality, temperature, and burn mortality does not appear to be linear and a larger dataset with increased temporal variation in burn timing would provide more clarity. Our study explores a narrow range of the burn conditions species have been and are exposed to, and we encourage the continuation and expansion of this research in other systems with broader variation in seasonality and timing of burns.

In addition to annual variation in mortality, burns appear to impact species differently. Species that begin activity earlier in the year at lower temperatures, like *T. sirtalis* (Trauth et al. 2004), are susceptible to mortality even when burns occur in late February, while species that begin activity later in warmer temperatures, like *C. constrictor* (DeGregorio et al. 2016), may be unaffected by early spring prescribed burns. *Lampropeltis calligaster* typically exhibits increased surface activity from mid-March to mid-April in WWPS, and *L. calligaster* accounted for ten of the 11 observed mortalities in the two burns that occurred in late March (2015 and 2019). Tallgrass prairie management plans have often championed the use of late spring burns to produce desired plant community composition characteristics (Owensby and Anderson, 1967), but this strategy is refuted by recent research suggesting that winter and early spring burns maximize biodiversity without negative effects to overall yield for livestock grazing (Towne and Craine, 2014). Prairie managers that embrace winter burns can maximize plant productivity and minimize reptile burn mortality, likely benefiting wildlife populations through both direct (i.e., reduced mortality) and indirect (i.e., diverse habitat structure) pathways. Ideally, experimental research would examine the effects of prescribed burns in other seasons. Pre-European burn regimes in the Great Plains appeared to peak in April, late summer, and early fall, contrasting the spring burns that are common now (Higgins, 1986; Engle and Bidwell TG, 2001). Thus, the mortality we observed might not align with what populations have historically experienced.

The snake populations we monitored from 2015–2022 generally did not appear to be in decline or suffer severe negative direct effects due to prescribed burns. Yet, we did document significant mortality for some species in certain years, which suggests that repeated instances of high annual burn mortality could occur and detrimentally affect snake populations without considerate planning. We documented burn mortality patterns that varied widely among species

and over time and highlight adaptive decision-making guidelines that could minimize snake burn mortality without negative vegetation management ramifications. Finally, we believe that detectability of animals during post-burn surveys is extremely low, suggesting that prescribed burns could have more severe direct effects on snake populations than previously expected, and we identify specific knowledge gaps related to direct burn mortality in snakes. Our study represents the first long-term monitoring program for burn mortality of a snake community and lays the groundwork for future research investigating how populations might respond to different burn management plans and mortality scenarios.

Acknowledgements

We thank Max Carnes-Mason, Dr. Larry Kamees, Dr. Chelsea Kross, Phil Vogrinc, Alex Baecher, Alex Meinders, Dr. Jackie Guzy, Dr. Jennifer Mortensen, Bailey Singleton, Dr. Meredith Swartwout, Gabriel Yerdon, Mary-Kate Shaver, Elliot Lassiter, Mitchell Pruitt, and many others for their work in the field. We thank Joe Woolbright, Bruce Shackleford, Environmental Consulting Operations Inc., Seth Pickens, Jeff Hickle and the City of Fayetteville for site access, information, and management work. We thank Dr. Lauren Maynard for insightful comments and edits to the manuscript.

Literature Cited

- Bragg, T. B. 1982. Seasonal Variations in Fuel and Fuel Consumption by Fires in a Bluestem Prairie. *Ecology* 63:7–11.
- Brockway, D. G., R. G. Gatewood, and R. B. Paris. 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management* 65:135–152.
- Burkle, L. A., J. A. Myers, R. T. Belote, and D. P. C. Peters. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. *Ecosphere* 6:1–14.

- Callaham, M. A., J. M. Blair, T. C. Todd, D. J. Kitchen, and M. R. Whiles. 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. *Soil Biology and Biochemistry* 35:1079–1093.
- Cavitt, J. F. 2000. Fire and a tallgrass prairie reptile community: Effects on relative abundance and seasonal activity. *Journal of Herpetology* 34:12–20.
- Collins, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *American Naturalist* 155:311–325.
- Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Rangeland Management* 51:258–264.
- Cross, M. D., K.V. Root, C. J. Mehne, J. McGowan-Stinski, D. Pearsall, and J. C. Gillingham. 2015. Multi-scale Responses of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*) to Prescribed Fire. *American Midland Naturalist* 173:346–362.
- Darracq, A. K., W. W. Boone, and R. A. McCleery. 2016. Burn regime matters: A review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. *Forest Ecology and Management* 378:214–221.
- DeGregorio, B. A., P. J. Weatherhead, M. P. Ward, and J. H. Sperry. 2016. Do seasonal patterns of rat snake (*Pantherophis obsoletus*) and black racer (*Coluber constrictor*) activity predict avian nest predation? *Ecology and Evolution* 6:2034–2043.
- Durbian, F. 2006. Effects of Mowing and Summer Burning on the Massasauga (*Sistrurus catenatus*). *American Midland Naturalist* 155:329–334.
- Engle, D., and Bidwell TG. 2001. The response of central North American prairies to seasonal fire. *Rangeland Ecology and Management* 54:2–10.
- Engstrom, R. T. 2010. First-order fire effects on animals: Review and recommendations. *Fire Ecology* 6:115–130.
- Frost Cecil C. 1998. Presettlement fire frequency regimes of the United States: a first approximation. *Tall Timbers Fire Ecology Conference Proceedings* 70–81.
- Fuhlendorf, S. D., R. F. Limb, D. M. Engle, and R. F. Miller. 2011. Assessment of Prescribed Fire as a Conservation Practice. Washington D.C.
- Gibbs, J. P., and W. G. Shriver. 2002. Estimating the Effects of Road Mortality on Turtle Populations. *Conservation Biology* 16:1647–1652.
- Grant, T. A., E. M. Madden, T. L. Shaffer, and J. S. Dockens. 2010. Effects of Prescribed Fire on Vegetation and Passerine Birds in Northern Mixed-Grass Prairie. *The Journal of Wildlife Management* 74:1841–1851.
- Griffiths, A. D., and K. A. Christian. 1996. The effects of fire on the frillneck lizard (*Chlamydosaurus kingii*) in northern Australia. *Australian Journal of Ecology* 21:386–398.

- Harris, K. A., J. D. Clark, R. D. Elmore, and C. A. Harper. 2020. Direct and Indirect Effects of Fire on Eastern Box Turtles. *The Journal of Wildlife Management* 84:1384–1395.
- He, T., B. B. Lamont, and J. G. Pausas. 2019. Fire as a key driver of Earth's biodiversity. *Biological Reviews* 94:1983–2010.
- Higgins, K. 1986. Interpretation and compendium of historical fire accounts in the northern Great Plains. Volume 161. US Department of the Interior, Fish and Wildlife Service.
- Hileman, E. T., R. B. King, and L. J. Faust. 2018. Eastern massasauga demography and extinction risk under prescribed-fire scenarios. *The Journal of Wildlife Management* 82:977–990.
- Hingtgen, T. 2000. Prescribed Burning: Observations on the Interaction Of Wildlife And Fire in State Parks of Southwestern Florida. Tall Timbers Fire Ecology Conference Proceedings.
- Howze, J. M., and L. L. Smith. 2021. The influence of prescribed fire on site selection in snakes in the longleaf pine ecosystem. *Forest Ecology and Management* 481:118703.
- Jolly, C. J., C. R. Dickman, T. S. Doherty, L. M. van Eeden, W. L. Geary, S. M. Legge, J. C. Z. Woinarski, and D. G. Nimmo. 2022. Animal mortality during fire. *Global Change Biology* 28:2053–2065.
- Kaufman, G. A., D. W. Kaufman, and E. J. Finck. 1988. Influence of Fire and Topography on Habitat Selection by *Peromyscus maniculatus* and *Reithrodontomys megalotis* in Ungrazed Tallgrass Prairie. *Journal of Mammalogy* 69:342–352.
- Knapp, D. D., and J. Howze. 2018. Prescribed fire affects diurnal vertebrate use of Gopher Tortoise (*Gopherus polyphemus*) burrows in a Longleaf Pine (*Pinus palustris*) forest Amphibian population ecology *Herpetological Conservation and Biology* 13(3):551–557.
- Komarek, E.V. 1969. Fire and Animal Behavior. Tall Timbers Fire Ecology Conference Proceedings 9:161:207.
- Laake J.L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep. 2013–01, Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA.
- Means, D. B., and H. W. Campbell. 1981. Effects of prescribed fire on amphibians and reptiles. Pages 89–96 in Wood G.W., editor. Prescribed fire and wildlife in southern forests. Belle Baruch Forest Science Institute, Clemson University, Georgetown, South Carolina.
- Nippert, J. B., L. Telleria, P. Blackmore, J. H. Taylor, and R. C. O'Connor. 2021. Is a Prescribed Fire Sufficient to Slow the Spread of Woody Plants in an Infrequently Burned Grassland? A Case Study in Tallgrass Prairie. *Rangeland Ecology & Management* 78:79–89.
- Owensby, C. E., and K. L. Anderson. 1967. Yield response to time of burning in the Kansas Flint Hills. *Journal of Rangeland Management* 20:12–16.
- Panzer, R. 2002. Compatibility of Prescribed Burning with the Conservation of Insects in Small, Isolated Prairie Reserves. *Conservation Biology* 16:1296–1307.

