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Contrasting Patterns of Migration and Habitat Use in Neighboring Rattlesnake Populations

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ABSTRACT.—Contrasting movements and habitat use may occur among snakes, and these differences may reflect important local responses to habitat variation and/or signify that broad, unimodal approaches to species conservation are too coarse. Fine-scale differences in these behaviors (e.g., between neighboring conspecifics) may be underappreciated because studies either focus exclusively on one (sub)population, and/or the animals are not compared across relevant ecological boundaries. We report on a striking dichotomy of seasonal migration behavior between Rattlesnakes (*Crotalus oreganus*) using two neighboring den sites. The snakes at one site undertook long-distance (2.9 ± 0.57 km [mean \pm SD], highly directional migratory behavior that was consistent across years and individuals. These movements carried them out of the habitat normally associated with these animals in this region (grassland steppe) and into higher elevation forests, a habitat not previously reported for these animals. Conversely, snakes at another den only 21 km away were nonmigratory (0.97 ± 0.54 km) and remained in grassland habitat throughout the year. Landscape and other environmental factors may have been responsible for the difference in the behavior of these two denning groups, suggesting that our knowledge of what dictates the migratory behavior of animals such as snakes is far from complete. Stereotyping the habitat use and behavior of any snake population is potentially misleading, and more thorough exploration is needed on how these animals alter their local movement patterns in response to changes in landscapes and habitat configurations, including potential climate change effects.

Divergent individual movement patterns within animal populations have been well documented, particularly those that are sex biased (Greenwood, 1980; Gregory et al., 2009; Pusey, 1987) or linked to a well-defined life-history stage. More recently, it has become apparent that even individuals sharing the same life history or reproductive traits can exhibit divergent patterns of movement (Olsson and Greenberg, 2004; Wysujack et al., 2009; Hebblewhite and Merrill, 2011). Although determining the extent, scale, and conditions by which movement patterns differ between neighboring populations is important, it also is difficult. As a result, cost, logistics, and/or local conservation issues often result in research being focused on one particular group or subset of a widespread population. The data from these focused studies are then extrapolated over a larger range for the animal, and important, insightful differences in movement patterns between groups of animals in proximity to one another remain undiscovered.

Although snakes often are cryptic in nature, the movement ecology of these animals has been well studied, and contrasting movements and habitat use have been reported. These differences have been shown between different age classes or individuals in different stages of reproduction. For example, juvenile and adult snakes in temperate climes often use different overwintering dens (Gregory, 1984; Larsen and Hare, 1992), and patterns of movement and habitat use have been shown to differ between gravid and nongravid females, between males and females, and between males and all other groups (Macartney, 1985; Reinert and Zappalorti, 1988; Charland and Gregory, 1995; Durbian et al., 2008). Geographic variation in movement patterns on a large scale also has been demonstrated: seasonal movements of garter snakes have long been known to be much greater in northern populations compared to populations farther south, presumably in response to a change in resource priorities and availability (Gregory and Stewart, 1975; Larsen, 1987). More recently, Parker and Anderson (2007) demonstrated “behavioral polymorphism,” whereby individual

Midget Faded Rattlesnakes (*Crotalus oreganus concolor*) either undertook straight-line movements, often followed by multidirectional movements in a summer range, or made multidirectional movements throughout the active season. This body of work suggests that patterns of space use may be more variable within snake populations than generally assumed. However, significant differences between neighboring, conspecific groups of snakes have not been well documented.

During the course of an empirical study on Western Rattlesnakes (*Crotalus oreganus*) near their northern limits (Gomez, 2007), we detected striking differences in the movement patterns (and habitat use) occurring between two neighboring denning groups of snakes. This work focused on adult male snakes because previous study on this and other *Crotalus* species indicated that this sex typically undertakes lengthy seasonal migrations between winter and summer habitats, whereas female movements often are tied to their reproductive status in a given year (Reinert and Zappalorti, 1988; Duvall and Schuett, 1997; Marshall et al., 2006). Hence, for a short-term study, male movements furnished more comparable data. The striking differences between these two groups of animals also revealed habitat use by the animals not previously documented for the species in this part of their range.

