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Overwintering Habitat Selection of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) in the Longleaf Pine Ecosystem

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Abstract.—**The Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) is currently under review for listing as Threatened under the U.S. Endangered Species Act. A more thorough understanding of its year-round ecology is necessary to recover populations. Overwintering ecology is poorly understood, but underground refugia are thought to be an important winter habitat requirement. Therefore, we radio-tracked 14 Eastern Diamondback Rattlesnakes from October 2018 to February 2019 in a Longleaf Pine (*Pinus palustris*) dominated landscape in southwest Georgia, USA, to investigate overwinter habitat and refugium selection. Within home ranges, snakes used Eastern Woodrat (*Neotoma floridana*) burrows (proportion of snakes that selected for this refugium: 0.50, proportion of refugia available per hectare: 0.02, $P = 1.0$), Nine-banded Armadillo (*Dasypus novemcinctus*) burrows (0.36, 0.11, $P = 0.42$), and stump holes (0.29, 0.11, $P = 0.18$) in proportion to availability. Eastern Diamondback Rattlesnake use of Gopher Tortoise (*Gopherus polyphemus*) burrows approached statistical significance for selection (0.79, 0.23, $P = 0.057$), while snakes avoided tip-ups (0.14, 0.09, $P = 0.013$) and large down woody debris (0.00, 0.45, $P < 0.001$). Snakes used all land cover types in proportion to availability except closed-canopy hardwood forests and non-forested land cover types (agricultural fields and wetlands), which were avoided. Poorly drained soils were avoided but all other soil classes were used in proportion to availability. Management to provide overwintering habitat for Eastern Diamondback Rattlesnakes should focus on maintaining open-canopy upland forests on well-drained soils with a range of refugium types. If Gopher Tortoise or other animal burrows are not present, retention of pine stumps or limits on their harvest should be considered.**

Key Words.—ecology; home range; management; radio-telemetry; snake; underground refugia

Introduction

Microhabitats are vital to the ability of terrestrial vertebrates to cope with changing environmental conditions and meet basic life-history needs (Whiles and Grubaugh 1996; Farallo and Miles 2016; Liang et al. 2017). For some vertebrates living in temperate ecosystems, microhabitats that provide thermal refuge during winter (hereafter refugia) are important for survival (Balogová et al. 2017). Some animals create their own thermal shelters in the form of burrows, whereas others rely on burrows of other species or other naturally occurring refugia. Ensuring presence of suitable refugia across the landscape may be an important management objective for refugium-dependent species.

The Eastern Diamondback Rattlesnake (*Crotalus adamanteus*; hereafter Eastern Diamondback; Fig. 1) is a large-bodied pit viper native to the Coastal Plain of the southeastern U.S. that has experienced significant population declines throughout its range (Martin and Means 2000; Means 2017). It is currently under review for listing by the U.S. Fish and Wildlife Service under the Endangered Species Act (U.S. Fish and Wildlife Service 2012). The Eastern Diamondback is associated with open-canopy habitats, which included Longleaf Pine (*Pinus palustris*) forest across much of its historical range (Martin and Means 2000). Waldron et al. (2008) described the Eastern Diamondback as a remnant species of the once widespread Longleaf Pine savanna, highlighting the importance of open habitats for the conservation of this species. Recent studies investigating habitat use in areas of pine forests have documented selection of these open-canopy habitats (Waldron et al. 2006, 2008; Hoss et al. 2010). Additionally, Waldron et al. (2006) found that Eastern Diamondbacks avoided closed-canopy pine plantations and Hoss et al. (2010) found a negative association with agricultural areas. Hoss et al. (2010) additionally found that Eastern Diamondbacks selected home ranges with high habitat heterogeneity, potentially because snakes selected the smallest possible home ranges that still provided access to all critical resources, including refugia.