- Pike, D. A., L. Pizzatto, B.A. Pike, and R. Shine. (2008). Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89(3):607-611.
- Powell, A. F. L. A. 2008. Responses of breeding birds in tallgrass prairie to fire and cattle grazing. *Journal of Field Ornithology* 79:41–52.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>
- Row, J. R., G. Blouin-Demers, and P. J. Weatherhead. 2007. Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). *Biological Conservation* 137:117–124.
- Russell, K. R., D. H. van Lear, and D. C. Guynn. 1999. Prescribed Fire Effects on Herpetofauna: Review and Management Implications. *Wildlife Society Bulletin* 27:374–384.
- Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecological Applications* 19:1253–1263.
- Simmons, M. T., S. Windhager, P. Power, J. Lott, R. K. Lyons, and C. Schwoppe. 2007. Selective and Non-Selective Control of Invasive Plants: The Short-Term Effects of Growing-Season Prescribed Fire, Herbicide, and Mowing in Two Texas Prairies. *Restoration Ecology* 15:662–669.
- Steen, D. A., L. M. Conner, L. L. Smith, L. Provencher, J. K. Hiers, S. Pokswinski, B. S. Helms, and C. Guyer. 2013. Bird assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecological Applications* 23:134–147.
- Towne, E. G., and J. M. Craine. 2014. Ecological Consequences of Shifting the Timing of Burning Tallgrass Prairie. *PLOS ONE* 9:e103423.
- Webb, J. K., B. W. Brook, and R. Shine. 2002. Collectors endanger Australia's most threatened snake, the broad-headed snake *Hoplocephalus bungaroides*. *Oryx* 36:170–181.
- White G.C, Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*. 46:120–139.
- Wilgers, D. J., and E. A. Horne. 2006. Effects of Different Burn Regimes on Tallgrass Prairie Herpetofaunal Species Diversity and Community Composition in the Flint Hills, Kansas. *Journal of Herpetology* 40(1):73–84.
- Wilgers, D. J., V. A. Horne, R. K. Sandercock, and A. W. Volkmann. 2006. Effects of Rangeland Management on Community Dynamics of the Herpetofauna of the Tallgrass Prairie. *Herpetologica* 62(4):378–388.
- Winder, V. L., L. B. McNew, J. C. Pitman, and B. K. Sandercock. 2017. Space Use of Female Greater Prairie-Chickens in Response to Fire and Grazing Interactions. *Rangeland Ecology and Management* 70:165–174.

Winton, S. A., C. A. Bishop, and K. W. Larsen. 2020. When protected areas are not enough: low-traffic roads projected to cause a decline in a northern viper population. *Endangered Species Research* 41:131–139.

Tables

Table 1. Species-specific mark-recapture model structures used to generate populations estimates for seven snake species from Woolsey Wet Prairie Sanctuary from 2015–2021. Parameters vary by species-specific model and include: apparent survival (S), probability of first detection (p), and the probability of recapture(c), the number of individuals available to enter the population throughout the study (Nsuper), and rate of entry into the population from the super population via births and immigration (pent). Parameters were allowed to vary by primary sampling period (year), secondary sampling period (session), or were held constant(.).

Species	Model Formulation	Model Structure
<i>C. constrictor</i>	Open – POPAN	S(.),p(.),pent(~year),Nsuper(.)
<i>L. calligaster</i>	Open – POPAN	S(.),p(.),pent(~year),Nsuper(.)
<i>L. holbrooki</i>	Open – POPAN	S(.),p(.),pent(~year),Nsuper(.)
<i>N. erythrogaster</i>	Robust	S(.),p=c(session), f0(session), $\gamma' = \gamma''$.
<i>R. grahamii</i>	Closed	p(.), p=c, f0(.)
<i>T. proximus</i>	Robust	S(.),p=c(session),f0(session), $\gamma' = \gamma''$.
<i>T. sirtalis</i>	Robust	S(.),p=c(session),f0(session), $\gamma' = \gamma''$.

Table 2. Observed burn mortalities for each species and the full snake community from post-burn surveys at Woolsey Wet Prairie Sanctuary from 2015–2022. Number of burn mortalities/ha of burn area is calculated from Year Total/ the 16.6 ha area of the Woolsey Wet Prairie Sanctuary restored section.

	<i>C. constrictor</i>	<i>L. calligaster</i>	<i>L. holbrooki</i>	<i>N. erythrogaster</i>	<i>T. proximus</i>	<i>T. sirtalis</i>	<i>R. grahamii</i>	Year Total	# Mortalities/ha Burn Area
2015	0	3	1	0	0	0	0	4	0.24
2016	0	2	0	6	4	15	8	35	2.11
2017	0	1	0	0	2	3	0	6	0.36
2018	0	2	0	0	0	2	1	5	0.30
2019	0	7	0	0	0	0	0	7	0.42
2020	0	0	0	0	0	0	0	0	0
2021	0	0	0	0	1	1	0	2	0.12
2022	0	0	0	0	0	0	0	0	0
Species Totals	0	15	1	6	8	21	9	60	

Figures

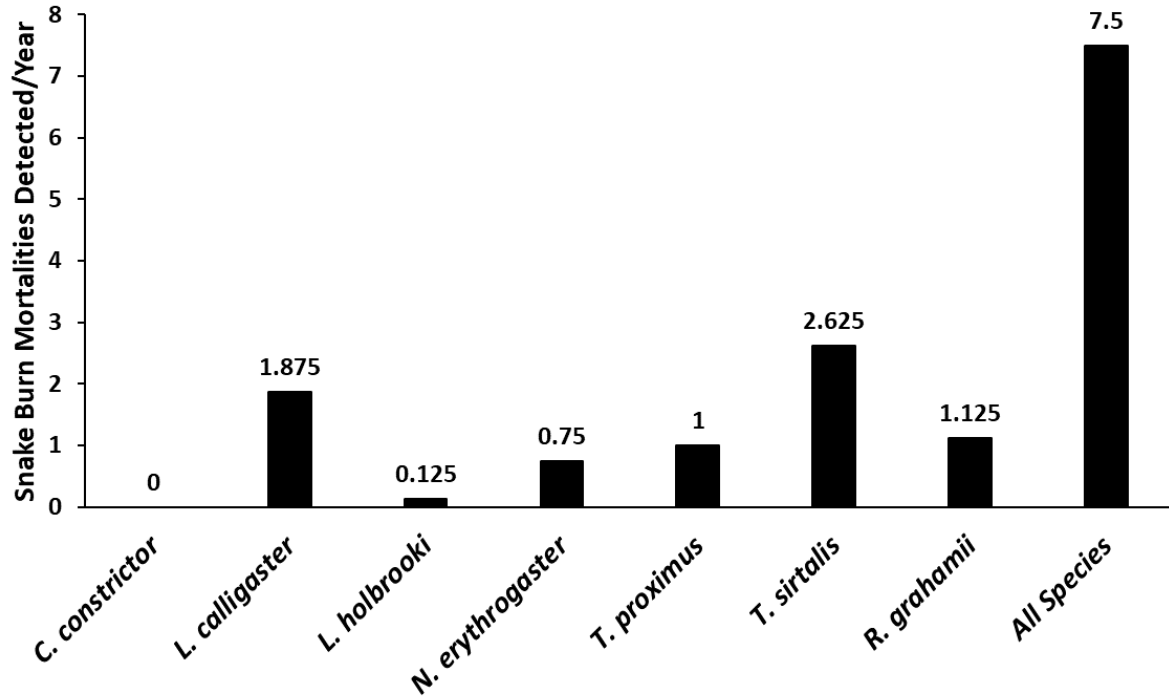


Figure 1. Average number of snake mortalities detected per year during visual surveys after annual prescribed burns at Woolsey Wet Prairie Sanctuary from 2015–2022.

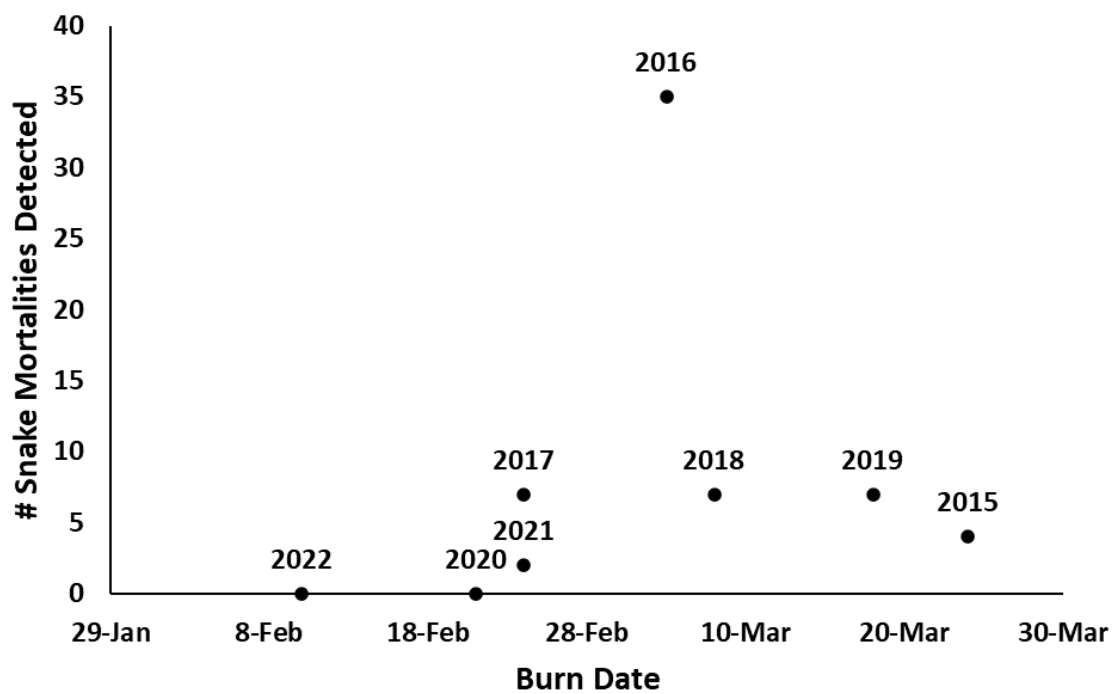


Figure 2. Number of snake mortalities detected during visual surveys after annual prescribed burns at Woolsey Wet Prairie Sanctuary from 2015–2022.