MATERIALS AND METHODS

We selected two study sites near the city of Kamloops ($50^{\circ}43'N$, $120^{\circ}25'W$) in British Columbia. Rattlesnake hibernacula in this area are restricted to lower elevation grassland steppe, presumably due to a combination of climate (earlier snowmelt, longer summers) and geology. The topography at site 1 was generally rugged with abundant bedrock outcrops on steep, south-facing slopes above a large waterbody (Kamloops Lake), but also included flat terrain in the upper elevations. This site contained two hibernacula approximately 500 m apart. Elevation at site 1 ranged from 350 to 1350 m. Habitat associations corresponded to the elevational gradient and changed from low-lying grasslands and open ponderosa pine (*Pinus ponderosa*) forests to interior Douglas-fir (*Pseudotsuga menziesii*) stands (Meidinger and Pojar, 1991). Site 2 was located entirely in low-lying grassland habitat at approximately 550-m

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elevation, with the lone hibernaculum in the area being within several hundred meters of urban developments. The straight-line distance between the two study sites was 21 km, with no major physical impediment to connectivity on the landscape (e.g., a major lake, mountain ridge, or other drastic change in ecosystem type). Although no precise estimates of the number of snakes at either den were available, throughout the study incidental captures of rattlesnakes at and in the general vicinity of each den were reasonably similar (site 1, 84; site 2, 63).

We used radiotelemetry to study the movement patterns of eight snakes in each of 2005 and 2006. Radiotransmitters (SM1, Holohil Systems Incorporated, Ontario, Canada) weighed between 3.2 and 5.2 g and comprised <5% of the snake's body mass. Veterinarians in the Animal Health Technology Program at Thompson Rivers University used surgical methods similar to those outlined in Reinert and Cundall (1982) to implant the radiotransmitters in snakes. Our overall sample sizes were ultimately set by the number of animals we could effectively monitor, given the snakes' propensity for extensive movements and the constraints of switching between the two sites (site 1 was particularly difficult to access). We also opted to track a subset of the animals over both years (with transmitter replacement), as no information existed on whether individuals followed similar movement paths from year to year. We thus had no a priori reason to believe individuals would demonstrate the same movement patterns over successive years, and collecting data of this nature was worth sacrificing larger samples of different individuals. In subsequent analyses comparing movements between years, we therefore treated these individuals as independent units in each year, with our focus being on demonstrating patterns within the two groups in each year.

We collected data between April and October 2005 and between April and July 2006. Animals were located with a handheld receiver as often as possible, typically one or two times per week. Locations (universal transverse mercators) of radiotagged rattlesnakes were recorded with a hand-held global positioning system (Garmin Ltd.), and the spatial accuracy of recorded locations was typically within 5 m. Due to this potential source of error, we considered a movement to be any change in location >10 m. Analyses were conducted in R version 2.4.1 (Ihaka and Gentleman, 1996).

To quantify an individual's movement pattern, we used net displacement and distribution of bearings. Net displacement refers to the total distance (maximum straight-line distance) between the beginning and end of a path (Turchin, 1998). We calculated net displacement for each individual using the Multiple Minimum Distance Extension Tool for ArcGIS 9.0. For each snake, we combined the directions of travel between all pairs of locations for an individual's distribution of bearings. We considered the migratory movements of each individual as a single path and defined migratory movements as those movements that occurred once the individual had moved from the den entrance until it attained the maximum displacement from the den.

To identify the individuals that oriented their migratory movements (i.e., nonrandom distribution of movements, or "directed" snakes), we applied Rao's spacing test to each snake's distribution of bearings in each year, to test the hypothesis of uniformity against a hypothesis of modality. This test was used because the data did not follow a Von-Mises distribution (circular equivalent to a normal distribution). We tested only those snakes that moved more than five times, as

required by the test statistic (Bergin, 1991). To test whether directed snakes from a den migrated toward a common bearing, we applied Rao's spacing test to the distributions. Critical values published by Russell and Levitin (1995) were used to test the hypothesis that the data points were distributed uniformly.