Most studies on Eastern Diamondbacks have largely focused on home ranges or within home range habitat

Figure 1. A telemetered Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) coiled in a Nine-banded Armadillo (*Dasypus novemcinctus*) burrow, September 2018, in Baker County, Georgia, USA. (Photographed by Chris Murphy).

selection to inform management decisions (Martin and Means 2000; Hoss et al. 2010) and little information exists on selection of habitat features such as winter refugia. However, use of Gopher Tortoise (*Gopherus polyphemus*) burrows by Eastern Diamondbacks is well-documented (Means and Grow 1985; Timmerman 1995; Means 2005, 2017; Smith et al. 2017). Gopher Tortoises have declined across their range (Tuberville et al. 2009), however, and could be absent in areas where they were once sympatric with Eastern Diamondbacks. Means (2017) also documented use of and site fidelity to stump holes and stressed their potential importance as refugia for Eastern Diamondbacks. Since colonization of Nine-banded Armadillos (*Dasypus novemcinctus*; hereafter Armadillo) in the southeastern U.S., studies also have documented Eastern Diamondbacks using Armadillo burrows as refugia (Timmerman 1995; Means 2017; Smith et al. 2017).

Additional studies are needed to better understand Eastern Diamondback overwintering ecology and habitat requirements. Previous studies documenting refugium use provide insight into refugia used, but no studies have quantified refugium selection relative to availability. Additionally, no studies have specifically investigated habitat use and home range size during winter. To address these knowledge gaps, our objective was to investigate Eastern Diamondback overwinter refugium and habitat selection in a Longleaf Pine-dominated landscape.

Materials and Methods

Study site.—We conducted this study on Ichauway, the 11,800-ha research site of the Jones Center located in Baker County, Georgia, USA. The site is dominated by Longleaf Pine savanna with a Wiregrass (*Aristida beyrichiana*) understory that occurs predominantly on sandy and loamy sand soils. Most of the Longleaf Pine forest at Ichauway is naturally regenerated second growth with trees approaching 100 y old. Additional land cover types include Mixed Pine Hardwood Forests, Bottomland Hardwood Forests, shrub/scrub, and forested and unforested isolated seasonal wetlands. Ichauway is managed for Northern Bobwhite (*Colinus virginianus*) populations and approximately 2% of the property is maintained as wildlife openings. Prescribed fire is applied on a 2-y rotation as the primary forest management tool across the site. During late fall and winter (October-February; the time frame of this study), Ichauway experiences mean daily highs of 21° C (range, 0°–38° C) and mean daily lows of 7° C (range, 10°–24° C) with annual rainfall averaging 48 cm (range 26–76 cm; data from 2000–2019; http://www.georgiaweather.net/). Southwest Georgia lies roughly in the middle of the range of the Eastern Diamondback with a more temperate climate than southern and coastal parts of the range (Martin and Means 2000).

Data collection.—We collected Eastern Diamondbacks through road cruising surveys (n = 4), box trap arrays (n = 5), and incidental encounters (n = 5) from August to October 2018. We held captured snakes in the laboratory under a heat lamp kept on a 12-h light-dark cycle creating a temperature hotspot of 29° C on one side of the enclosure and an ambient room temperature of 24° C on the other with access to water (Murphy and Armstrong 1978). We held snakes for no more than two weeks before transmitter attachment. We attached 17 × 8.5 × 5.5 mm, 3.4 g Holohil BD-2 transmitters (Carp, Ontario, Canada) using the subdermal stitch method (Riley et al. 2017). Transmitters did not exceed 1% of the body mass of a snake. We attached transmitters below the 20th subcaudal scale on all snakes except smaller females whose tails were smaller in diameter at that location than the transmitters. For these small females, we attached transmitters at the 10th subcaudal scale. We did not radio-instrument any small males as attachment at that part of the tail could injure the hemipenes. We held snakes 24–36 h post-transmitter attachment and we released them within 100 m of the capture location away from the road or snake trap where they were captured. Mean snout-vent length (SVL) and weight of radio-tagged individuals was 1,129.2 cm (range, 950.0–1,270.0 cm) and 1,342 g (range, 811–2,194 g), respectively, for the 10 males and 928.6 cm (range, 834.5–993.5 cm) and 602 g (range, 484–660 g), respectively, for the four females.

