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Road Ecology and Microhabitat Assessment of Black Hills Red-bellied Snakes and Smooth Greensnakes in an Isolated Mountain Range

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Abstract.—**Understanding species habitat use and population threats is important to inform effective conservation management. In 2016, we conducted a road ecology and microhabitat project for Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae*) and Smooth Greensnakes (*Opheodrys vernalis*) in the northern Black Hills of South Dakota. Both species are of conservation importance. We surveyed more than 1,700 km of rural, unpaved roads and analyzed data for 75 snakes. Road-adjacent microhabitats were similar where either species was found, suggesting syntopy. Areas with rocky substrates and denser, taller herbaceous vegetation were seasonally favored by both species: flat mesic meadows were indicative of active season habitat and steep south/southwest-facing slopes were typical of overwintering habitat. We found that temporal factors (e.g., coinciding with seasonal ingress) best predicted snake activity on roads, especially for certain areas. High rates of road mortality (78.6%) throughout the study area, however, are concerning. Because roads bisect important seasonal habitat features, and both species are small and relatively non-vagile, they are likely susceptible to vehicle strikes, even at relatively low traffic volumes along local roads. Road mortality is likely a significant driver of population decline. Because of their overlap in natural history, likelihood of road mortality, and similarities in habitat use, we recommend wildlife managers consider umbrella-concept conservation strategies, especially in important seasonal habitats and migration corridors.**

Key Words.—activity; conservation; habitat association; migration; *Opheodrys vernalis*; roadkill; seasonality; *Storeria occipitomaculata*

Introduction

Understanding ecological characteristics, habitat associations, and threats to populations of species are invaluable to inform effective wildlife management decisions (Böhm and Popescu 2016; Dodd 2016; Pike 2016). Roads often present barriers to wildlife and fragment habitat for many species, including herpetofauna (Baxter-Gilbert et al. 2015; Monge-Velázquez et al. 2022). Roads can also directly and indirectly affect behavior and movement, which can stress population dynamics (Shine et al. 2004; Bennett 2017; Lutterschmidt et al. 2019). Road mortality of at-risk species highlights the need for studies of road effects (e.g., traffic rates, roadside habitat) on species (Jones et al. 2011; Jochimsen et al. 2014). Understanding the characteristics of where and when road mortality occurs can guide more effective mitigation efforts (Langen et al. 2009; Garrah et al. 2015; Lutterschmidt et al. 2019).

Red-bellied Snakes (*Storeria occipitomaculata*) and Smooth Greensnakes (*Opheodrys vernalis*) are small (about < 370 mm SVL), cryptic snakes primarily found throughout much of the Temperate Deciduous Forests and mesic Grasslands of the eastern two-thirds of the U.S. and southern Canada (Ernst and Ernst 2003). Both species are insectivorous, and communal overwintering in hibernacula can occur, sometimes in inactive ant mounds (Lang 1969; Cairns et al. 2018). Interestingly, *S. occipitomaculata* (and possibly *O. vernalis*) also use active ant mounds during summer months (Pisani and Busby 2011; Harris and Savage 2020). Both taxa have isolated populations in the montane Black Hills of western South Dakota and northeastern Wyoming and carry special conservation status there (Smith and Quinn 2012). The Black Hills Red-bellied Snake (*S. o. pahasapae*) is considered a Species of Greatest Conservation Need (SGCN) in South Dakota and Wyoming (Smith and Stephens 2003; Smith and Quinn 2012) and is included on the Regional Forester's list of Sensitive Species (RFSS) of the U.S. Forest Service (USFS) for the Rocky Mountain Region (Region 2). *Opheodrys vernalis* has SGCN status in Wyoming and is monitored by the South Dakota Natural Heritage Database (Redder et al. 2006); range-wide population declines are a concern (Blais et al. 2021). These two species are sympatric in the Black Hills and often co-occur in similar microhabitats, including hibernacula (pers. obs.).

Both species are relatively non-vagile and have limited home range sizes (Smith and Stephens 2003; Redder et al. 2006). Lang (1969) found that *S. occipitomaculata* in Minnesota moved less than a few hundred meters from hibernacula in one active season. Active season home ranges of *O. vernalis* appear relatively small and tracked daily movements seldom exceed five meters (Sacerdote-Velat et al. 2014). A phylogeographic assessment of *O. vernalis* revealed low heterozygosity and the likelihood of limited gene flow among many western populations, including the Black Hills (Blais et al. 2021). Although some differentiation exists among *S. o. pahasapae* and other *S. occipitomaculata* populations (Pyron et al. 2016; Dieter and Ronningen 2017), refined ecological or evolutionary analyses of *S. o. pahasapae* are unresolved and much valuable information remains unknown. Because *O. vernalis* and *S. o. pahasapae* may share similar habitat and life-history traits (e.g., seasonality and reproductive phenology; Redder et al. 2006; Cairns et al. 2018), new data may serve to benefit both species.

Some roadways in the Black Hills have caused considerable mortality for both species of snakes (Jodi Massie et al., unpubl. report); however, certain localities of high activity, as judged by observations of frequent road mortality, are lacking in quantitative analyses. Also uncharacterized and unknown are knowledge of habitats and environmental variables associated with activity of these species (Smith and Quinn 2012). More information about activity and seasonal habitat use are warranted for both species, which can better guide multiple-use management decisions and potential mitigation measures.

Here, we describe our findings from a road ecology study of *O. vernalis* and *S. o. pahasapae* in the northern Black Hills of South Dakota. Our objectives were to (1) assess road activity by these snakes; (2) characterize road-adjacent habitat used and available to both species in relation to seasonal usage; and (3) determine important extrinsic factors (e.g., ambient conditions, traffic) affecting their activity. Because neither species is known to move far, and many known road segments run parallel with perennially flowing streams that may act as movement barriers, it is likely that these snakes spend a considerable amount of their lifetimes in areas adjacent to where they are found on roads. Thus, roadside vegetation plots likely reflect proximity to active season habitat as well as overwintering den sites. Additionally, locations where snakes are commonly observed may be areas where these species are abundant. These data are valuable for non-vagile species with vulnerable populations. Understanding road ecology in areas that have moderate or increasing traffic volumes has direct implications to support our contention that road mortality may be affecting populations of these species. Taken together, unraveling ecological data for these understudied species should provide valuable information to guide effective conservation management.