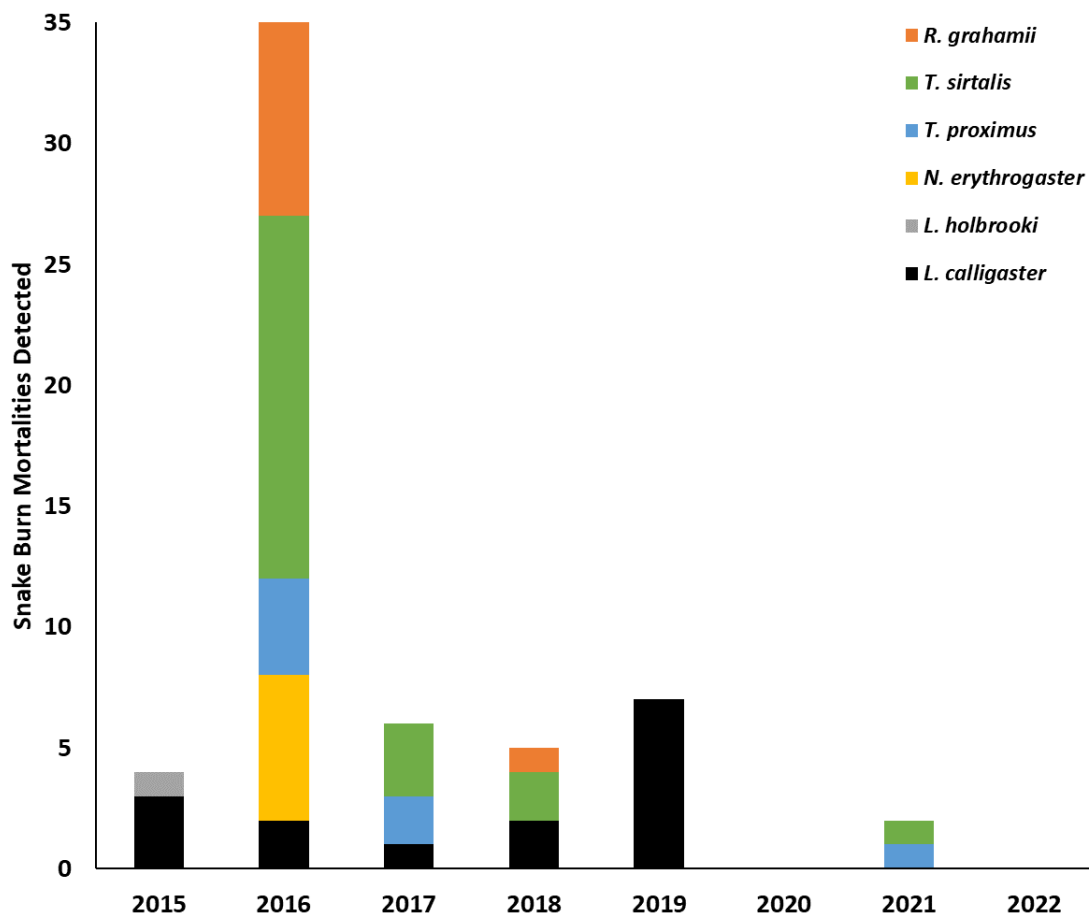


Figure 3. Species composition of snake burn mortalities detected by year at WWPS from 2015–2022. *Coluber constrictor* not included, as no mortalities were found.

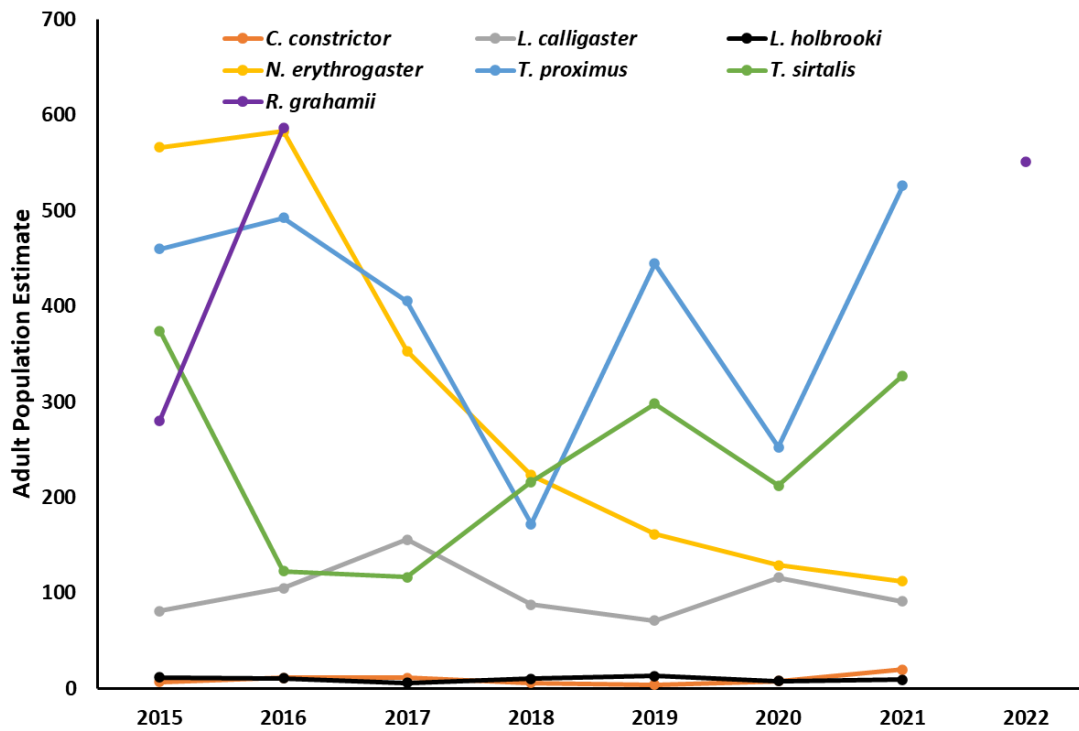


Figure 4. Annual mark-recapture adult population estimates for seven snake species from Woolsey Wet Prairie Sanctuary from 2015–2022.

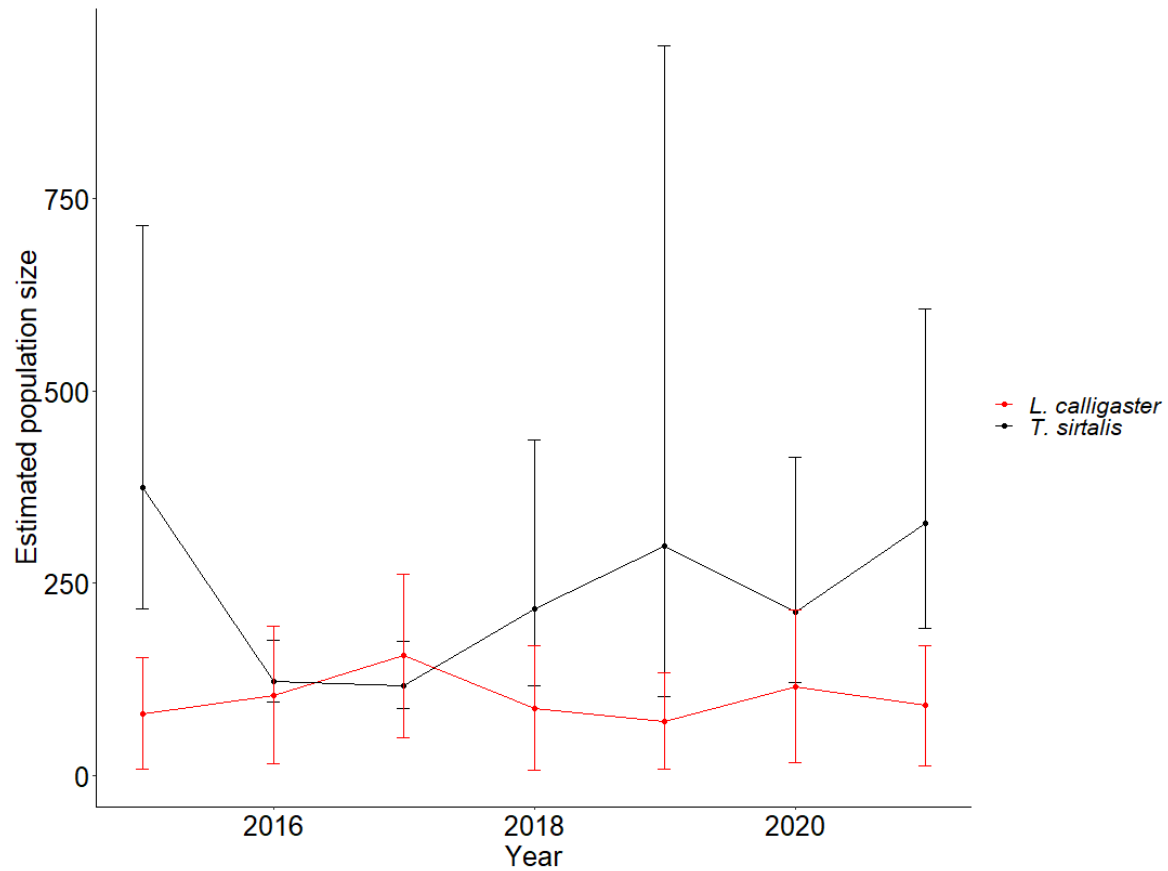


Figure 5. Annual mark-recapture adult population estimates for *Lampropeltis calligaster* and *Thamnophis sirtalis* from Woolsey Wet Prairie Sanctuary from 2015–2021. Error bars represent 95% confidence intervals.

IACUC Approval Forms



Office of Research Compliance

MEMORANDUM

TO: J.D. Willson

FROM: Craig N. Coon, Chairman
Institutional Animal Care
And Use Committee

DATE: May 8, 2013

SUBJECT: IACUC Protocol APPROVAL
Expiration date : **May 3, 2016**

The Institutional Animal Care and Use Committee (IACUC) has **APPROVED** Protocol #13041 - "Anthropogenic Impacts on Herpetofaunal Biodiversity in Arkansas". You may begin this study immediately.

The IACUC encourages you to make sure that you are also in compliance with other UAF committees such as Biosafety, Toxic Substances and/or Radiation Safety if your project has components that fall under their purview.

In granting its approval, the IACUC has approved only the protocol provided. Should there be any changes to the protocol during the research, please notify the IACUC in writing [via the Modification Request form] prior to initiating the changes. If the study period is expected to extend beyond **04-04-2016** you must submit a new protocol. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines for research involving animal subjects.

cnc/car

cc: Animal Welfare Veterinarian

Administration Building 210 • University of Arkansas • Fayetteville, AR 72701-1201 • 479-575-4572
Fax: 479-575-3846 • <http://vpred.uark.edu/199>
The University of Arkansas is an equal opportunity/affirmative action institution.