We tracked snakes twice/week by homing and recording locations using a handheld GPS unit (Garmin eTrex 30x, Garmin LTD, Olathe, Kansas, USA) with ≤ 10 m accuracy. If the snake was in a refugium, we recorded refugium type, which included stump holes, large down woody debris (> 25 cm diameter), upturned root systems (tip-ups), and burrows of Gopher Tortoises, Armadillos, and Eastern Woodrats (*Neotoma floridana*; hereafter Woodrat). We attempted to visually confirm snake presence in refugia and determine the distance of a snake from burrow entrances using a Gopher Tortoise burrow camera (Environmental Management Systems, Canton, Georgia, USA). We only recorded distance from burrow entrance if the snake was stationary and at least partially coiled at the time of measurement. We determined land cover type and soil drainage classification (described below) at each snake location from existing land cover data (Jones Center at Ichauway, unpubl. data).

Data analysis.—We generated winter home ranges for snakes as 100% minimum convex polygons (MCP; Mohr 1947) using ArcMap 10.7.1 (Esri, Redlands, California, USA) as suggested by Row and Blouin-Demers (2006). When calculating MCPs, we omitted locations from October and February that were > 250 m from the majority of overwinter locations of a snake; the mean distance moved for these months in another Eastern Diamondback population (Means 2017). We considered these locations as representing snakes immigrating to or emigrating from their winter home ranges. We created 100-m buffers around home ranges for surveys of refugia potentially available to snakes and estimated availability of each refugium type using Line Transect Distance Sampling (Buckland et al. 2001) within each buffered home range of a snake. Transects were 10 m apart to ensure as thorough of a survey as possible. We recorded refugium locations using an Archer 2 Handheld Computer with a Geode sub-meter GPS receiver (Juniper Systems, Wels, Austria). We calculated perpendicular distances from transects to observed refugia in ArcGIS 10.7.1 (Esri, Redlands, California, USA). We generated abundance and density estimates for each refugium type in each snake home range using Distance v7.3 (Thomas et al. 2010).

We used a permutation-based combination of sign tests in package phuassess (Fattorini et al. 2017) in R 3.4.1 (R Development Core Team 2017) to investigate selection of land cover types and soil drainage classes across the landscape (second-order) and selection of refugium types and land cover types within home ranges (third order; Johnson 1980). We defined potential habitat types from existing land cover data as: pine forest (pine; 51.5% of the terrestrial area of the study site), pine dominated mixed pine/hardwood forest (pine/HW; 50–80% pine; 15.0% of study site), hardwood dominated mixed pine/hardwood forest (HW/pine; 50–80% hardwood; 8.3% of study site), hardwood forest (HW; 7.4% of study site), shrub scrub (shrub/scrub; 4.6% of study site), wildlife food plots and other agricultural fields (ag; 10.4% of study site), and wetlands (2.9% of study site; Jones Center at Ichauway, unpubl. data). We obtained soil drainage class information from the US Geological Survey Official Soil Series Descriptions and Series Classification (https://soilseries.sc.egov.usda.gov) and grouped soil drainage classes into three categories: excessively drained (47.8% of study site), well drained (41.6% of study site), and poorly drained (10.5% of study site). We derived habitat availability across the landscape (all of Ichauway) from 328 randomly generated points, which was equal to the number of snake telemetry locations, using ArcMap (Esri, Redlands, California, USA). Permutation-based combination of sign tests uses the proportion of animals that used a certain habitat more than available to examine selection. For tests with P-value < 0.05, proportions > 0.5 indicate selection for a habitat type (used proportionally more than available) and proportions < 0.5 indicate avoidance (used proportionally less than available). Tests with P-values > 0.05 indicate use in proportion to availability. P-values are combined into an overall test statistic that is permutated to test for overall habitat selection similar to the initial test of habitat selection using Wilks' lambda when using a compositional analysis (Aebischer et al. 1993).