Materials and Methods

Study site.—Our study site was located on the USFS Northern Hills Ranger District in Lawrence and Pennington counties, South Dakota, at elevations between 1,100–1,949 m (Fig. 1). The Black Hills of western South Dakota and northeastern Wyoming are an approximate 200 × 100 km domal uplift rising from about 915–1,065 m elevation in the surrounding plains, to 2,207 m at the highest peak (Hoffman and Alexander 1987). The climate in the Black Hills is semi-arid but varies considerably with elevation driven in part by complex topography, variable wind patterns, and inconsistent snowpack depths (Hoffman and Alexander 1987; Froiland 1990). Lower elevations are more xeric, with highly variable temperature, that transitions towards mesic conditions with elevation.

The biotic communities of the Black Hills consist mostly of Rocky Mountain Montane Conifer Forest (Brown et al 2007), dominated by Ponderosa Pine (*Pinus ponderosa*). Patches of other trees, such as birches (*Betula* spp.), cottonwoods and aspens (*Populus* spp.), and spruces (*Picea* spp.), are interspersed (Froiland 1990; Parrish et al. 1996). Trees typical of Eastern Deciduous Forest biomes, such as Bur Oak (*Quercus macrocarpa*) and Hophornbeam (*Ostrya virginiana*), can be found in low to mid elevation drainages along the northern and eastern portions of the Black Hills. Willows (*Salix* spp.) are found near bottomland creeks, and mesic, herbaceous meadows with few or no trees are not uncommon (Froiland 1990). Many small lotic hydrological networks are sinuously interspersed through the bottomlands, and man-made reservoirs serve as the only large lentic waterbodies (Fontaine et al. 2001; Dieter and Ronningen 2017).

Road ecology.—Coinciding with the active season of *O. vernalis* and *S. o. pahasapae* between late spring and fall of 2016, we conducted repeated road cruise surveys (Jones et al. 2011) in the northern Black Hills of South Dakota. Snow cover lasting until late spring and periodic snowstorms in October can limit the active season window in our study area (pers. obs.). We divided a 55.5 km route into five sampling segments: (1) Black Fox; (2) Higgins Gulch; (3) Long Draw; (4) Rochford, and (5) Roughlock Falls. All roads were rural, unpaved with dirt or aggregate substrates (e.g., limestone), and

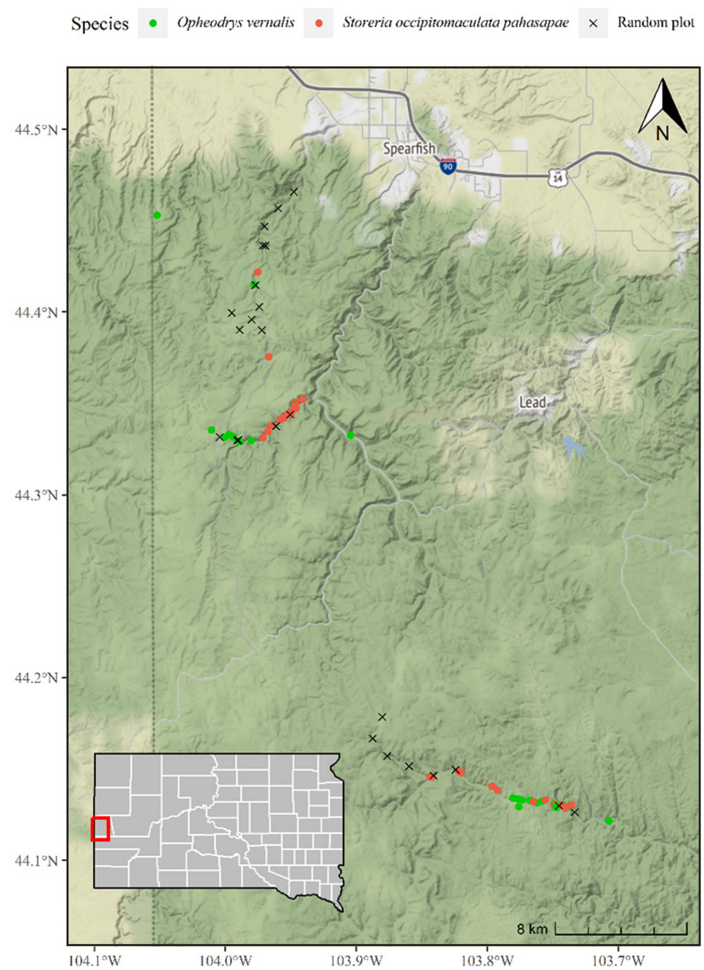

Figure 1. Observations of Smooth Greensnakes (*Opheodrys vernalis*; green) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae*; red) during road cruise surveys in the northern Black Hills of South Dakota, USA, June-October 2016. (Map data from Stamen Maps via the ggmap and sp R packages: Bivand et al. 2013; Kahle and Wickham 2013).

some had seasonal closures (e.g., 15 December to 15 May; https://www.fs.usda.gov/detail/blackhills/maps-pubs/?cid=FSEPRD533421). Segments were classified as local roads (https://opendata2017-09-18t192802468z-sdbit.opendata.arcgis.com/) and residential development along segments was sparse or absent. We controlled for variation in diurnal activity of *Opheodrys* and *Storeria* by starting surveys at different times of day (range, 0800–1430) and staggering survey directions. We cruised at speeds < 40 km/h and recorded traffic as the number of vehicles encountered during transit (Lutterschmidt et al. 2019). Some surveys were restricted due to assorted road closings, extreme weather changes, and for the Crow Peak Wildfire of 2016 along the Higgins Gulch segment. The latter prohibited surveys on that segment from 24 June to 27 July.

When we encountered snakes, we used GPS units (GPSMap64s, Garmin Ltd., Olathe, Kansas, USA; GeoExplorer 2008 series, Trimble Inc., Sunnyvale, California, USA) to collect elevation and geocoordinates. We divided elevation into 50 m bins (range, 1,100–1,949 m) for downstream analyses. When possible, we recorded snout-vent length (SVL, ± 1.0 mm), tail length (TL), mass (± 0.1 g), and whether we found snakes alive- or dead-on-road (hereafter, AOR, DOR). Because *O. vernalis* and *S. o. pahasapae* are small and sensitive, we did not attempt to determine the sex of snakes. We removed all DOR snakes off roadways.