Office of Research Compliance

MEMORANDUM

TO: John David Willson
FROM: Craig N. Coon, Chairman
DATE: May 6, 2016
SUBJECT: IACUC Approval
Expiration Date: May 5, 2019

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # 16067 "Anthropogenic Impacts on Herpetofaunal Biodiversity in Arkansas"

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond May 5, 2019 you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/aem

cc: Animal Welfare Veterinarian



UNIVERSITY OF
ARKANSAS

Office of Research Compliance

To: John David Willson
Fr: Craig Coon
Date: April 8th, 2019
Subject: IACUC Approval
Expiration Date: April 4th, 2022

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol # **19074: Anthropogenic Impacts on Herpetofaunal Biodiversity in Arkansas**.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, please notify the IACUC in writing (via the Modification form) prior to initiating the changes. If the study period is expected to extend beyond April 4th, 2022, you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy the IACUC cannot approve a study for more than 3 years at a time.

The following individuals are approved to work on this study: JD Willson, Chelsea Kross, Ethan Royal, Meredith Swartwout, Mitchell Pruitt, Jennifer Mortensen, Brian Becker, Brett DeGregorio, Brett DeGregorio, and Bailey Singleton. Please submit personnel additions to this protocol via the modification form prior to their start of work.

The IACUC appreciates your cooperation in complying with University and Federal guidelines involving animal subjects.

CNC/tmp



UNIVERSITY OF ARKANSAS

Office of Research Compliance

To: J.D. Willson
From: Jeff Wolchok
Date: March 17, 2022
Subject: IACUC Approval
Expiration Date: March 16, 2025

The Institutional Animal Care and Use Committee (IACUC) has APPROVED your protocol #22019, *Anthropogenic Impacts on Herpetofaunal Biodiversity*.

In granting its approval, the IACUC has approved only the information provided. Should there be any further changes to the protocol during the research, you must notify the IACUC in writing (via the Modification form) and receive approval prior to initiating the changes. If the study period is expected to extend beyond the above expiration date, you must submit a newly drafted protocol prior to that date to avoid any interruption. By policy, the IACUC cannot approve a study for more than three years at a time.

The following individuals are approved to work on this study: J.D. Willson, Ethan Royal, Ethan Hollender, Elliot Lassiter, and Mitchell Pruitt. You must submit personnel additions to this protocol via the modification form prior to their starting work.

The IACUC appreciates your cooperation in complying with University and federal guidelines involving the care and use of animals.

JCW/rek

1424 W. Martin Luther King, Jr. • Fayetteville, AR 72701
Voice (479) 575-4572 • Fax (479) 575-6527

The University of Arkansas is an equal opportunity/affirmative action institution.

I, Dr. John D. Willson, certify that Ethan J. Royal completed the training as require by the Institutional Animal Care and Use Committee (IACUC) for work completed in Chapter 3.



7/21/2022

John D. Willson, Ph.D.

Date

Associate Professor

Department of Biological Sciences

Chapter 4

Quantifying detection probability to account for spatial and methodological variation: a case
study of squamate reptiles

Ethan J. Royal

and

John D. Willson

Abstract

Many reptile species currently lack adequate population data to generate meaningful distribution and abundance estimates, hindering our understanding of their ecologies and conservation statuses. Even species that are well represented in parts of the literature may have poorly understood population dynamics and distributions due to the low species detection probabilities that are a common feature of squamate reptiles. Variation in detection probability can be driven by sampling method, environmental conditions, habitat type, population density, individual observer, and presently unidentified latent sources. The failure to appropriately quantify detection probability can inappropriately influence estimates of occupancy, abundance, and covariate relationships. Thus, it is imperative that studies aim to explicitly quantify detection probabilities relevant to their specific system and research questions prior to extensive sampling. We present a case study demonstrating quantifiable differences in detection probabilities 1) within species between two regions in their ranges, 2) between two common reptile survey methods between regions and among species, and 3) among species within each region. We present the first rigorous comparison of species- and method-specific detection probabilities in different regions across their ranges. Finally, we highlight the risks of relying solely on the literature for study design and the importance of quantifying the scale of survey effort needed to produce meaningful inference related to occupancy and abundance via pilot studies prior to the implementation of large-scale field work.

Introduction

Globally, many reptile species are suffering severe, well documented population declines (Gibbons et al., 2000), yet thousands of species across many taxa lack sufficient data for assessment. These gaps in knowledge represent fundamental barriers to the effective

implementation of vital conservation actions (Tingley et al., 2016; Henrique De Oliveira Caetano et al., 2022), and they persist due to challenges, such as geopolitical conditions, regional research biases, rapid rates of species discovery and description, and small geographic range sizes (Tingley et al., 2016). For reptiles, a primary reason for the lack of sufficient data is their incredibly low detection rates (Kéry and Schmidt 2008; Durso et al., 2011; Royal et al., 2022). The ecological, behavioral, and physiological characteristics of reptiles that contribute to low detectability include nocturnal activity, cryptic color patterns, use of inaccessible habitats (i.e., subterranean, aquatic, arboreal, or densely vegetated), sedentary foraging behaviors, small home range sizes, and highly seasonal activity patterns (Mazerolle et al., 2007). Compounding these issues, detectability can vary among species within a site, among individuals within a population, and among populations within a species (Iknayan et al., 2014). Failure to account for imperfect detection resulting in the acceptance of false negatives (cases of non-detection when a species is truly present) can severely bias inferences of species occupancy, covariate effects on species distributions, and conservation status (Tyre et al., 2003; Gu and Swihart 2004; Ruiz-Gutiérrez and Zipkin 2011; Tingley and Beissinger 2013). Detection for squamate reptiles can be affected by abundance, environmental conditions, body size, and myriad factors related to survey method and individual observers (Kery 2002; Durso et al., 2011; Willson et al., 2011; Durso and Seigel 2015; Lardner et al., 2015; Rodda et al., 2015a). That detection is both an integral piece of understanding species' ecologies and subject to such a wide variety of influences highlights the need to rigorously quantify and account for detection processes in research efforts (Rodda et al., 2015b). Thus, the characteristics that alter detectability must be understood and accounted for when designing studies in order to collect meaningful data.

Researchers have long recognized variability in capture rates among sampling methods using analyses based on raw capture numbers or capture per unit effort metrics that do not account for detection probability (Ryan et al., 2002; Kuhnz et al., 2005; Bartman et al., 2016). Recent research has begun to investigate underlying variation in detection by explicitly comparing detection probabilities of complementary methods (Kyle et al., 2022). In studies targeting multiple squamate reptile species, employing a combination of common survey methods, including visual encounter surveys (VES) and checking artificial cover objects (ACOs), has often yielded the highest capture rates and species richness due variation in the effectiveness of given methods among species (Adams et al., 1999; Doan 2003; Hutchens et al., 2009; Michael et al., 2012; Carpio et al., 2015). While the use of multiple sampling methods can improve overall detection probability, it may not guide accurate inferences about occupancy or abundance due to differences in detection probability among habitat types. Furthermore, it is possible that detection probability and local densities are not necessarily linked (Nafus et al., 2015; Rodda et al., 2015a). In response to these difficulties, some have argued that estimation of detection probabilities is often not meaningful when detections are sparse, and thus recommend ignoring detection entirely (Welsh et al., 2013). However, this recommendation is only reasonable in extreme cases, as it ignores the complexities of abundance-detection relationships, confounds occupancy with detection, and decreases inferential power related to occupancy patterns (Guillera-Arroita et al., 2014). When faced with low detection probability and sparse data, the course of action should instead be to increase sampling effort and explicitly quantify detection probabilities across a range of methods and habitat types. This method allows researchers to implement optimal sampling strategies and thus generate meaningful estimates of occupancy and abundance (Steen 2010; Guillera-Arroita et

al., 2014). Unfortunately, little is known about how method-specific detection probabilities might vary for a species among different habitat types across its range.

As climate conditions and landcover types change across a species' range, their habitat requirements and associations are likely to change with it. For example, Chandler et al. (2021) suggested that eastern indigo snake (*Drymarchon couperi*) habitat associations shifted across their range due to interactive effects of climate and physical habitat structure. Furthermore, as the climatic, structural, and ecological conditions change across a species' range, behavioral differences can emerge. For example, a species' daily activity patterns, foraging behaviors, and microhabitat use may differ from one region to another due to a confluence of environmental and ecological factors (Bashey and Dunham 1997; Downes and Shine 1998). These observed variations in activity patterns and habitat use may alter detection probabilities in ways that likely vary by method. However, to our knowledge, there is no research that explicitly compares the species-specific detection probabilities of common squamate reptile survey methods (i.e., visual encounter surveys (VES) and artificial cover objects (ACOs)) among populations occupying different habitat types across their ranges.

Here, we investigated how detection probabilities of ten common squamate species vary between two common reptile sampling methods and between two open-canopy habitat types in distinct regions within the species' ranges. We leveraged datasets from two landscape-scale community occupancy studies targeting reptile assemblages in open-canopy pine forests in Northwest Louisiana (Royal et al., 2022) as well as remnant and restored tallgrass prairies and oak savannahs in Northwest Arkansas (Royal et al., *In Review*). These studies used identical sampling protocols for VES and ACO surveys, repeated surveys at each site, and featured overlapping species that were captured in both regions. Using hierarchical multi-species occupancy models

that account for imperfect and method-specific detection, we compared method-specific detection probabilities of four lizard species and six snake species to determine if VES and ACO surveys differ in effectiveness between regions. We had three predictions for these systems: 1) That detection probability would vary considerably by survey method (VES and ACO) within each region; 2) Using VES, snake and lizard detection probabilities would be significantly higher in Louisiana open-canopy pine forests; and 3) Snake and lizard detection probabilities would exhibit a positive relationship with increasing survey temperatures.