We used a one-tailed t-test to determine differences in snake distance from refugium entrance between Gopher Tortoise and Armadillo burrows. We investigated influence of refugium density on winter home range size using Analysis of Covariance (ANCOVA) in R 3.4.1 (R Development Core Team 2017). We included SVL as an additional covariate to account for variation attributed to body size, as body size was a predictor of annual home range size of another large-bodied snake in this ecosystem (Hyslop et al. 2014). For both tests, α = 0.05.

Results

We documented Eastern Diamondbacks using six refugium types: Gopher Tortoise, Armadillo, and Eastern Woodrat burrows; stump holes; large down woody debris; and tip-ups. Gopher Tortoise burrows were the most commonly used refugium type comprising 41% (n = 94) of all underground locations, followed by Armadillo burrows (20%, n = 46), stump holes (13%, n = 29), Woodrat burrows (11%, n = 26), large down woody debris (11%, n = 25), and tip-ups (4%, n = 8). Snakes were further from the burrow entrances (t = 2.325, df = 29, P = 0.027) in Gopher Tortoise burrows (mean = 149.5 cm, standard deviation = 102.8, n = 21) than Armadillo burrows (mean = 81.6 cm, standard deviation = 53.4, n = 22).

Across all snake home ranges, large down woody debris had the highest density (mean density per ha with 95% confidence intervals = 7.33, 6.44–8.34) of all refugium types, followed by Gopher Tortoise burrows (3.77, 3.22–4.41), Armadillo burrows (1.88, 1.45–2.44), stump holes (1.77, 1.41–2.20), tip-ups (1.47, 1.170–1.855), and Woodrat burrows (0.25, 0.134–0.473). Eastern Diamondbacks used Gopher Tortoise burrows (proportion of snakes that selected for [ps] this refugium = 0.79, proportion of refugia available [pa] per hectare: 0.23, P = 0.057), Woodrat burrows (ps = 0.50, pa = 0.02, P = 1.00), Armadillo burrows (ps = 0.36, pa = 0.11, P = 0.424), and stump holes (ps = 0.29, pa = 0.11, P = 0.180) in proportion to availability (hereafter, proportionally used refugia) within home ranges. Eastern Diamondbacks avoided tip-ups (ps = 0.14, pa = 0.09, P = 0.013) and large down woody debris (ps = 0.00, pa = 0.45, P < 0.001) relative to availability within home ranges (overall P < 0.001).

The results for habitat selection across the landscape suggest selection for certain habitat types (overall P = < 0.001). Snakes used pine (ps = 0.50, proportion of habitats available [ph] across study site = 0.52, P = 1.00) and pine/HW (ps = 0.50, ph = 0.15, P = 1.00) in proportion to availability. Snakes avoided HW/pine (ps = 0.14, ph = 0.08, P = 0.013), HW (ps = 0.14, ph = 0.07, P = 0.013), wetland (ps = 0.07, ph = 0.03, P = 0.002), shrub/scrub (ps = 0.21, ph = 0.05, P = 0.057), and ag (ps = 0.00, ph = 0.10, P < 0.001) land cover types. We detected no selection of land cover types within winter home ranges (i.e., all land cover types were used proportionally; overall P = 0.184). Excessively drained (ps = 0.57, proportion of soil drainage classes available [pd] across study site = 0.48, P = 0.791) and well drained (ps = 0.43, pd = 0.42, P = 0.791) soils were used proportional to availability, whereas poorly drained soils were avoided (ps = 0.07, pd = 0.11, P = 0.001; overall P = 0.004). Winter home range size was not significantly influenced by refugium density ($F_{1,11}$ = 1.636, P = 0.227; Fig. 2). Home range size was, however, positively influenced by body size ($F_{1,11}$ = 5.042, P = 0.046; Fig. 2).