Because it is difficult to decipher when an animal is killed on a road, capturing recent weather patterns in the days prior to surveys may approximate the conditions when animals move on to a road (Rendall et al. 2021). We obtained daily weather data from three stations located in the northern Black Hills (https://www.weather.gov/wrh/climate?wfo=unr); these data included daily minimum, maximum, and mean ambient air temperature (± 0.1° C), mean temperature departure from normal, i.e., 30-y means according to the National Ocean and Atmospheric Administration (NOAA), and total precipitation (± 0.1 mm). We followed Rendall et al. (2021) by deriving mean values of daily weather recency from all three stations for survey dates and up to 8 d before surveys, i.e., our mean survey interval plus one standard deviation. For AOR snakes, we used a Kestrel 3000 anemometer (Nielsen-Kellerman, Inc., Boothwyn, Pennsylvania, USA) to record ambient air temperature (± 0.1° C) and relative humidity (± 0.1%). Because of variability in wind speed due to habitat heterogeneity along the route (e.g., canyon corridors to open meadows), we categorized wind speed according to the Beaufort Scale (https://www.spc.noaa.gov/faq/tornado/beaufort.html). We categorically recorded precipitation (none, drizzle, light rain, showers), and cloud cover (< 10%; 10–25%; 25–50%; 50–75%; > 75%).

Microhabitat assessment.—We assessed microhabitat via vegetation plots adjacent to each observed snake on road locality. Because *O. vernalis* and *S. o. pahasapae* size may hinder them from crossing perennial, swift-flowing streams, we restricted vegetation plots to areas between roads and creeks. To sample vegetation, we marked plot centers 15 m from the edge of the road from capture sites. We randomly selected which side of the road to measure plots. If a creek was < 15 m from the edge of the road, we centered plots at the mean distance between the creek and road. Within 5-m circular plots (about 78.5 m^2) from the central point, we quantified trees and used a densiometer to estimate percentage canopy cover (Smith and Stephens 2003). We used a clinometer to estimate steepest downhill slope and aspect along the steepest incline. Grassland height can indicate grazing pressure (Uresk et al. 2009) and may be important in quantifying habitat suitability for *O. vernalis* and *S. o. pahasapae* (Smith and Stephens 2003; Redder et al. 2006). Therefore, we used Robel Poles to estimate herbaceous height of grasses and forbs, averaged across four cardinal directions (Uresk and Benzon 2007; Hollis Marriott, unpubl report).

We estimated ground cover composition in 1 m circular plots (ca. 3.1 m^2) within plot centers. These data included percentages of barren ground, rocks, woody debris, herbaceous growth (i.e., grasses and forbs), and leaf litter. We also conducted microhabitat assessments at random points throughout our survey route to assess habitat available to the snakes. These encompassed areas where both snakes were known to occur, which was determined using state and federal databases (see Fig. 1). We omitted plot assessment on private land.

Statistical analyses.—Relationships of contextual (e.g., time, traffic) and environmental factors (e.g., precipitation, temperature) can impact road usage by animals (Siers et al. 2016). Thus, we performed Generalized Linear Mixed Models with a Poisson distribution in the R package lme4 (Bates et al. 2015) to understand snake activity on roadways, proxied here as the total snakes of both species observed per segment. Candidate predictors included month, traffic, and weather recency values of daily minimum temperature and total precipitation; we accounted for road segments as a random effect and (log) segment length as an offset term. To mitigate multicollinearity among temperature variables ($r > 0.9$), we selected daily minimum because it performed best with the data in preliminary assessment; all other covariates were below correlation threshold ($r < 0.6$). We performed backwards elimination to remove uninformative parameters from models (Leroux 2019) and used the AICcmodavg package (Mazerolle 2020) to select optimal models following the lowest corrected Akaike Information Criterion (ΔAICc > 2) method (Venables and Ripley 2013). We tested models for overdispersion and used the R package MuMIn (Barton 2020) to assess marginal pseudo-R^2, i.e., a coefficient of determination of variance explained by fixed effects.

We used a Kruskal-Wallis test to assess snakes per road segment, and a Chi-squared test to assess differences between species counts at the two most productive segments. Because road mortality has been a recent and growing concern in the Black Hills region (Jodi Massie et al. unpubl. report), we used Kendall's tau to explore the association between traffic counts and total DORs encountered per survey. Because no differences existed in relative traffic volumes by weekday or weekend (Mann-Whitney $U = 59.5$, $P = 0.478$; see Rendall et al. 2021), and both species are distributed throughout our sampling frame, we pooled across survey day of week. We also used a Spearman Rank Correlation to assess if elevational occurrences were correlated between species. We used Chi-squared and *t*-tests to assess weather variables between species for AOR observations.

For microhabitat analyses, we first used Factor Analysis of Mixed Data (FAMD) in the FactoMineR package (Lê et al. 2008) to explore qualitative and quantitative associations in the habitat data. Due to insufficient variation among finite characteristics of trees, we only retained the total number of trees (deciduous + coniferous) within plots. Next, we performed mixed effect Logistic Regressions in the glmmTMB package (Brooks et al. 2017) to analyze microhabitat differences between snake-associated (i.e., used by either species) versus random sites. Predictor variables included slope, aspect, elevation, canopy, total trees, all percentage cover composition classes, and mean herbaceous height. We included road segment as a random effect. We again used the backwards elimination process and ΔAICc to select optimal models. We repeated microhabitat analyses to assess differences in microhabitat associations between *O. vernalis* and *S. o. pahasapae*.