We defined the major habitat types in our study area following the designations used by Meidinger and Pojar (1991) and widely adopted by government ministries and other organizations in British Columbia. These were bunchgrass (*Pseudoroegneria spicata*), ponderosa pine (*Pinus ponderosa*), and two subzones of the interior Douglas-fir zone. This information was captured from geographic information system layers using ArcGIS 9, ArcView GIS 3.3 and several other program extensions (Hooge and Eichenlaub, 1997; Environmental Systems Research Institute, 1999).

To define "used habitat" at site 1, we systematically recorded the habitat types that occurred at 100-m intervals along the migration paths of six radiotagged snakes in 2005 and four radiotagged snakes in 2006. To define "available habitat" at site 1, we used the maximum distance attained from the den by a radiotagged snake to define the radius of the area centered around the denning site; we then used ArcGIS 9 to randomly select locations from the area (1,000 times in 2005 and 2006; water bodies excluded). We used a logistic regression model to indicate the direction of association with each habitat type. Habitat type was converted to dummy variables, and ponderosa pine was the reference category (Zar, 1999). Site 2 was composed entirely of bunchgrass habitat; thus, comparisons of second-order habitat use at site 2 were not possible.

RESULTS

During the 2 yr of this study, 11 individual snakes furnished movement data through telemetry. Five of these snakes were tracked in both years, providing information on the tendency of snakes to repeat their movements. The telemetered snakes were located 10.4 ± 2.7 (mean \pm SD, $n = 8$) times in 2005 and 10.9 ± 3.4 ($n = 8$) times in 2006. This provided eight sets of snake movements in 2005, and another eight in 2006. Over these 16 cases, the maximum displacement distance that the radiotagged snakes moved from their dens averaged 2,188 m (SD = 1,118 m). However, there were very notable differences between the two sites. The mean maximum distance that the site 1 snakes were found from their den site was 2,922 m (SD = 573, $n = 10$), whereas the site 2 snakes moved much shorter distances (966 m, SD = 542 m, $n = 6$; the difference between these values was statistically significant [$t_{14} = 6.74$, $P < 0.0001$]).

There were eight cases in which the animals directed their movements toward a fixed bearing (Rao's spacing test stat > critical value at $P = 0.05$) and eight cases in which this did not occur (Rao's spacing test stat < critical value at $P = 0.05$). The latter included just two of eight snakes from site 1, but all of six snakes from site 2 that were tracked from the den to the summer range. The eight snakes from site 1 that showed directed movement did not migrate toward random bearings from the den in 2005 ($n = 5$) or in 2006 ($n = 3$, Rao's spacing test stat > critical value, $P = 0.001$). Instead, their migration pathways were concentrated toward the northeast (Fig. 1). Maximum distance from the den of directed snakes differed from that of nondirected snakes ($t_{14} = -3.95$, $P = 0.001$): for the most part, snakes that directed their migratory movements toward a fixed bearing moved twice as far from the den site as snakes whose movements were not directed.