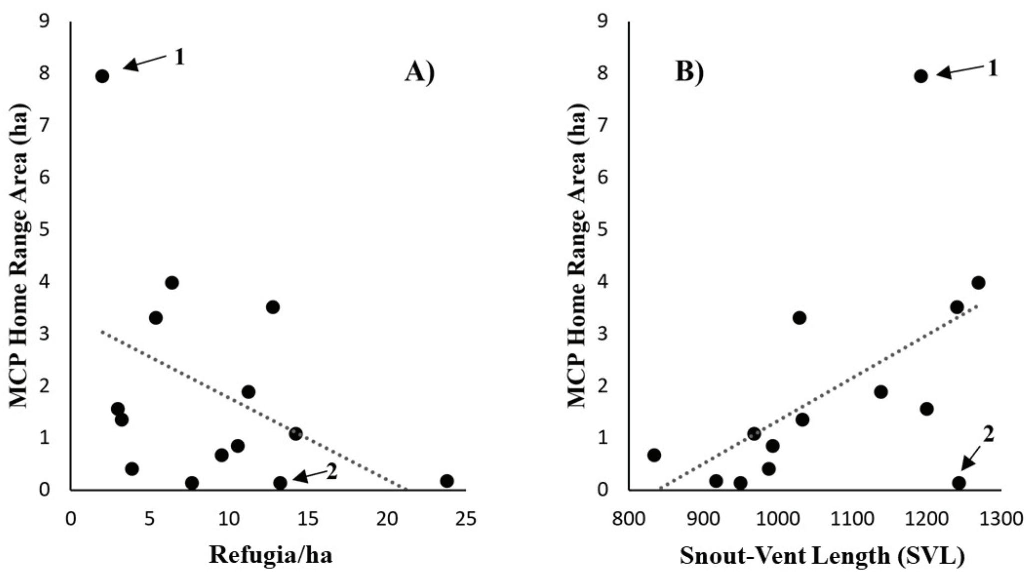

Figure 2. (A) Relationship between winter home range size (ha) and refugium density of 14 radio-tracked Eastern Diamondback Rattlesnakes (*Crotalus adamanteus*) in Baker County, Georgia, USA. Refugia included in this analysis are Gopher Tortoise (*Gopherus polyphemus*), Nine-banded Armadillo (*Dasypus novemcinctus*), and Eastern Woodrat (*Neotoma floridana*) burrows and stump holes. (B) Relationship between winter home range size (ha) and snout-vent length (SVL) of 14 radio-tracked Eastern Diamondback Rattlesnakes in Baker County, Georgia, USA. In both panels, snakes 1 and 2 are marked for discussion in the text.

Discussion

Eastern Diamondbacks used animal-made burrows and stump holes as overwintering refugia in proportion to availability, whereas they avoided large down woody debris and root tip ups. The apparent lack of selection for any of these particular refugium may be because they all provide appropriate microhabitats for overwintering Eastern Diamondbacks. Thus, when all are present on the landscape, availability likely has greater influence on refugium use than preference for a particular refugium. Timmerman (1995) documented a higher proportion of Eastern Diamondbacks using Armadillo burrows than Gopher Tortoise burrows in peninsular Florida. In contrast, Means (2005) documented a higher proportion of telemetered Eastern Diamondbacks using stump holes than Gopher Tortoise burrows in the Florida Panhandle. Timmerman (1995) suggested that apparent preference for Armadillo burrows may be related to warmer temperatures at lower latitudes and therefore less need for thermal buffering, considering Armadillo burrows are shallower on average than Gopher Tortoise burrows. Means (2005) suggested the deep taproot of Longleaf Pines combined with the additional structural complexity as a possible explanation for snakes selecting stump holes over Gopher Tortoise burrows. Neither of these studies, however, quantified relative availability of refugia within snake home ranges or across the landscape. Thus, it is possible that Armadillo burrows and stump holes were more available on the respective study sites. These refugia could be of higher value in parts of the range of Eastern Diamondbacks, such as North Carolina and South Carolina, that are outside that of the Gopher Tortoise.