Because previous data suggested that these snakes used meadows in the active season and rocky hillsides for overwintering den sites during the inactive season (Smith and Stephens 2003; Jodi Massie et al. unpubl. report), we subdivided microhabitats accordingly. For example, both Rochford and Roughlock Falls segments have south-southwesterly facing slopes (mean slope = 34.8° ± (SD) 6.3°); mean aspect = 214.5° ± (SD) 71.8°) along the north side of roadways and meadows with nearby streams south of the roads. We used Analysis of Variance (ANOVA) and Multivariate Analysis of Variance (MANOVA) tests to describe levels of each species and random points against microhabitat factors (slope, aspect, canopy cover, ground cover composition, and herbaceous height) in seasonally designated habitats, respectively. We conducted analyses in program R v.4.1.1 (R Core Team, 2021). We set α to 0.05 and report mean ±1 standard deviation for applicable tests unless specified otherwise. We used R packages ggmap (Kahle and Wickham 2013) and sp (Bivand et al. 2013) to generate the sampling map.

Results

Road ecology.—Between 2 June and 27 October 2016, we completed 35 road cruise surveys (160 segments; about 1,768.6 km). We surveyed routes approximately every 4.4 ± (standard deviation) 3.2 d and mean survey duration was 112.5 ± 27.9 min. We detected 36 *O. vernalis* and 39 *S. o. pahasapae* (Fig. 1). Body sizes for *O. vernalis* were mean SVL = 218.4 ± 63.9 mm, TL = 84 ± 31.3 mm, and mass = 5.4 ± 4.6 g. For *S. o. pahasapae*, mean SVL = 178.2 ± 34.4 mm, TL = 54.0 ± 12.4 mm, and mass = 3.2 ± 2.0 g. A notable observation was a gravid *S. o. pahasapae* with four near-term embryos found freshly DOR on 8 August 2016 in the Rochford area. Reproductive data for this taxon are sparse (Smith and Quinn 2012); average daily conditions of the area in the week prior were 21.8° C (1.3° C above 30-y mean) and 1.4 mm precipitation; survey cloud cover ranged 50–75%. We encountered 16 non-target species: 13 Terrestrial Gartersnakes (*Thamnophis elegans*); one Plains Gartersnake (*T. radix*); one Common Gartersnake (*T. sirtalis*); and one unidentified snake, but we omitted them from analyses.

We encountered at least one *O. vernalis* or *S. o. pahasapae* in 34 of 160 segments surveyed (21.3%) and 0.04 snakes/km overall. Activity for both species was highest on the Rochford segment (50.7% of all detections), followed by Roughlock Falls (34.7%), Higgins Gulch (4.0%), and Black Fox (1.3%); miscellaneous sightings accounted for 9.3% of observations. Because we did not detect any snakes on the Long Draw segment, it was omitted from analyses. The number of snakes detected was not equal across segments ($H = 26.3$, df = 3, $P < 0.001$; Table 1). There was no difference, however, in abundance of the two species at the two most productive segments ($\chi^2 = 0.051$, df = 1, $P = 0.821$). Despite relatively low traffic counts per segment (mean = 2.2 ± 3.5 vehicles) or survey (mean = 9.3 ± 6.4 vehicles), we found significantly more snakes DOR (n = 55, 78.6%) than AOR (n = 15, 21.4%) when assuming equivalent frequencies ($\chi^2 = 11.2$, df = 1, $P < 0.001$). Increased traffic volume was associated with more DOR snakes ($\tau = 0.297$, $P = 0.026$; Fig. 2).

Activity.—We detected live *O. vernalis* slightly later in the day (mean = 1241 ± 129 min) but not significantly different than observations of *S. o. pahasapae* (mean = 1134 ± 122 min; $t = 1.206$, df = 10, $P = 0.256$). In biweekly (14-d) spans between 1 June and 14 August, we detected no more than five individuals of either species (Fig. 3). We recorded an uptick in detections, however, between 30 August and 28 September. We did not detect either species after 30 September. Weather conditions were equivalent between AOR observations of species, including relative humidity ($t = -0.078$, df = 10.993, $P = 0.939$), temperature ($t = 0.254$, df = 3.851, $P = 0.813$), and wind ($\chi^2 = 1.190$, df = 4, $P = 0.756$). Mean ambient conditions at capture were 22.9 ± 3.7° C for temperature and 39.0 ± 9.9% for relative humidity. Modes were Beaufort 2 (termed rustling leaves) for wind category and 25–50% for cloud cover. We did not observe live snakes during active rain or wind speeds above Beaufort Scale 3.

Table 1. Summary of road ecology surveys in the northern Black Hills of South Dakota, USA, June-October 2016. Data are split by road segment and total individuals detected on surveys for Smooth Greensnakes (*Opheodrys vernalis* = OPVE) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae* = STOC). Traffic depicts the number of vehicles encountered along each segment during surveys. Duration and traffic values are mean ± standard error.

Road Segment (surveys)	Length (km)	Duration (min)	Traffic	OPVE (n)	STOC (n)
Black Fox (n = 30)	7.7	19.3 ± 0.8	0.5 ± 0.2	1	0
Higgins Gulch (n = 30)	14.2	31.9 ± 1.2	0.9 ± 0.2	2	1
Long Draw (n = 30)	13.0	30.0 ± 0.8	1.0 ± 0.3	0	0
Rochford (n = 35)	11.4	39.6 ± 2.0	1.8 ± 0.3	17	21
Roughlock Falls (n = 35)	9.2	29.2 ± 1.9	6.3 ± 0.9	10	16

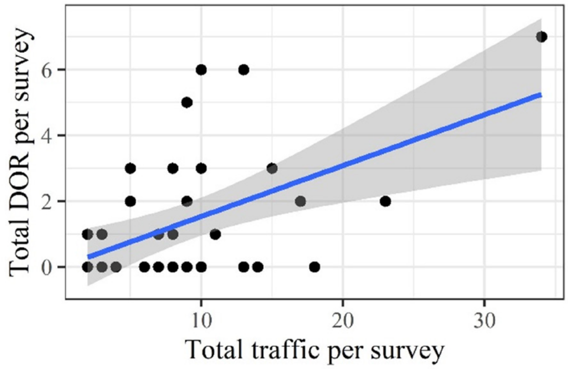

Figure 2. Relationship of traffic (i.e., number of cars) to dead-on-road (DOR) Smooth Greensnakes (*Opheodrys vernalis*) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae*) encountered per 55.5 km road cruise survey in the northern Black Hills of South Dakota, USA, June-October 2016. The blue line and grey shading represent fit (Kendall's $\tau = 0.297$, $P = 0.026$) and 95% confidence intervals.