Methods

Herpetofaunal Surveys

We performed seven repeated rounds of paired surveys (VES and ACO) at 81 open-canopy pine forest sites in Louisiana during 2017–2019 (Royal et al., 2022/Chapter 1) and six rounds at 34 prairie sites in Northwest Arkansas during 2018–2019 (Royal et al., *In review*/Chapter 2). In both studies, we conducted surveys between Mar–Jul, during noted active seasons for our target species in each region. Each paired survey used in this analysis consisted of one person-hour of diurnal VES effort and an ACO check of five 122 x 81 x 1.3-cm plywood coverboards placed 10 m apart on transects located at least 30 m from site boundaries. We captured and identified all reptiles and amphibians encountered during these surveys, noted the relevant sampling method (VES or ACO), and released all captured animals at the end of each survey. We also measured air temperature (°C) at the start of each survey for use as a potential predictor of detection (Kestrel™ 2500; Kestrel, Boothwyn, PA, USA). Our sampling methods and study sites are further detailed in Royal et al., (2022)/Chapter 1 and Royal et al., *In Review*/Chapter 2.

Adapting our datasets for use in this analysis involved two primary steps. First, Arkansas prairie surveys originally included two person-hours of VES effort and ten coverboards for ACO checks. During these surveys, we noted if captures occurred during the first or second person-hour of VES effort, and we recorded the coverboard where each capture occurred, with coverboards numbered 1–10 at each site. Thus, to create a dataset comparable to our one person-hour VES, five ACO surveys from Louisiana, we filtered captures from the first person-hour of VES effort and only included ACO captures from five randomly selected coverboards at each site (coverboard numbers 3, 4, 6, 8, and 9) to generate an unbiased Arkansas prairie dataset. In total, Louisiana sampling consisted of seven paired rounds of VES and ACO checks at 81 sites and Arkansas sampling consisted of six paired rounds of VES and ACO checks at 34 sites. Second, we selected a suite of species that are found in both regions and are regularly targeted using VES and ACO surveys. This group consisted of four lizards and six snakes: six-lined racerunner (*Aspidoscelis sexlineatus*), common five-lined skink (*Plestiodon fasciatus*), prairie lizard (*Sceloporus consobrinus*), ground skink (*Sincella lateralis*), eastern racer (*Coluber constrictor*), prairie kingsnake (*Lampropeltis calligaster*), common kingsnake (*Lampropeltis getula*), western ratsnake (*Pantherophis obsoletus*), western ribbon snake (*Thamnophis proximus*), and common garter snake (*Thamnophis sirtalis*).

Statistical Analysis

We used multi-species hierarchical Bayesian occupancy models developed by Ribeiro et al., (2018) to explicitly examine method-specific detection probabilities for each species in each region, as well as method-specific overall detection probabilities of the species group in each region. These models are designed to evaluate relationships between site occupancy covariates (landscape characteristics, site management regimes, etc.) and target species, while also

accounting for imperfect detection using repeated surveys (Zipkin et al., 2009). Multi-species (or community) occupancy models also improve individual parameter estimates for rare species by considering them within the context of the larger group of ecologically similar species (Dorazio et al., 2006). Our models assumed static occupancy with no extinction or colonization over the study period, given the short duration of the studies relative to the lifespans of our focal taxa and the lack of intense management action likely to impact occupancy during the study period. We have used these models to investigate detection relationships, and thus do not explore occupancy patterns (but see Royal et al., 2022/Chapter 1 and Royal et al., *In Review*/Chapter 2 for studies addressing occupancy relationships in these systems).

We created a binary encounter matrix for each region, representing detection (1) or non-detection (0) for each species at each site during each survey. A binary latent state variable, $z_{i,j}$, indicated the presence of species i at site j if $z_{i,j} = 1$ and indicated absence if $z_{i,j} = 0$. The occupancy probability ($\Psi_{i,j}$) was then modeled as a Bernoulli random process, $z_{i,j} \sim \text{Bernoulli}(\Psi_{i,j})$. Species i could only be detected at site j during survey k ($y_{i,j,k} = 1$) conditional upon the occurrence of species i at site j ($z_{i,j} = 1$), and detection probability ($p_{i,j,k}$) was modeled as a Bernoulli random variable: $y_{i,j,k} | z_{i,j} \sim \text{Bernoulli}(z_{i,j} \cdot p_{i,j,k})$. We used a logit link function to estimate occupancy probability of each species at each site without the use of any occupancy covariates ($\Psi_{i,j}$):

$$\text{logit}(\Psi_{i,j}) = \alpha_{0i}$$

We also used a logit-link function to model method-specific (VES vs. ACO) detection probabilities for each species ($p_{i,j,k}$), and a detection covariate for survey temperature:

$$\text{logit}(p_{i,j,k}) = \beta_{0i, \text{SurveyType}} + \beta_{1i} * \text{Temperature}_{j,k}$$

Parameter $\beta_{0i, SurveyType}$, the detection intercept, represents the detection probability for each species specific to the survey method used (VES or ACO). We standardized the values for survey temperature to set means of zero and standard deviations equal to 1 before inclusion in the models to allow comparison of model coefficients as effect sizes (Zipkin et al., 2009). We used separate models with identical structures for lizards and snakes in the Arkansas (AR) and Louisiana (LA) datasets. Thus, we ran four separate models (AR lizards, AR snakes, LA lizards, LA snakes) that allowed comparison of method-specific detection probabilities for each species between the two regions.

We fit our occupancy models using JAGS version 4.3.0 (Plummer 2016) called through R (R Core Team 2021) and the package jagsUI version 1.5.2 (Kellner 2016). We used non-informative prior distributions for the community parameters and ran the models with three Markov chains with 100,000 iterations, 50,000 burn-in iterations, 10,000 iterations for the adaptive phase, and a thinning rate of 20. We then visually inspected the chains for convergence on each monitored parameter and statistically evaluated convergence using R-hat value thresholds of <1.1 .

Results

We recorded 57 VES captures and 12 ACO captures of our six target snake species in Louisiana, and 73 VES captures and 32 ACO captures of the target snake species in Arkansas. We recorded 1,512 VES captures and 123 ACO captures of the four target lizard species in Arkansas, and 132 VES and 33 ACO captures of the target lizard species in Louisiana (see Royal et al., 2022 for Louisiana capture details). When considering the full suite of species, VES detection was a more effective sampling method than ACO checks, resulting in higher detectability of lizards (mean VES detection: 0.12 and 0.38 in AR and LA, respectively; mean ACO detection: 0.06 and 0.06 in AR and LA, respectively) and snakes (mean VES detection: 0.07 and 0.03 in AR and LA,

respectively; mean ACO detection: 0.02 and 0.01 in AR and LA, respectively) in both Arkansas and Louisiana.

Method-specific detection probabilities varied widely by species, region, and survey method (Table 1), but were generally low (<0.1) with a few exceptions. Species-specific detection probabilities within each region (i.e. Arkansas ACO vs. VES detection probabilities) were higher for VES than for ACO sampling in all cases. For snakes, the differences in detection probability between VES and ACO sampling within region were generally small and 95% credible intervals (CIs) overlapped widely in most cases (Figs. 1, 2). For lizards, VES produced significantly higher detection probabilities (95% CIs not overlapping) in many cases, particularly in Louisiana sampling (Figs. 1, 2). When comparing the same sampling method between regions, ACO sampling was generally more effective for snakes in Arkansas than in Louisiana, although 95% CIs were widely overlapping (Fig 3). The inverse was true for lizards, as ACO sampling was more effective in Louisiana, albeit with widely overlapping 95% CIs in most cases (Fig. 3). Visual encounter surveys produced higher detection probabilities for snakes in Arkansas than for snakes in Louisiana, again with widely overlapping 95% CIs (Fig. 4). Lizards tended to be more detectable by VES in Louisiana than in Arkansas, with significant differences for *S. lateralis* and *S. consobrinus* and a notable difference in *A. sexlineatus* (Fig. 4).

Temperature did not have a significant influence on community detection probability in either region. The only significant (95% CIs not overlapping zero) species-specific responses were positive relationships between increasing temperature and detection for *A. sexlineatus* (95% CIs: 0.7–1.5) in Louisiana and *C. constrictor* in Arkansas (95% CIs: 0.2–1.2).

Discussion

In this study, we leveraged landscape-scale reptile community datasets from two distinct regions of the southeastern US to investigate how method- and species-specific detection probabilities might differ between regions. We documented significant differences in detection probabilities for multiple species between sampling methods within a region and within a sampling method between regions. Reptiles are notoriously difficult to detect, particularly in cases where the need for standardized sampling of multiple species precludes the use of highly specialized sampling methods for target species (Mazerolle et al., 2007). In such cases, researchers typically default to a combination of several general sampling methods that will ideally present an accurate representation of the underlying reptile community (Kuhnz et al., 2005; Dorcas and Willson 2009; Hutchens and DePerno 2009; Carpio et al., 2015). However, there are acknowledged gaps in our understanding of how detection probability produced by commonly employed methods may vary spatially and temporally (Mazerolle et al., 2007; Durso and Seigel 2015).

Our first hypothesis was supported, as we found that species-specific detection probability varied considerably between VES and ACOs within each region. Visual encounter surveys produced higher detection probabilities for all species when comparing VES vs. ACOs within both Arkansas and Louisiana (Figs. 1, 2), with significant differences for lizards in most cases. While VES and ACO detection probabilities for snakes had widely overlapping 95% CIs when comparing within regions, the differences in mean detection probabilities are notable and relevant to future study designs (Figs. 1, 2). For example, detection probabilities based on VES compared to ACOs were 8x higher for *P. obsoletus* in both Arkansas and Louisiana, 7.5x and 2.4x higher for *C. constrictor* in Arkansas and Louisiana, respectively, and 16.5x and 5.8x higher for *T. sirtalis* in Arkansas and Louisiana, respectively (Table 1). These are meaningful differences that could

improve detection probabilities, and therefore occupancy and abundance estimates, if considered in future research.