Our results suggest that although Eastern Diamondbacks use shallow refugia such as Armadillo burrows, they may prefer deeper refugia provided by Gopher Tortoise burrows on our study site. Selection for Gopher Tortoise burrows approached statistical significance with nearly 80% of telemetered snakes using Gopher Tortoise burrows more than what was available. Mean length of Armadillo (McDonough et al. 2000) and Gopher Tortoise burrows (Hansen 1963; Diemer 1986) in Florida have been reported at 0.56 m and 4.5 m, respectively. Therefore, Gopher Tortoise burrows may allow snakes to select from a greater range of temperatures for thermoregulation (Douglass and Layne 1978). Means (2017) reported that Eastern Diamondbacks in the Florida Panhandle had lower overwinter mean body temperatures in stump holes than Gopher Tortoise burrows. Shallow refugia such as Armadillo burrows and stump holes may still provide adequate thermal buffering. Means (2017) points to the mean temperature of Eastern Diamondbacks using stump holes of around 10° C being similar to mean overwintering temperatures in other *Crotalus* species living in temperate environments (Jacob and Painter 1980; Brown 1982). Mean temperature of Eastern Diamondbacks using Gopher Tortoise burrows was higher at around 13° C.

Our study demonstrated that location of refugia on the landscape is important in management of this species. Eastern Diamondbacks overwintered in open-canopy, pine-dominated forests or shrub/scrub habitats and avoided closed-canopy land cover types such as hardwood-dominated forests. Previous studies have demonstrated Eastern Diamondback preference for open habitats, citing increases in prey base and basking opportunities as the mechanism (Martin and Means 2000; Waldron et al. 2006, 2008; Hoss et al. 2010; Means 2017). Selection for open habitats in winter likely allows for similar increases in basking opportunities, which has been documented in other *Crotalus* species (Jacob and Painter 1980; Gienger and Beck 2011). For example, Northern Pacific Rattlesnakes (*Crotalus oreganus*) in Washington, USA, select south facing slopes in winter that receive more sunlight than north facing slopes (Gienger and Beck 2011). Additionally, considering winter foraging has been documented in Eastern Diamondbacks (Means 2017), basking opportunities provided by open habitats may be important to facilitate digestion. Finally, this could be related to availability of Gopher Tortoise burrows, which is higher in open-canopied pine forests than in other forest types on Ichauway (Jones Center at Ichauway, unpubl. data).

It was not surprising that snakes avoided agricultural areas in winter. Because these areas are plowed and replanted annually, they generally lack underground refugia. Although edges of agricultural areas may provide foraging opportunities for snakes during the active season (Waldron et al. 2006), their presence in winter home ranges could increase overall home range size due to the lack of suitable refugia. Two snakes in our study, both males of similar size (1,193.5 mm and 1,243.5 mm SVL), had different winter home range sizes compared to other similarly sized study snakes. The home range of Snake 1 was larger than average and included 54% non-forested habitats (agriculture and wetland) with 2.0 preferred refugia (animal burrows and stump holes)/ha whereas the home range of the second snake was smaller than average and consisted of 0% non-forested habitat with 13.3 preferred refugia/ha. Although Eastern Diamondbacks generally avoided selecting winter home ranges within nonforested habitats, the differences between these snakes suggests that when a large portion of these land cover types is present in their home range, snakes move farther over the course of the season to find suitable microhabitats. Similar relationships between home range size and avoided land cover types within home ranges has been documented in other snake species. Home range size of Bullsnakes (*Pituophis catenifer*) in the midwestern U.S. increases with increasing area of avoided habitat types likely due to increased movement needed to find suitable habitat (Kapfer et al. 2010). Increased movement could result in increased overwinter mortality from vehicles, predation, or exposure to low temperatures (Bonnet et al. 1999). These negative effects of fragmented habitats could be compounded by high site fidelity and low dispersal probability of Eastern Diamondbacks, which limits their ability to adjust home ranges in response to land use changes (Waldron et al. 2013). Ichauway is predominantly open-canopied forest with readily available refugia. This, in combination with a small sample size, could be the reason we did not see a significant relationship between refugium density and winter home range size. Annual home range data would have allowed us to determine if there were seasonal differences in home range selection related to refugium density.