After accounting for effects from road segments, two competing models best described snake abundance on roads; both included month as a predictor (marginal R^2m = 0.905) but differed by daily minimum temperature, though the effects of the latter appeared negligible (R^2m = 0.904; Table 2). After adjusting for effects from daily minimum temperature, predicted counts of snakes increased from 0.15/segment (95% Confidence Interval [CI] = 0.03–0.70) and 0.07/segment (95% CI = 0.01–0.42) during June and July, respectively, to 0.40/segment (95% CI = 0.09–1.77) during August and 0.38/segment (95% CI = 0.09–1.64) in September.

Microhabitat analyses.—We analyzed 68 microhabitat plots in this study (*O. vernalis* n = 17; *S. o. pahasapae* n = 27; random n = 24; Table 3). We omitted vegetation plots for 10 *O. vernalis* observations that would have been on private land. The first three dimensions from FAMD analyses accounted for 46.3% of plot variation. The most representative and contributing variables to dimension 1 were herbaceous and leaf litter cover classes, dimension 2 was driven by vegetation height, and road segment and species contributed most to dimension 3. There was no apparent multivariate cluster separation for individual road segment or by species or random points, however (Fig. 4). Two competing models as well as an intercept-only model best described differences between snake associated sites versus random points (Table 4). Fitted models shared the following covariates: mean canopy density and substrate cover compositions of rock and herbaceous vegetation (R^2m = 0.205) but differed by mean herbaceous height (R^2m = 0.238) but there was uncertainty among covariates. That is, confidence intervals were widely dispersed, which partly explains why these models did not outperform an intercept-only

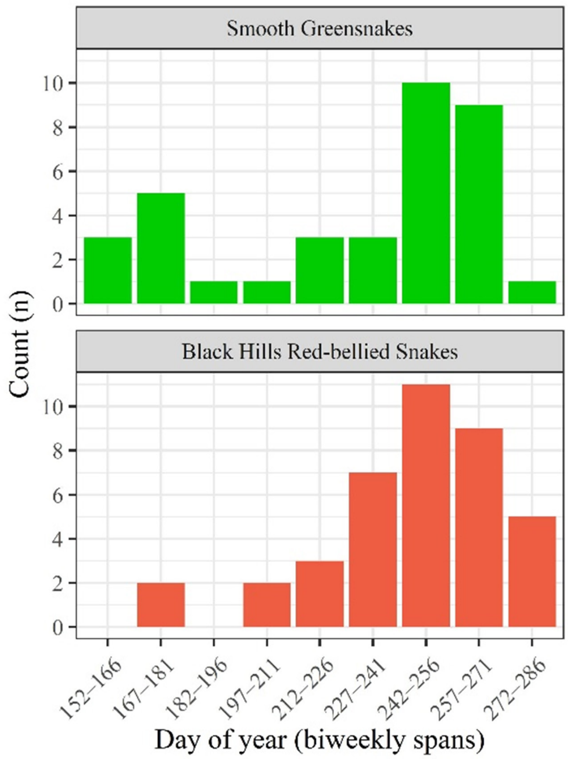

Figure 3. Activity on roadways for Smooth Greensnakes (*Opheodrys vernalis*, green) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae*, red) during road cruise surveys in the northern Black Hills of South Dakota, USA, June-October 2016. Data are reported as counts of each species encountered, alive or dead, and partitioned within biweekly spans of day of year; first detection was 10 June (day 161) and last occurred on 30 September (Day 274).

Table 2. Mixed effect models for predicting total snakes on roads. Model selection was based on change in corrected Akaike Information Criterion (ΔAICc) method (Venables and Ripley 2013). Variables are K = the number of model parameters, ω = relative model weight, R^2m = marginal coefficient of determination for fixed effects. Abbreviations are mo = month that survey occurred, traf = counts of traffic encountered, off = offset term ([log] segment length), and seg = survey sublevel sampling segment, as a random effect. For weather recency (≤ 8 d prior to and including survey date), TminC = mean minimum daily ambient temperature (°C), depC = average temperature departure from 30-y mean, and pr = mean daily precipitation (mm).

Model	K	AICc	ΔAICc	ω	R^2m
~ mo + off + (1|seg)	6	221.01	0.00	0.63	0.905
~ mo + TminC + off + (1|seg)	7	222.83	1.82	0.25	0.904
~ mo + TminC + traf + off + (1|seg)	8	225.00	3.99	0.09	0.903
~ mo + TminC + traf + pr + off + (1|seg)	9	227.28	6.27	0.03	0.903
~ mo + TminC + traf + pr + depC + off + (1|seg)	10	229.62	8.61	0.01	0.903
~1 + (1|seg)	2	250.84	29.83	0.00	--

Table 3. Microhabitat composition associated with Smooth Greensnakes (*Opheodrys vernalis* = OPVE) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae* = STOC) and random points in the northern Black Hills of South Dakota, USA, June-October 2016. Variables were measured within circular plots: herbaceous (i.e., grasses, forbs) height was determined by averaging four cardinal-direction measurements from Robel poles. Values represent means ± standard error.

Microhabitat Characteristics	OPVE (n = 17)	STOC (n = 27)	Random (n = 24)
Elevation (m)	1,667 (± 12.1)	1,664 (± 15.9)	1,656 (± 40.4)
Aspect (°)	125.3 (± 27.4)	112.2 (± 24.2)	122.2 (± 21.6)
Slope (°)	18.5 (± 4.4)	18.0 (± 3.5)	16.2 (± 2.9)
Canopy (%)	18.4 (± 6.9)	45.1 (± 7.2)	25.1 (± 5.6)
Rock (%)	17.9 (± 5.9)	9.4 (± 2.9)	5.6 (± 2.1)
Wood (%)	5.6 (± 3.2)	5.4 (± 1.1)	6.6 (± 2.1)
Herbaceous (%)	64.4 (± 7.9)	65.4 (± 5.4)	63.3 (± 6.5)
Litter (%)	9.7 (± 3.7)	18.3 (± 4.5)	19.9 (± 4.8)
Barren (%)	2.4 (± 0.8)	0.4 (± 0.3)	4.0 (± 1.7)
Herbaceous height	33.2 (± 5.1)	51.5 (± 6.2)	33.9 (± 3.5)
Total trees	6.8 (± 1.8)	17.1 (± 2.5)	10.6 (± 3.7)