Species-specific detection probabilities from VES were generally higher in Louisiana for lizards, thus partially supporting our second hypothesis. Visual encounter survey detection probabilities were significantly higher in Louisiana compared to Arkansas for *S. consobrinus* (0.35 in LA vs. 0.04 in AR) and *S. lateralis* (0.67 in LA vs. 0.17 in AR). Although the differences were not significant and the 95% CIs overlapped, *A. sexlineatus* (0.19 in LA vs 0.07 in AR) and *P. fasciatus* (0.27 in LA vs. 0.16 in AR) followed the same trend. We believe that these trends are related to structural conditions that alter activity or visibility to observers. *Aspidoscelis sexlineatus* and *S. consobrinus* are both heliothermic, diurnally surface-active species that shuttle between microhabitats to balance thermoregulation, foraging, and other behaviors. *Scincella lateralis* is a diurnally surface-active species that primarily forages in the leaf litter. We believe that the movements of these small-bodied species are far more visible to observers in the bare soil and comparatively open groundcover found in open-canopy pine forests than in dense prairie vegetation. Lizard detection probabilities using ACOs were also generally higher in Louisiana, but there was considerable uncertainty, except for in *P. fasciatus*. The detection probabilities were higher in Louisiana for both methods, which suggests that higher population densities might be partially responsible for these differences. Relevant density estimates for these species are lacking in the literature, but *A. sexlineatus* and *S. consobrinus* exhibited lower occupancy in Arkansas than Louisiana (Royal et al., 2022 for LA and unpublished data for AR). A pattern exhibiting decreasing detection with decreasing abundance would be consistent with observed relationships among detection, occupancy, and abundance documented in other studies (Gaston et al., 2000; Kéry 2002; Kéry and Royle 2020). However, these relationships are not always predictable and the role of

habitat conditions in shaping detection regardless of density should not be ignored (Nafus et al., 2015; Boback et al. 2020).

In contrast to VES detection probabilities for lizards, VES detection probabilities for snakes were higher in Arkansas than Louisiana, although detection probabilities for snakes were uniformly low (≤ 0.10 in all cases) and featured wide 95% CIs (Table 1). Detection probabilities for snakes using ACOs were also higher in Arkansas than in Louisiana and, as seen in within-region comparisons, the proportional differences in detection probabilities of snakes between ACOs in Arkansas versus Louisiana and VES in Arkansas versus Louisiana were considerable. ACO surveys in Arkansas produced detection probabilities 7.7x higher for *C. constrictor*, 3.3x higher for *L. calligaster*, 28.5x higher for *L. holbrooki*, 3.5x higher for *T. proximus*, and 6.5x higher for *T. sirtalis* than those seen in Louisiana. Similarly, VES detection probabilities in Arkansas were 2.4x higher for *C. constrictor*, 3.7x higher for *P. obsoletus*, and 2.3x higher for *T. sirtalis* than those seen in Louisiana VES. Given that denser vegetative groundcover in Arkansas should theoretically make visual detections more difficult and that snake detection probabilities for both methods were higher in Arkansas, we believe that regional differences in snake detection probabilities are likely due to higher densities in Arkansas. We documented lower occupancy probabilities for each of the six snake species in Louisiana than in Arkansas (Royal et al., 2022 for LA and unpublished data for AR), consistent with previously reported detection-occupancy-abundance relationships (Gaston et al., 2000; Kery 2002). Additionally, four of our target species (*C. constrictor*, *L. calligaster*, *L. holbrooki*, and *P. obsoletus*) are vulnerable to nest predation by invasive red imported fire ants (RIFA; *Solenopsis invicta*; Swartwout and Willson 2022), and *L. holbrooki* has experienced significant population declines in many parts of the southeast where RIFA are common (Swartwout 2021). We observed RIFA nests during surveys at nearly all of our

Louisiana sites, including under ACOs, while they were relatively rare in Arkansas prairie sites (pers. obs.). Declines due to RIFA invasion, along with naturally lower occupancy in open-canopy pine forests relative to other habitat types (Steen et al., 2012), could be driving the detection disparities documented between regions. Alternatively, the open groundcover conditions found in open-canopy pine forest sites might lead to reduced surface activity during the day when surveys occur, and snakes in this habitat type might be more reliant on subterranean or arboreal microhabitats.

We have explicitly identified disparities in detection probabilities using widespread survey methods for a group of common reptiles that could have significant implications for efforts attempting to describe distributions and reptile community composition. Our results suggest that there are considerable regional differences in the species-specific efficacies of widely used herpetofaunal sampling methods. Many herpetofaunal studies design sampling procedures based on literature from disparate parts of species' ranges and subsequently encounter challenges related to low detection probabilities. We suggest that the regional variation in detection probabilities we document here illustrates the limitations of relying on literature from disparate portions of species' ranges, and we emphasize the need to quantify those local detection parameters through pilot studies. Additionally, our study echoes previous calls to quantify the scale of survey effort necessary to supply adequate data before implementing landscape-scale monitoring projects (Steen 2010; Guillera-Aroita et al., 2014). We relied upon relatively low survey effort for both methods, particularly for ACO checks, in which we used only five coverboards. In cases where ACO checks of five coverboards produced detection probabilities of only 0.05, scaling effort up to include 30 coverboards would likely produce detection probabilities approaching 0.3, resulting in a much richer dataset. Understanding issues of effort beforehand via pilot studies will allow much richer

and reliable inferences related to occupancy and abundance at the project's completion. Our study represents an important step in the explicit quantification of detection probability and lays the groundwork for future projects to meaningfully account for patterns of variability in species-specific and regional detection.

Acknowledgements

We would like to again thank all those who contributed to the field work that produced the data used in this manuscript, and who were listed in the Acknowledgments of Chapters 1 and 2. We thank Lauren Maynard for helpful comments on early drafts of the manuscript.

Literature Cited

- Adams, M. J., S. D. West, and L. Kalmbach. 1999. Amphibian and Reptile Surveys of U.S. Navy Lands on the Kitsap and Toandos Peninsulas, Washington. *Northwestern Naturalist* 80:1–7.
- Balouch, S., D. A. Driscoll, A. Naseer, M. Rais, and T. S. Doherty. 2022. Impacts of land cover on reptile movement and habitat use in farming landscapes. *Animal Conservation*.
- Bartman, J. F., N. Kudla, D. R. Bradke, S. Otieno, and J. A. Moore. 2016. Work Smarter, Not Harder: Comparison of Visual and Trap Survey Methods for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*).
- Bashey, F., and A. E. Dunham. 1997. Elevational variation in the thermal constraints on and microhabitat preferences of the greater earless lizard *Cophosaurus texanus*. *Copeia* 725–737.
- Boback, S. M., M. G. Nafus, A. A. Yackel Adams, and R. N. Reed. 2020. Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. *Ecosphere* 11:e03000.
- Carpio, A. J., M. Cabrera, and F. S. Tortosa. 2015. Evaluation of methods for estimating species richness and abundance of reptiles in olive groves. *Herpetological Conservation and Biology* 10:54–63.
- Doan, T. M. 2003. Which Methods Are Most Effective for Surveying Rain Forest Herpetofauna? Reptile Database View project Global Assessment of Reptile Distributions. *Journal of Herpetology* 37:72–81.
- Dorazio, R. M., J. A. Royle, B. O. Soderstrom, S. Soderstro, S. Soderstrom, A. Glimska'r, and G. Glimska'r. 2006. Estimating Species Richness and Accumulation by Modeling Species Occurrence and Detectability. *Ecology* 87:842–854.
- Dorcas, Michael E. and Willson, J. D. 2009. Snakes: Ecology and Conservation. Eds. S. J. Mullin and R. A. Seigel. Comstock Publishing Associates.

- Durso, A. M., and R. A. Seigel. 2015. A Snake in the Hand is Worth 10,000 in the Bush. *Journal of Herpetology* 49(4):503-506.
- Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. *Journal of Applied Ecology* 37:39–59.
- Gibbons, J.W., D.E. Scott, A.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The Global Decline of Reptiles, Déjà Vu Amphibians. *BioScience* 50(8):653-666.
- Gu, W., and R.K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation* 116:195–203.
- Guillera-Aroita, G., J.J. Lahoz-Monfort, D.I. MacKenzie, B.A. Wintle, and M.A. McCarthy. 2014. Ignoring Imperfect Detection in Biological Surveys Is Dangerous: A Response to ‘Fitting and Interpreting Occupancy Models’. *PLOS ONE* 9:e99571.
- Henrique De Oliveira Caetano, G., D.G. Chapple, R. Grenyer, T. Raz, J. Rosenblatt, R. Tingley, M. Böhm, S. Meiri, and U. Rollid. 2022. Automated assessment reveals that the extinction risk of reptiles is widely underestimated across space and phylogeny. P. Jordano, editor. *PLOS Biology* 20:e3001544.
- Hutchens, S.J., Deperno, and Christopher S. 2009. Efficacy of Sampling Techniques for Determining Species Richness Estimates of Reptiles and Amphibians.
- Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2014. Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology & Evolution* 29:97–106.
- Jones, K. B., and W. G. Whitford. 1989. Feeding Behavior of Free-Roaming *Masticophis flagellum*: An Efficient Ambush Predator. *The Southwestern Naturalist* 34:460.
- Kellner, K. 2016. jagsUI: A Wrapper Around rjags to Streamline JAGS Analyses. R package version 1.4.4.
- Kéry, M. 2002. Inferring the Absence of a Species: A Case Study of Snakes. *The Journal of Wildlife Management* 66:330.
- Kéry, M., and J. Royle. 2020. *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced*.
- Kéry, M., and B. R. Schmidt. 2008. Imperfect detection and its consequences for monitoring for conservation. *Community Ecology* 9:207–216.
- Kuhnz, L. A., R. K. Burton, P. N. Slattery, Oakden, and James M. 2005. Microhabitats and Population Densities of California Legless Lizards, with Comments on Effectiveness of Various Techniques for Estimating Numbers of Fossorial Reptiles. Source: *Journal of Herpetology* 39:395–402.