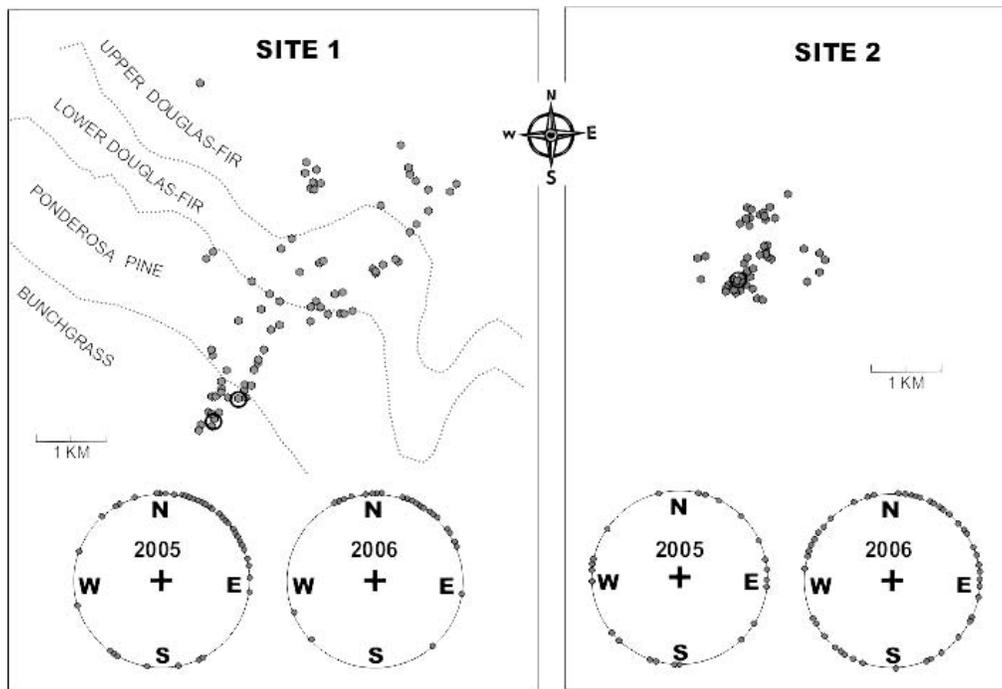


FIG. 1.—Locations and directionality of rattlesnakes radiotracked from two denning sites (site 1, left; site 2, right). Open circles on maps indicate precise location of entrances to hibernacula (two at site 1, one at site 2). Top section of each panel is a map showing the locations collected on the telemetered snakes ($n = 10$ for site 1, $n = 6$ for site 2). Note identical scales on each map. Snakes in site 1 also left the bunchgrass habitat typically associated with the species and travelled in a northeasterly direction, taking them into several different vegetation zones (at increasing elevation). Snakes at site 2 never left the bunchgrass zone surrounding the den. Orientation plots at the bottom of each panel show consistent directionality trends at each site, across the 2 yr of the study.

In site 1, we sampled habitat type from 340 points along paths used by six rattlesnakes in 2005 and four rattlesnakes in 2006 and from 2,000 points within the area available to snakes during the summer. A logistic regression model showed that habitat type significantly reduced the deviance of the null models in both years (2005: likelihood ratio $\chi^2 = 10.76$, $df = 2$, $P = 0.005$; 2006: likelihood ratio $\chi^2 = 15.43$, $df = 2$, $P < 0.001$), but correctly predicted only 56 and 59% of habitat types, marginally better than 50%. Compared with ponderosa pine and bunchgrass habitat, rattlesnakes were positively associated with interior Douglas-fir in 2005 and 2006 (2005: coefficient = 0.28, Wald $\chi^2 = 6.99$, $P = 0.0083$; 2006: coefficient = 0.41, Wald $\chi^2 = 9.27$, $P = 0.0023$).

As mentioned, five individual rattlesnakes were tracked in both 2005 and 2006 (site 1, $n = 3$; site 2, $n = 2$). Data from these snakes showed consistent movement patterns of individuals from year to year (Fig. 2), with the snakes from site 1 all travelling nearly the same elongated pathways, whereas the snakes at site 2 displayed consistent less-elongated movements, albeit using similar areas of the landscape. Overall, the maximum straight-line distance that these animals moved from their dens ranged from 297 to 3,568 m, and the snakes attained the same maximum distance between years ($t_4 = 0.10$, $P = 0.92$).

DISCUSSION

Our key finding was that mature male snakes at the two neighboring dens exhibited highly differentiated movement patterns during the annual migration period, with males at one location (site 1) travelling farther from their hibernacula than previously reported for the species. These differences were consistent across the 2 yr of our study, and individual animals

tracked in successive years were consistent in terms of the maximum distance attained from their respective dens. These results provide clear evidence that migratory behavior and habitat use in a species can vary tremendously, even between neighboring groups of individuals. Certainly, a diversity of movements and habitat use has been demonstrated in snakes, including variation in these behaviors within the same species (Macartney, 1985; King and Duvall, 1990; Blouin-Demers and Weatherhead, 2002; Brown, 2006; Jørgensen, 2009). However, our study is one of the first to show such striking, simultaneous differences in movements and habitat use between neighboring groups. This can be attributed partly to the spatial scale at which these animals operate; but nonetheless, our results show that the resolution at which we categorize habitats for animals (and then draw inferences about movements) may need to be re-examined for certain species.