model. For example, with canopy overstory of 25%, the odds of a microhabitat site being used by snakes versus a random location was 36% (CI = 9–75%), increasing to 59% (CI = 20–89%) at 50% overstory, and 79% (95% CI = 29–97%) at 75% overstory, after accounting for other covariates. Similarly, microhabitats with rocky substrate cover were more likely to be used by snakes than random when rock comprised 15% (snake-used: 59%, CI = 22–89%) and at least 30% (snake-used: 82%, CI = 33–98%) of a plot, after accounting for other covariates. Conversely, snakes were less likely to be associated with herbaceous ground cover unless it comprised at least 83% of plots (snake-used: 51%, CI = 17–84%); when herbaceous cover was ≤ 50%, predicted probabilities of it being used by a snake versus at random was 20% (CI = 3–66%). At median vegetation height, the predicted probability being used by snakes versus random was 32% (CI = 8–72%), but probabilities of snake-use increased with vegetation height albeit with wide intervals. We note that plots on sloped hillsides often had rocky talus piles indicative of overwintering hibernacula whereas flatter plots tended to be in mesic meadows. We conclude that differences between used and random sites had much overlap across all survey segments.

Elevation was correlated between taxa ($r_s = 0.895$, $P = 0.002$); *O. vernalis* were detected primarily at elevations between 1,550–1,799 m (mode, 1,650–1,699 m) and *S. o. pahasapae* were found from 1,500–1,899 m (mode, 1,600–1,699 m). Two competing models best explained microhabitat difference between the two species of snakes (Table 4). Models shared the covariates barren cover, leaf litter, and total trees (R^2m = 0.455) but differed by mean canopy cover (R^2m = 0.504); however, differences appeared subtle or with much uncertainty in dispersion. For instance, the predicted probability of microhabitats without barren cover (i.e., 0%) to be associated with *S. o. pahasapae* than *O. vernalis* was 63% (95% CI = 38–82%), but at 10% barren cover, the likelihood of being used by *S. o. pahasapae* dropped to 1% (95% CI = 0–54%). That is, *O. vernalis* was the species more likely to be in spots with bare patches, though barren composition never exceeded 10%, and *S. o. pahasapae* appears to avoid it altogether (Table 3). The three other covariates in top models were related to trees, which favored *S. o. pahasapae*. Plots were more likely to be used by *S. o. pahasapae* than *O. vernalis* when there were at least 15 trees (72%, CI = 46–89%), canopy overstory density at least 50% (75%, CI = 42–93%), and subsequent leaf litter substrate of at least 35% (71%, CI = 35–92%; Table 3).

Table 4. Mixed effect logistic regression models for predicting microhabitat composition differences of the response (*Res*) of (A) snake-associated versus random plots and (B) between Smooth Greensnakes (*Opheodrys vernalis*) and Black Hills Red-bellied Snakes (*Storeria occipitomaculata pahasapae*). Model selection was based on the change in corrected Akaike Information Criterion (ΔAICc) method (Venables and Ripley 2013). Variables are K = the number of model parameters. ω = relative model weight, and R^2m = marginal coefficient of determination for fixed effects. Abbreviations are bare = barren cover (%), can = mean canopy density (%), elev = elevation above sea level (m), herb = herbaceous cover (%), litt = leaf litter (%); rock = rock cover (%), tree = total number of trees, vegH = mean vegetation height, wood = woody debris cover (%), and seg = road segment, as a random effect.

Model	K	AICc	ΔAICc	ω	R^2m
A					
~ can + herb + rock + (1|seg)	5	77.04	0.00	0.30	0.205
~ 1 + (1|seg)	2	78.42	1.38	0.15	--
~ can + herb + rock + vegH + (1|seg)	6	78.78	1.74	0.12	0.238
~ rock + vegH + (1|seg)	4	79.77	2.73	0.08	0.070
~ herb + (1|seg)	3	80.34	3.29	0.06	0.004
~ can + elev + herb + rock + vegH + wood + (1|seg)	8	81.91	4.87	0.03	0.265
B					
~ bare + litt + tree + (1|seg)	5	51.90	0.00	0.39	0.455
~ bare + can + litt + tree + (1|seg)	6	52.31	0.41	0.32	0.504
~ bare + can + litt + (1|seg)	5	54.72	2.83	0.09	0.398
~ bare + litt + (1|seg)	4	56.56	4.66	0.04	0.287
~ bare + can + herb + litt + tree + vegH + (1|seg)	8	57.93	6.03	0.02	0.502
~ 1 + (1|seg)	2	63.00	11.10	0.00	--

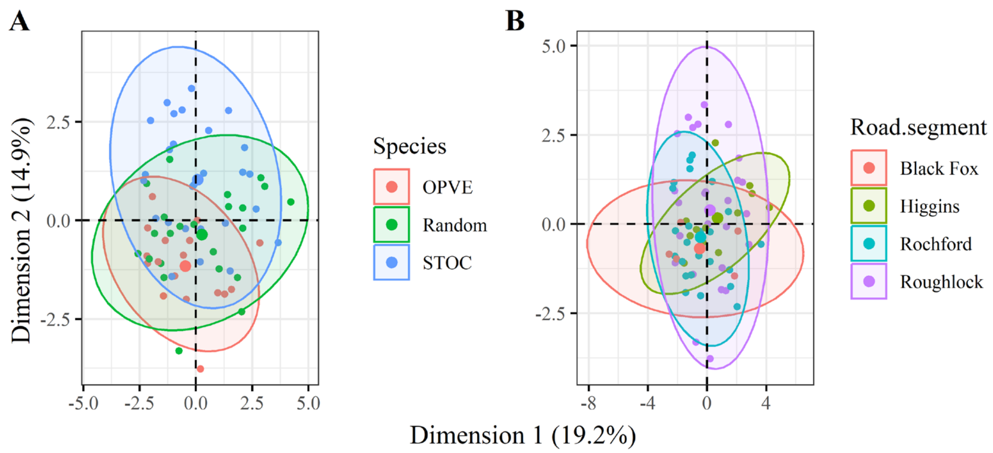

Figure 4. Multivariate biplots of roadside microhabitat composition in the northern Black Hills of South Dakota, USA in 2016. Data include aspect, elevation, canopy density, total trees, mean herbaceous height, and percent cover classes (barren, rock, wood, herbaceous, and leaf). Data are partitioned by (A) species levels (Smooth Greensnakes [*Opheodrys vernalis* = OPVE] and Black Hills Red-bellied Snakes [*Storeria occipitomaculata pahasapae* = STOC]) and random points; and (B) individual route segments. Enlarged points depict sublevel centroids.