- Kyle, K. E., M. C. Allen, J. Dragon, J. F. Bunnell, H. K. Reinert, R. Zappalorti, B. D. Jaffe, J. C. Angle, and J. L. Lockwood. n.d. Combining surface and soil environmental DNA with artificial cover objects to improve terrestrial reptile survey detection. *Conservation Biology*.
- Lardner, B., G. H. Rodda, A. A. Y. Adams, J. A. Savidge, and R. N. Reed. 2015. Detection Rates of Geckos in Visual Surveys: Turning Confounding Variables into Useful Knowledge. *Journal of Herpetology* 49:522–532.
- Mazerolle, M. J., L. L. Bailey, W. L. Kendall, J. A. Royle, S. J. Converse, and J. D. Nichols. 2007. Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies. <https://doi.org/10.1670/07-061.1> 41:672–689.
- Michael, D. R., R. B. Cunningham, C. F. Donnelly, D. B. Lindenmayer, D. R. Michael, R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 2012. Comparative use of active searches and artificial refuges to survey reptiles in temperate eucalypt woodlands. *Wildlife Research* 39:149–162.
- Nafus, Melia G, Amy A Yackel Adams, Page E Klug, Gordon H Rodda, M G Nafus, A A Yackel Adams, P E Klug, and G H Rodda. 2015. Habitat type and structure affect trap capture success of an invasive snake across variable densities. *Ecosphere* 9(8):e02339.
- Plummer, M. 2016. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vienna, Austria.
- Ribeiro, J. W., T. Siqueira, G. L. Brejão, and E. F. Zipkin. 2018. Effects of agriculture and topography on tropical amphibian species and communities. *Ecological Applications* 28:1554–1564.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rodda, G. H., A. A. Y. Adams, E. W. Campbell, and T. H. Fritts. 2015*a*. General Herpetological Collecting is Size-Biased for Five Pacific Lizards. *Journal of Herpetology* 49:507–512.
- Rodda, G. H., K. Dean-Bradley, E. W. Campbell, T. H. Fritts, B. Lardner, A. A. Y. Adams, and R. N. Reed. 2015*b*. Stability of Detectability over 17 Years at a Single Site and other Lizard Detection Comparisons from Guam. *Journal of Herpetology* 49:513–521.
- Royal, E. J., D. U. Greene, D. A. Miller, and J. D. Willson. 2022. Influence of landscape and vegetation characteristics on herpetofaunal assemblages in Gulf Coastal Plain pine forests. *The Journal of Wildlife Management* 86:e22199.
- Ruiz-Gutiérrez, V., and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. *Ecosphere* 2:1–14.
- Ryan, T. J., T. Philippi, Y. A. Leiden, M. E. Dorcas, T. B. Wigley, and J. W. Gibbons. 2002. Monitoring herpetofauna in a managed forest landscape: effects of habitat types and census techniques. *Forest Ecology and Management* 167:83–90.

- Shine, R. 1987. Intraspecific variation in thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porphyriacus* (Elapidae). *Journal of Herpetology* 21:165–177.
- Steen, D. A. 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation and Biology* 5:183–188.
- Steen, D. A., C. J. W. McClure, J. C. Brock, D. C. Rudolph, J. B. Pierce, J. R. Lee, W. J. Humphries, B. B. Gregory, W. B. Sutton, L. L. Smith, D. L. Baxley, D. J. Stevenson, and C. Guyer. 2012. Landscape-level influences of terrestrial snake occupancy within the southeastern United States. *Ecological Applications* 22:1084–1097.
- Swartwout, M. 2021. The Role of Reptile-Invertebrate Interactions in Enigmatic Reptile Declines. Dissertation, University of Arkansas, Fayetteville, AR.
- Swartwout, M. C., and J. D. Willson. 2022. Southeastern US Snake Species are Vulnerable to Egg Predation by Red Imported Fire Ants (*Solenopsis invicta*). *Herpetologica* 78:139-144.
- Tingley, M. W., and S. R. Beissinger. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology* 94:598–609.
- Tingley, R., S. Meiri, and D. G. Chapple. 2016. Addressing knowledge gaps in reptile conservation. *Biological Conservation* 204:1–5.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving Precision and Reducing Bias in Biological Surveys: Estimating False-Negative Error Rates. *Ecological Applications* 13:1790–1801.
- Welsh, A. H., D. B. Lindenmayer, and C. F. Donnelly. 2013. Fitting and Interpreting Occupancy Models. *PLOS ONE* 8:e52015.
- Willson, J. D., C. T. Winne, and B. D. Todd. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. *The Journal of Wildlife Management* 75:36–45.
- Zipkin, E. F., A. Dewan, and J. Andrew Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology* 46:815–822.

Tables

Table 1. Summary of species-specific detection probabilities for ACO and VES surveys in Arkansas and Louisiana from 2017-2019.

Species	ACO Mean Detection (95% CI)		VES Mean Detection (95% CI)	
	Arkansas	Louisiana	Arkansas	Louisiana
<i>A. sexlineatus</i>	0.01 (0.00 - 0.03)	0.01 (0.00 - 0.02)	0.08 (0.04 - 0.16)	0.19 (0.13 - 0.26)
<i>P. fasciatus</i>	0.01 (0.00 - 0.02)	0.04 (0.02 - 0.06)	0.17 (0.10 - 0.32)	0.28 (0.23 - 0.33)
<i>S. consobrinus</i>	0.00 (0.00 - 0.02)	0.03 (0.01 - 0.04)	0.05 (0.01 - 0.15)	0.36 (0.31 - 0.41)
<i>S. lateralis</i>	0.09 (0.05 - 0.14)	0.12 (0.09 - 0.14)	0.18 (0.12 - 0.26)	0.68 (0.64 - 0.72)
<i>C. constrictor</i>	0.03 (0.01 - 0.06)	0.004 (0.00 - 0.02)	0.07 (0.05 - 0.12)	0.03 (0.01 - 0.09)
<i>L. calligaster</i>	0.03 (0.01 - 0.07)	0.01 (0.00 - 0.03)	0.06 (0.03 - 0.12)	0.04 (0.02 - 0.09)
<i>L. holbrooki</i>	0.06 (0.03 - 0.12)	0.002 (0.00 - 0.02)	0.06 (0.03 - 0.11)	0.03 (0.01 - 0.09)
<i>P. obsoletus</i>	0.01 (0.00 - 0.04)	0.003 (0.00 - 0.02)	0.10 (0.06 - 0.17)	0.03 (0.00 - 0.09)
<i>T. proximus</i>	0.02 (0.01 - 0.06)	0.01 (0.00 - 0.02)	0.06 (0.03 - 0.13)	0.04 (0.01 - 0.09)
<i>T. sirtalis</i>	0.01 (0.00 - 0.04)	0.002 (0.00 - 0.01)	0.08 (0.04 - 0.14)	0.03 (0.01 - 0.09)

Figures

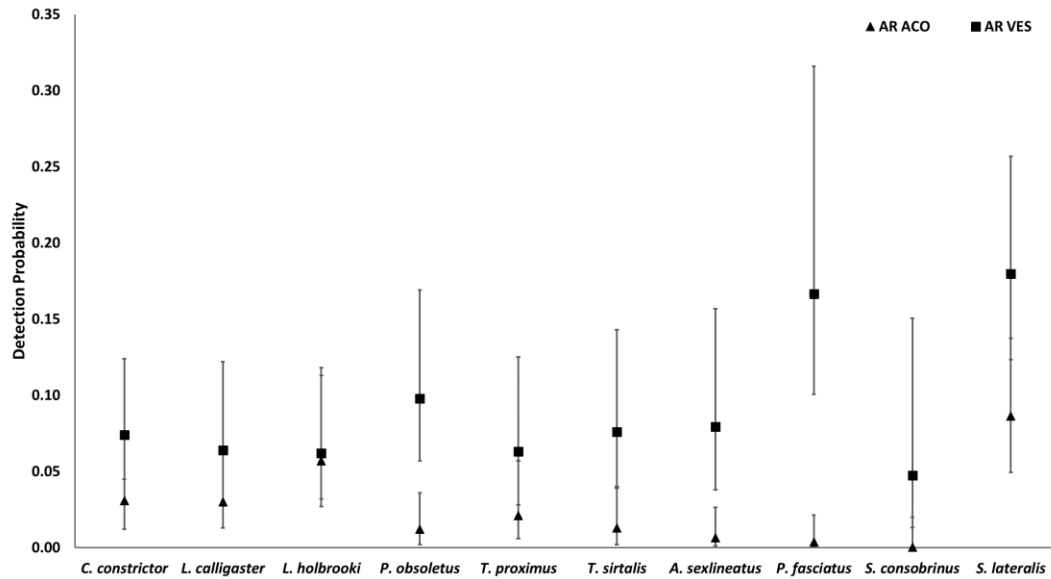


Figure 1. Mean species-specific detection probabilities for ACO and VES sampling in Arkansas prairie sites from 2017–2019. Bars represent 95% credible intervals.

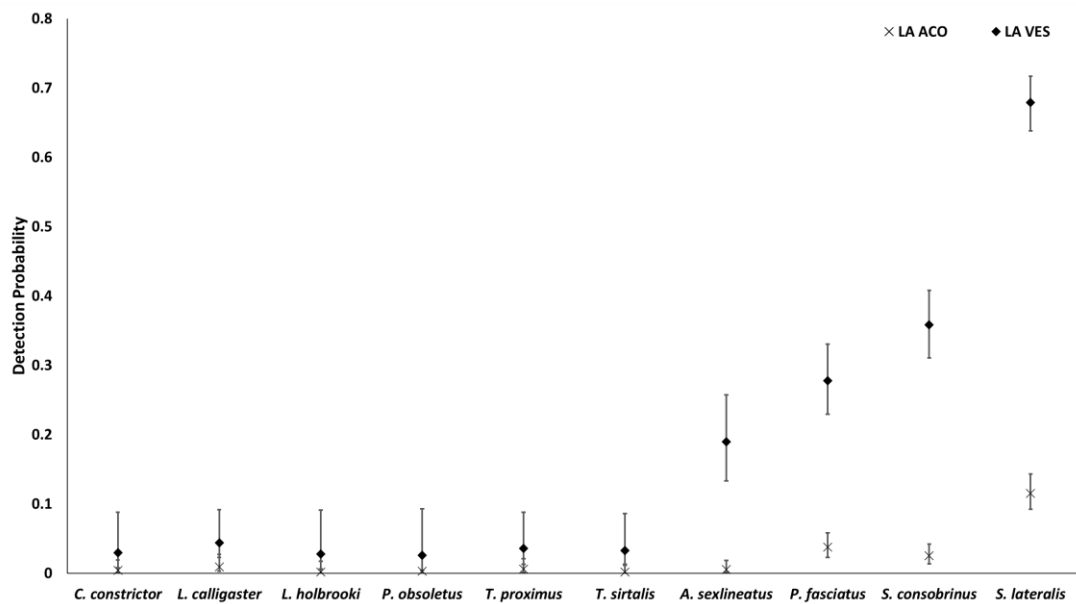


Figure 2. Mean species-specific detection probabilities for ACO and VES sampling in Louisiana open-canopy pine forest sites from 2017–2019. Bars represent 95% credible intervals.