Despite our small sample sizes, the patterns we observed seem reasonably fixed in the two groups of animals. We saw no evidence of variation in annual movements by those animals that were tracked over two consecutive field seasons. Consistent movement patterns for snakes (including den fidelity) also have been reported previously by Jenkins and Peterson (2005) and Parker and Anderson (2007). Migratory and contrasting sedentary behaviors are well documented in avian literature, leading Berthold (1999) to propose that the proportion of migrants and residents within a population may be determined by selection and microevolution. Environmental factors including the distribution of resources and habitats also have been shown to affect migration (Alerstam et al., 2003).

What factors then are responsible for the different movement patterns exhibited in this study? Two experimental approaches to investigating the phenomenon of divergent movement

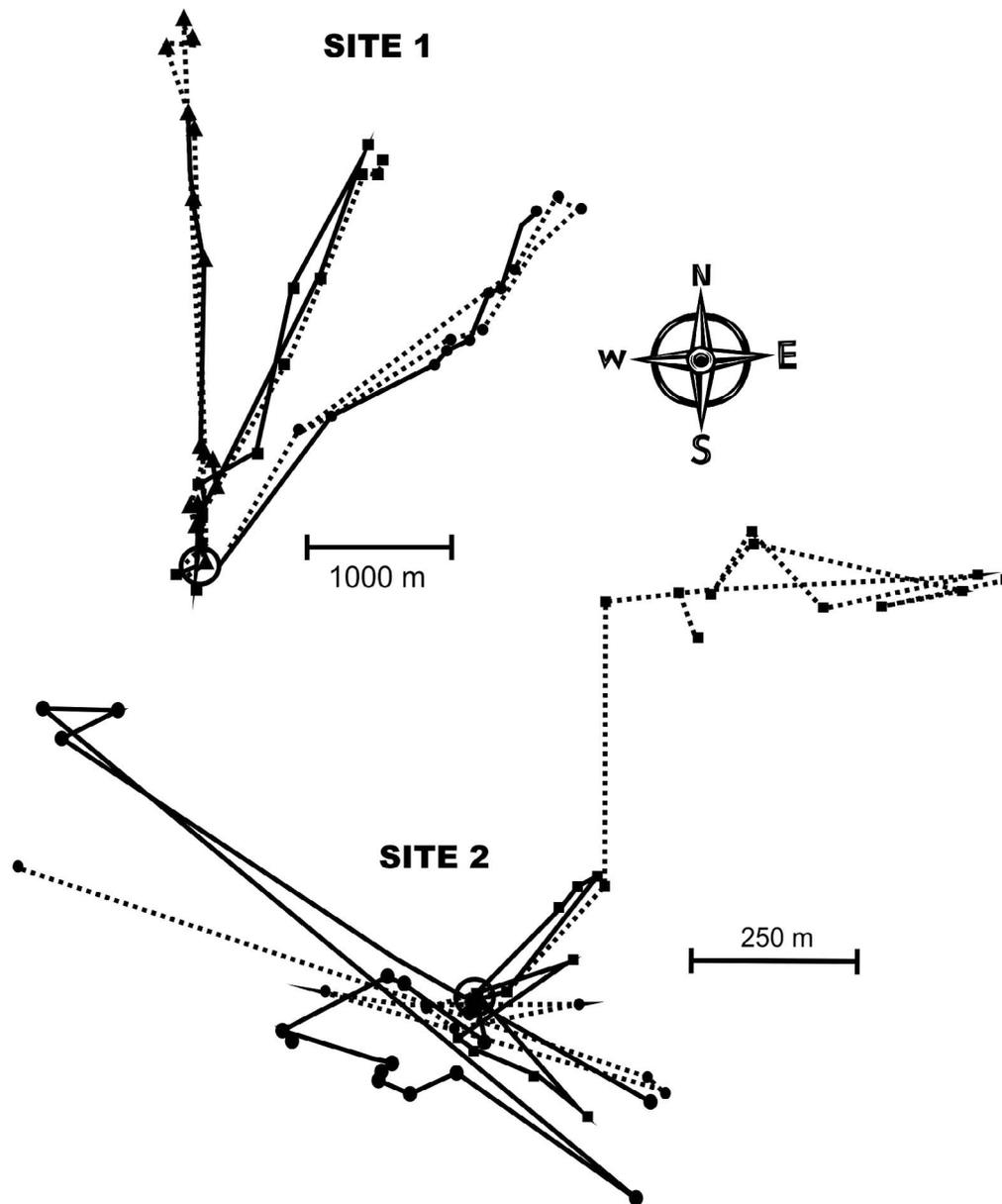


FIG. 2.—Comparisons of annual movement patterns of individual snakes tracked in both years of study. Locations for each individual snake are depicted by the same symbol type within each of the two illustrations. Broken lines represent movements in 2005, and solid lines represent movements in 2006. Note the differences in scale of the two maps. At site 1, three snakes showed very similar elongated, long-distance movement patterns when compared from year to year. At site 2, two snakes showed relatively less consistency in movement pattern and magnitude, although each snake still tended to occupy roughly the same parts of the landscape over the 2 yr.

behavior (and the relative effects of genetic and environmental factors) would be as follows: 1) manipulation of environmental resources and 2) reciprocal translocations of animals into populations showing different movement behaviors. The former would be particularly valuable if before the manipulation, an individual's migration strategy has been identified as either long-distance or sedentary. Taylor et al. (2005) found no relationship between home range size and supplemental feeding of female timber rattlesnakes; this work could be repeated with migration strategy as the dependent variable. Manipulation of resources may be preferable over reciprocal transplant experiments because translocated rattlesnakes are known to exhibit atypical movement patterns (Reinert and Rupert, 1999; Brown et al., 2009), likely resulting from their strong fidelity and imprinting to specific hibernating sites. To

our knowledge, no published study exists on the reciprocal transplant of snakes, but see Olsson et al. (2006) for an example of using this approach to demonstrate that the migratory behavior of Brown Trout (*Salmo trutta*) is a plastic response influenced by growth opportunities.