For seasonal analyses, we only included Rochford and Roughlock segments as sample size were limited elsewhere. After partitioning the data for seasonally active and inactive habitats, we found significant differences for both slope ($F_{2,42}$ = 16.22, P < 0.001) and aspect ($F_{2,44}$ = 6.96, P = 0.002). *Post hoc* testing revealed no differences between snake species, but random sites grouped separately. We note that slope and canopy cover were not correlated (r_s = 0.187, P = 0.141).

Among seasonal microhabitat surface composition, we found that mean herbaceous height and percentages of rock, herbaceous cover, and leaf litter were significant variables to describe habitat composition (Wilk's lambda = 0.705, P = 0.001). Steeper sites had more rock and leaf litter and less plant and herbaceous growth than the flatter meadow sites. We also found no significant difference between species in both the active and inactive season habitats (Wilk's lambda = 0.640, P = 0.115). Concordant to our modeled results, the two snake species generally used similar microhabitats between active and inactive seasons.

Discussion

It is well known that roads affect snake populations and are a major cause of mortality (Shine et al. 2004; Andrews et al. 2008; Jochimsen et al. 2014). Spatial and temporal data can inform effective wildlife management strategies (Garrah et al. 2015; Lutterschmidt et al. 2019; Monge-Velázquez et al. 2022), and it is important to understand road-adjacent habitat that snakes may be using (Wagner et al. 2021). We found temporal, by-month differences for when both *O. vernalis* and *S. o. pahasapae* were active on roads. The relatively high rates of activity beginning in the last week of August throughout September likely signals the period of ingress towards overwintering hibernacula, as also found in the Black Hills (Jodi Massie et al., unpubl. report) and elsewhere (Ernst and Ernst 2003; Rutherford and Cairns 2020). Seasonal migration phenology is likely important for temperate species occupying a region where the onset of unfavorable wintry conditions can appear rapidly (Hamann 1943; Blais 2017). Ectotherms caught out in rapid temperature declines may not survive unless they are near refuges that reach below the frost layer (Churchill and Storey 1992; Storey 2006). This is undoubtedly true for *O. vernalis* and *S. o. pahasapae* in the Black Hills. Although dramatic and unpredictable weather in the Black Hills can restrict sampling during spring egress (i.e., late April to early June), prior efforts (Jodi Massie et al., unpubl. report; pers. obs.) suggest road activity for these two snakes during spring egress are similar to fall ingress.

Given the abundance of both species along certain road segments but not others, we were not surprised to find differences among road segments. Both species were already known at the Rochford segment, which consists of a large area of mesic meadows and south-facing rocky slopes with suspected hibernacula (Jodi Massie et al., unpubl. report). We expected a relatively high abundance of both species at the Roughlock Falls area based on incidental sightings prior to this study (pers. obs.).

Snakes are generally susceptible to mortality on both high and low traffic roads due to their activity and movement behaviors, especially near ecotones (Wagner et al. 2021). This may be especially true for small snakes such as *O. vernalis* and *S. o. pahasapae* due to their slow rate of movement (Ernst and Ernst 2003; Smith and Quinn 2012; Sacerdote et al. 2014). Our data revealed a concerningly high frequency (almost 80%) of snakes found DOR. This is despite the characteristics of the roads we sampled (i.e., unpaved, local road classification, relatively low traffic volumes). When in proximity to important habitat resources, roadkill rates may be high even if traffic rates are low (Hallisey et al. 2022). We acknowledge, though, that imperfect detection and between-survey carcass accumulation and persistence may in part explain higher DOR than AOR frequencies (Cabrera-Casas et al. 2020; Hallisey et al. 2022).

It is challenging to know when a snake was killed on a road, how long it persists, and how DOR rates relate to daily traffic volume (Santos et al. 2011; Cabrera-Casas et al. 2020). Rural roadways, like those in this study, may not be reliably monitored for traffic. We found daily traffic records for only the Rochford segment, albeit data were recorded discretely approximately every 3 y from four stations (https://opendata2017-09-18t192802468z-sdbit.opendata.arcgis.com/). Despite detecting a significant association between traffic and the number of DOR snakes, our DOR results may be conservative in respect to daily traffic rates in the Black Hills. For example, extrapolating our Rochford per-survey traffic rates to per-day estimates (mean = 63.1 ± 61.8 vehicles/d) represent roughly 28% of estimated average daily traffic captured from the Rochford stations, circa 2011 and 2020 (mean = 225.1 ± 90.4 vehicles/d). Our concerns remain as we have detected fewer snakes along Rochford during other projects and periodic road cruises since this 2016 study (pers. obs.). Fewer wildlife detections in formerly present areas may reflect population declines or extirpations (Barrientos et al. 2021). Our data suggest that roads are a significant mortality factor for small bodied and slow-moving ectotherms like *Opheodrys* and *Storeria*. Additional assessment of road-adjacent behavior and thermoregulatory resource preferences along movement corridors would add resolution to the road ecology of these taxa (Smith and Quinn 2012; Lutterschmidt et al. 2019; Mccardle et al. 2022).