Aversion to poorly drained soils by Eastern Diamondbacks was likely to avoid refugia that flood during rain events (Means 1982, 2017). Flooded refugia can be detrimental to overwinter survival due to drowning (Shine and Mason 2004) or risks associated with increased movements following displacement. One snake in our study abandoned its refugium in oak scrub habitat after it was flooded by a nearby creek; it then moved into adjacent upland pine habitat. The snake used two different tortoise burrows in the upland habitat before returning to the oak scrub habitat after the water receded. Additionally, Gopher Tortoises also avoid these poorly drained soil classes resulting in lower density of their burrows in these habitats. These results underscore the importance of considering soil drainage characteristics when managing for open-canopy habitat to support Eastern Diamondbacks.

Management implications.—Our study shows that typical Longleaf Pine management, creating open-canopy habitat on well-drained soils managed with frequent fire, provides optimal overwinter habitat for Eastern Diamondbacks. These management practices will also promote Gopher Tortoise populations, if present, and thereby provide burrows valuable to Eastern Diamondbacks. If Gopher Tortoise or other animal-made burrows are not present or uncommon in these areas, managers should consider retaining stumps or limiting their harvest to ensure presence of stump holes. Reducing habitat fragmentation from agricultural practices would also benefit this species as the presence of non-forested land cover types may increase home range sizes by potentially reducing refugium densities resulting in a higher probability of mortality in winter.

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Literature Cited

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Balogová, M., D. Jelić, M. Kyselová, and M. Uhrin. 2017. Subterranean systems provide a suitable overwintering habitat for *Salamandra salamandra*. International Journal of Speleology 46:321–329.

Bonnet, X., G. Naulleau, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

Brown, W.S. 1982. Overwintering body temperatures of Timber Rattlesnakes (*Crotalus horridus*) in northeastern New York. Journal of Herpetology 16:145–150.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, UK.

Diemer, J.E. 1986. The ecology and management of the Gopher Tortoise in the southeastern United States. Herpetologica 42:125–133.

Douglass, J.F., and J.N. Layne. 1978. Activity and thermoregulation of the Gopher Tortoise (*Gopherus polyphemus*) in southern Florida. Herpetologica 34:359–374.

Farallo, V.R., and D.B. Miles. 2016. The importance of microhabitat: a comparison of two microendemic species of *Plethodon* to the widespread *P. cinereus*. Copeia 104:67–77.

Fattorini, L., C. Pisani, F. Riga, and M. Zaccaroni. 2017. The R package "phuassess" for assessing habitat selection using permutation-based combination of sign tests. Mammalian Biology 83:64–70

Gienger, C., and D.D. Beck. 2011. Northern Pacific

Rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Canadian Journal of Zoology 89:1084–1090.

Hansen, K.L. 1963. The burrow of the Gopher Tortoise. Quarterly Journal of the Florida Academy of Sciences 26:353–360.

Hoss, S.K., C. Guyer, L.L. Smith, and G.W. Schuett. 2010. Multiscale influences of landscape composition and configuration on the spatial ecology of Eastern Diamond-backed Rattlesnakes (*Crotalus adamanteus*). Journal of Herpetology 44:110–123.

Hyslop, N.L., J.M. Meyers, R.J. Cooper, and D.J. Stevenson. 2014. Effects of body size and sex of *Drymarchon couperi* (Eastern Indigo Snake) on habitat use, movements, and home range size in Georgia. Journal of Wildlife Management 78:101–111.

Jacob, J.S., and C.W. Painter. 1980. Overwinter thermal ecology of *Crotalus viridis* in the north-central plains of New Mexico. Copeia 1980:799–805.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kapfer, J., C. Pekar, D. Reineke, J. Coggins, and R. Hay. 2010. Modeling the relationship between habitat preferences and home-range size: a case study on a large mobile colubrid snake from North America. Journal of Zoology 282:13–20.

Liang, C.T., R.L. Grasso, J.J. Nelson-Paul, K.E. Vincent, and A.J. Lind. 2017. Fine-scale habitat characteristics related to occupancy of the Yosemite Toad, *Anaxyrus canorus*. Copeia 105:120–127.