Situations in which extensive migration occurs in only a subset of the population may provide opportune conditions for understanding why and how movement patterns vary. In snakes, studies have focused primarily on the spatiotemporal distribution of resources to explain space use, but attention also should be given to the role that genetics may have in predisposing an individual to a particular migratory behavior. The application of partial migration theory to diverse taxa and ecosystems should help further our understanding of the movement patterns observed in nature (Chapman et al., 2011).

Our finding of divergent movement patterns is made more interesting by the fact that the lengthier movements took animals into habitats not normally associated with this species in this region. Typically, this species is linked to dry grassland steppes and open, sparsely treed habitat (Macartney, 1985; Bertram et al., 2001; COSEWIC, 2004; Brown, 2006; Matsuda et al., 2006), whereas in our study the use of Douglas-fir forests during the active season was significantly greater than the use of the other available types. Possibly the forested habitat in this location offered greater prey availability and/or suitable thermoregulatory opportunities. Simultaneous study of habitat use by rattlesnakes from numerous areas surrounded by similar habitat types would be needed to make such comparisons. Future studies should investigate whether rattlesnakes from populations in similar locations also migrate into these higher elevation forests.

Documenting (and eventually understanding) the factors responsible for divergent movement patterns such as seen here has important bearing on the conservation and management of species. The existence of strong differences in movement patterns may indicate a need to maintain a variety and distribution of resources on the landscape that meets the needs of both migratory and sedentary individuals. Although this will be challenging, it will likely be increasingly important as environmental conditions continue to be altered. Climate change and urbanization have been found to influence migratory behavior in various bird species, and the effects of these changes on migratory behaviors in other animals should be considered (Pulido and Berthold, 2004; Partecke and Gwinner, 2007).

Our findings add new layers of complexity to our understanding of the movement patterns and habitat use of this and other species. Not only may these parameters change for animals over their range (e.g., Constible et al., 2010) but also they may vary over much finer scales and population subunits. We encourage biologists, conservationists, and managers to exercise caution when extrapolating information on one confined group of animals to conspecifics over a larger area.

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