Characteristics of roadside-associated micro-habitat.—We found no obvious differences in occurrence between *O. vernalis* and *S. o. pahasapae*: they are largely sympatric in the northern Black Hills, and both species are associated with very similar habitat types (i.e., they are syntopic). Microhabitats were relatively indistinguishable and when covariate predictors differed, it was subtle and with much overlap as identified by wide confidence intervals. For example, areas with moderate tree density, especially species that provide equivalent light and shade (e.g., 50% canopy), and subsequent leaf litter may slightly favor *S. o. pahasapae* whereas *O. vernalis* may be found in somewhat more open and patchy habitats. Given past findings (Smith and Quinn 2012; Jodi Massie et al., unpubl. report) and our results here, the likelihood exists that where one species is found, the other could also be present. Additional research may parse out untested differences in habitat/microhabitat usage, niche partitioning, and distribution between the species. Additionally, there was much overlap between snake-used versus random, available microhabitats. Dense meadows with tall herbaceous cover as well as rocky areas with moderate overstory appear to be favorably associated with these snakes.

Previous work (Jodi Massie et al., unpubl. report) revealed stark habitat demarcation related to seasonal usage. For both species, meadows are used during the active season and rocky slopes are used during winter dormancy. This sharp habitat dichotomy exists along the east-west orientated roads at the Rochford and Roughlock Falls segments. We interpret steep, rocky, south-southwesterly slopes as potential hibernacula as similarly found for other temperate zone snakes (Prior and Weatherhead 1996; Fitzgerald et al. 2013), though we did not find den sites during this study. Additionally, adjacent mesic meadows intuitively represent a resource selection link for the insectivorous *O. vernalis* and *S. o. pahasapae* (Ernst and Ernst 2003; Smith and Stephens 2003). Given that higher herbaceous cover was favorable to both species, overgrazing or meadow habitat degradation may exacerbate pressures on resources required by *O. vernalis* and *S. o. pahasapae*. For example, grazing and associated livestock/agricultural practices may negatively affect *S. occipitomaculata* directly (e.g., avoidance) or indirectly (e.g., reduction of prey resources; Pisani and Busby 2011; Dieter and Ronningen 2017). Roads that bisect important habitat features and movement corridors where population densities are high may lead to greater roadkill events (Garrah et al. 2015; Siers et al. 2016; Bennet 2017; Hallisey et al. 2022).

Conservation concerns and management recom-mendations.—We provide resolution of previously unquantified road ecology and habitat associations for *O. vernalis* and *S. o. pahasapae*, two data-deficient species of conservation concern within the Black Hills. Roads that bisect south-facing rocky slopes and mesic meadowlands are associated with use by both species. Although the Rochford segment was already known to have high densities of these taxa (Jodi Massie et al., unpubl. report), we draw attention to the alarmingly high roadkill rates that we found. Because of their behavior and size, populations of *O. vernalis* and *S. occipitomaculata* elsewhere are likely to be affected by roads that bisect population centers or migration corridors.

Effective road mortality mitigation structures are generally focused on larger taxa (Baxter-Gilbert et al. 2015). In some cases, properly located underpasses (e.g., eco-passages, hose-bridges) can lower road mortality of small snakes, especially when coupled with increased signage and awareness (Manka 2016; Colley et al. 2017). Identifying appropriate locations for vehicle-animal conflict mitigation infrastructure is important (Langen et al. 2009; Garrah et al. 2015). We caution, however, that widespread or dispersed snake mortality zones creates difficulties for mitigation (Wagner et al. 2021) and multiple or alternative conservation strategies (e.g., citizen-science, activity, and occupancy studies) are worth consideration (Gratwicke et al. 2016; Crawford et al. 2020; Chyn et al 2021; Hallisey et al. 2022; Mccardle et al. 2022). In such cases, mitigation in key identified areas, such as seasonal migration corridors, may be more practical and feasible (Beaudry et al. 2010).

Road mortality is unlikely to be the only stressor on populations of these snakes. Monitoring populations that are fragmented, isolated, or may become isolated is imperative to understand both evolutionary and forecasted climate-related effects (Blais et al. 2021; Cox et al. 2022). Climate change, habitat loss, and fragmentation will continue to stress snake populations globally (Diele-Viegas and Rocha 2018), especially for insular montane species (Davis et al. 2015). For example, *O. vernalis* is a cool-climate snake with evidence of population contraction and reduced heterozygosity in parts of its range where it has warmed and dried over time (Blais et al. 2021), and *S. o. pahasapae* is allopatricly disjunct from other populations by a vast sea of grass with gene flow limitations (Pyron et al. 2016). Climate change in the Black Hills is likely to bring warmer and drier conditions (Fontaine et al. 2001), which can alter fire regimes and affect forest landscape structure (Brown 2006). A broader assessment of stressors (e.g., climate change, disturbance, habitat loss) on populations of both species would be useful.

Because of considerable overlap in habitat characteristics and distribution between the two species in the Black Hills, umbrella-concept management of one species may provide conservation benefits to the other (Branton and Richardson 2010). The logical suggestion is that management prioritize *S. o. pahasapae* because it is already of conservation concern at state and federal levels, which should coincidentally benefit *O. vernalis*. Resource managers should attempt to minimize the effects of ground disturbing activities (e.g., road construction, natural resource harvesting) to protect areas where snakes forage and overwinter (Burger et al. 2012; Maida et al. 2020). For example, some winter refuges for *O. vernalis* and *S. o. pahasapae* consist of talus that can shift easily underfoot. Fragility of talus composition emphasizes the importance of locating these microhabitats and mitigating disturbances to preserve important seasonal refuges. Loss or excessive alteration of habitat important to these species are in part due to long-term management practices. For example, fire suppression, overgrazing, overharvest of keystone species, silvicultural practices, and other anthropogenic demands are linked to structural community changes and aridification in the Black Hills since the late 1800s (Parrish et al. 1996). Contemporary management that sustains or increases mesic meadow habitats while mitigating overgrazing should favor both taxa (Dieter and Ronningen 2017). Jodi Massie et al. (unpubl. report) provide additional management recommendations for these snakes. Preventing further fragmentation and preserving migration corridors will be key (Blais et al. 2021), and such conservation umbrella strategies should benefit other biota that share their habitat. Further research is warranted to provide resolution of natural history and ecological data for *O. vernalis* and *S. o. pahasapae*, including distributions, demography, and phenology (e.g., seasonal migration relationships or impact to prey base). Long-term population trends for these snakes should be monitored as well as assessment of how contemporary landscape-level disturbances (e.g., wildfire, logging, mining; Webb and Shine 2008; Caven et al. 2017) affect these small snakes.

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