Martin, W.H., and D.B. Means. 2000. Distribution and habitat relationships of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*). Herpetological Natural History 7:9–34.

McDonough, C.M., M.J. DeLaney, P. Quoc Le, M.S. Blackmore, and W. Loughry. 2000. Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. Revista de Biologia Tropical 48:109–120.

Means, D.B. 1982. Responses to winter burrow flooding of the Gopher Tortoise (*Gopherus polyphemus* Daudin). Herpetologica 38:521–525.

Means, D.B. 2005. The value of dead tree bases and stumpholes as habitat for wildlife. Pp. 74–78 *In* Amphibians and Reptiles: Status and Conservation in Florida. Meshaka, W.E., and K.J. Babbitt (Eds.). Krieger Publishing Company, Malabar, Florida, USA.

Means, D.B. 2017. Diamonds in the Rough: Natural History of the Eastern Diamondback Rattlesnake. Tall Timbers Press, Tallahassee, Florida, USA.

Means, D.B., and G. Grow. 1985. The endangered Longleaf Pine community. ENFO (Environmental Information Center) 85:1–12.

Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.

Murphy, J.B., and B.L. Armstrong. 1978. Maintenance of rattlesnakes in captivity. Special Publication No. 3, University of Kansas Publications, Museum of Natural History, Lawrence, Kansas, USA. 40 p.

R Development Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Riley, J.L., J.H. Baxter-Gilbert, and J.D. Litzgus. 2017. A comparison of three external transmitter attachment methods for snakes. Wildlife Society Bulletin 41:132–139.

Row, J.R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia 2006:797–802.

Shine, R., and R.T. Mason. 2004. Patterns of mortality in a cold-climate population of garter snakes (*Thamnophis sirtalis parietalis*). Biological Conservation 120:201–210.

Smith, L.L., J.A. Cox, L.M. Conner, R.A. McCleery, and E.M. Schlimm. 2017. Management and restoration of Longleaf Pine ecosystems for wildlife. Pp. 233–251 *In* Ecological Restoration and Management of Longleaf Pine Forests. Kirkman, L.K., and S.B. Jack (Eds.). CRC Press, Boca Raton, Florida, USA.

Timmerman, W. 1995. Home range, habitat use, and behavior of the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) on the Ordway Preserve. Bulletin of the Florida Museum of Natural History 38:127–158.

Thomas, L., S.T. Buckland, E.A. Rexstad, J.L. Laake, S. Strindberg, S.L. Hedley, J.R. Bishop, T.A. Marques, and K.P. Burnham. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47:5–14.

Tuberville, T.D., Gibbons, J.W., and H.E. Balbach. 2009. Estimating viability of Gopher Tortoise populations. Technical Report No. ERDC/CERL TR-09-2, U.S. Army Engineer Research and Development Center, Champaign, Illinois, USA. 58 p.

U.S. Fish and Wildlife Service. 2012. Endangered and threatened wildlife plants; 90-Day finding on a petition to list the eastern diamondback rattlesnake as threatened. Federal Register 77:27403–27411.

Waldron, J.L., S.M. Welch, and S.H. Bennett. 2008. Vegetation structure and the habitat specificity of a declining North American reptile: a remnant of former landscapes. Biological Conservation 141:2477–2482.

Waldron, J., S. Bennett, S. Welch, M. Dorcas, J. Lanham, and W. Kalinowsky. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. Animal Conservation 9:414–420.

Waldron, J.L., S.M. Welch, S.H. Bennett, W.G. Kalinowsky, T.A. Mousseau. 2013. Life history constraints contribute to the vulnerability of a declining North American rattlesnake. Biological Conservation 159:530–538.

Whiles, M.R., and J.W. Grubaugh. 1996. Importance of coarse woody debris to southern forest herpetofauna. Pp. 94–100 *In* Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. McMinn, J.W., and D.A. Crossley, Jr. (Eds.). General Technical Report SE-94, U.S. Department of Agriculture, Forest Service, Asheville, North Carolina, USA.

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