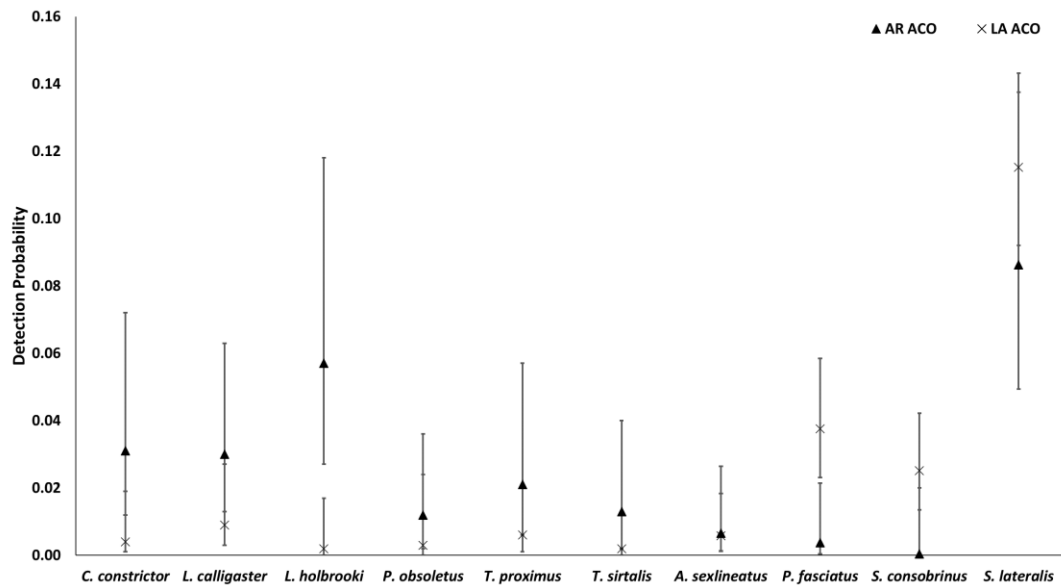


Figure 3. Mean species-specific detection probabilities for ACO sampling in Arkansas prairies and Louisiana open-canopy pine forest sites from 2017–2019. Bars represent 95% credible intervals.

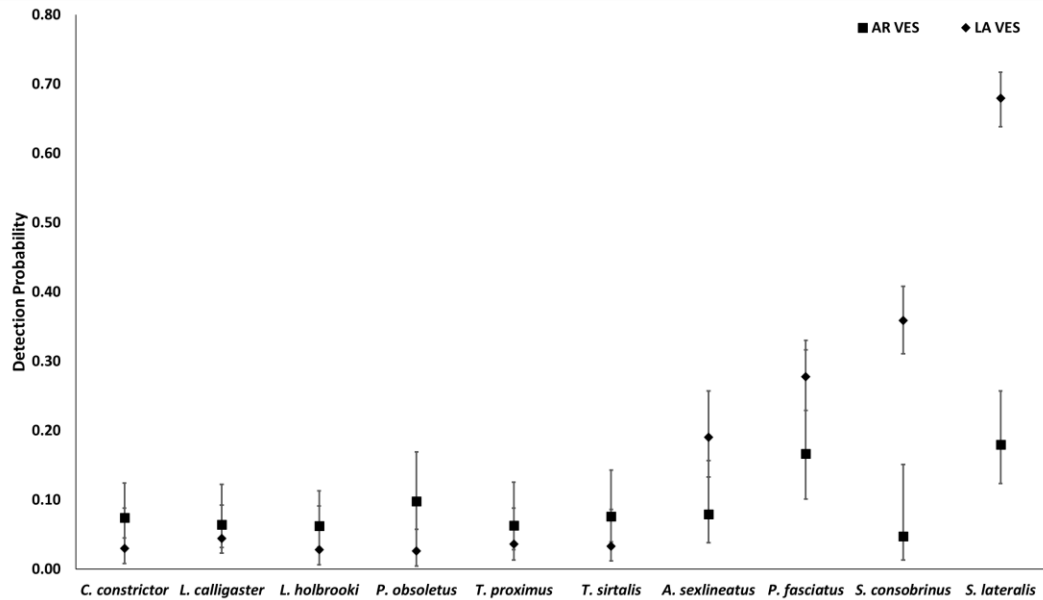


Figure 4. Mean species-specific detection probabilities for VES sampling in Arkansas prairies and Louisiana open-canopy pine forest sites from 2017–2019. Bars represent 95% credible intervals.

Conclusions

Habitat loss has resulted in declines for open-canopy-associated herpetofauna in many regions (Gibbons et al. 2000). However, significant knowledge gaps exist related to current distributions, habitat associations, and management effects. In this dissertation, I have addressed research gaps specific to herpetofauna associated with open-canopy pine savanna in the western Coastal Plain and with tallgrass prairie in the eastern edge of its range. I have also presented novel research related to the effects of prescribed burn mortality on a snake community in a fire-maintained prairie and highlighted the importance of rigorously quantifying the detection process for researchers attempting to assess the conservation status of difficult to detect herpetofauna.

In **Chapter 1**, we used repeated field surveys and hierarchical community occupancy models to examine the relationships among herpetofaunal community species richness, community and species-specific occupancy, and a suite of management, vegetation, and landscape covariates. We hypothesized that dominant overstory species (loblolly vs. longleaf) would not affect species richness or occupancy of open-pine-associated herpetofauna, and that open-pine-associated species occupancy would be highest at sites with sandy soils and open-canopy vegetation structure. We performed 7 rounds of surveys at 81 sites covering a range of management regimes, landscape characteristics, and vegetation conditions. We found that open-canopy-associated species richness and occupancy had positive relationships with open structural conditions in the canopy and understory, as well as with the presence of sandy soils. Sites with closed canopy conditions still harbored diverse herpetofaunal communities, suggesting that although they are not ideal for open-pine-associated species, they still provide significant value to regional diversity. We believe these results can be used to guide management practices that

balance the goals of working pine forests with conservation and provide valuable habitat for imperiled open-pine-associated herpetofauna.

In **Chapter 2**, we examined the status, habitat associations, and land-use and landscape characteristics that influence the distribution of another group of imperiled, open-canopy-associated herpetofauna, this time in the tallgrass prairies of Western Arkansas. We focused our efforts on an assemblage of nine prairie-associated species and hypothesized that community and species occupancy would be positively influenced by the presence of prairie mounds (indicating a lack of intense anthropogenic disturbance in a site), historic prairie area, and current open-canopy and herbaceous groundcover vegetation conditions. We performed 6 rounds of surveys at 34 sites and used hierarchical community occupancy models to examine occupancy-covariate relationships. Prairie mound density had a strong positive relationship with occupancy at both the community and species-specific levels, historic prairie area had a significant positive relationship with some species-specific occupancy probabilities, and current vegetation conditions showed no strong influence on occupancy at either level. We suggest that these species' current distributions are driven by historic land-use rather than current conditions, with sites that have experienced intense disturbance in the past having lost species with little chance of recolonization. Species appear to be able to persist in sites that have been spared intense disturbance, even in landscapes that are highly fragmented and contain only small prairie patches. Our findings can guide future conservation and management activities by providing tools to rapidly assess site potential and guide exploratory survey efforts.

In **Chapter 3**, we used a long-term population and burn mortality monitoring program at a restored prairie site to investigate the direct effects of prescribed burn management on a snake community. We used repeated mark-recapture field survey and post-burn mortality surveys

conducted over an eight-year period to quantify direct burn mortality and track long-term population trends for seven snake species. Mark-recapture population estimates suggest that snake populations are relatively stable and are not suffering apparent declines due to burn mortality. However, we did document burn mortality for six species, with instances of 4-8% of a species' estimated adult population being killed in a single burn. We highlight cases of temporary population dips following these mortality events and identify detectability issues clouding our understanding of true mortality rates. We also discuss annual variation in burn mortality patterns related to burn seasonality and local environmental conditions at the time of the burn that could be used to guide management planning to minimize mortality.

In **Chapter 4**, we use data collected in **Chapters 1** and **2** to describe cases of variation in detection probability that can skew our understanding of species distributions and obfuscate inferences related to habitat associations and conservation status. We used a hierarchical community occupancy model structure that explicitly quantifies species- and method-specific detection probabilities, and we examine detection probability variation among and within ten species of squamate reptiles using two common survey methods and from two distinct portions of their ranges: tallgrass prairies in Western Arkansas and open-canopy pine savannas in Northwest Louisiana. We demonstrated that detection probabilities of squamate reptiles can vary considerably via combinations of species-, method-, and region-specific patterns. While these findings are specific to a group of ten species using two survey types in two regions, they highlight the important differences in detection probabilities produced in different scenarios. In order to account for these differences, researchers should explicitly quantify local and species-specific detection parameters using pilot studies before implementing large-scale survey efforts. Overreliance on established methods from other systems and failure to incorporate study-specific

understanding of detection processes invites inaccurate interpretation of the occupancy, abundance, and habitat association patterns that are vital to effective conservation efforts.

This dissertation yields significant insight into the conservation statuses, occupancy patterns, and habitat associations for two assemblages of open-canopy-associated herpetofauna in heavily disturbed, dynamic landscapes. We provide management tools and guidance in both cases that will hopefully inform successful conservation action moving forward. We also investigate more specific challenges to herpetofauna conservation by documenting direct effects of prescribed fire management on snake populations and explicitly quantifying oft-ignored sources of variation in detection probability. We believe that the totality of this work contributes significantly to the conservation of imperiled, open-canopy-associated herpetofauna.

Literature Cited

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653-666.