

# Migration and disturbance: impact of fencing and development on Western Rattlesnake (*Crotalus oreganus*) spring movements in British Columbia

Jared R. Maida, Christine A. Bishop, and Karl W. Larsen

**Abstract:** Due to increasing anthropogenic pressures, including land-use transformation globally, the natural process of animal migration is undergoing alterations across many taxa. Small-scale migrants provide useful systems at workable scales for investigating the influence of disturbance and landscape barriers on natural movement patterns and migrations. The Western Rattlesnake (*Crotalus oreganus* Holbrook, 1840) in British Columbia, Canada, is a small, migrant predator that undertakes seasonal spring movements from its communal hibernaculum to summer hunting and mating grounds and reverses its movements in autumn. From 2011 to 2016, we examined changes to spring migration movements in 27 male Western Rattlesnakes encountering both mitigative fencing barriers and disturbed habitats. Individuals moving through disturbed habitats or intercepted by mitigative fencing demonstrated shorter migration distances and reduced spring path sinuosity compared with individuals migrating in undisturbed habitats. Specifically, individuals encountering a fence during spring movements completed shorter total spring migration path lengths and occupied smaller home ranges over the course of the entire active season. Total spring migration distance also was strongly associated with the distance that individuals traveled until they first encountered human disturbance. This study contributes significantly to our knowledge of how fencing barriers may impact normal behavioural patterns in smaller vertebrates.

**Key words:** migration, *Crotalus oreganus*, disturbance, movement ecology, wildlife fencing, Western Rattlesnake.

**Résumé :** En raison de pressions d'origine humaine croissantes, dont les changements d'utilisation du sol à l'échelle planétaire, le processus naturel de migration animale subit des modifications chez de nombreux taxons. Les espèces migrant sur de petites distances constituent des systèmes dont l'échelle des déplacements se prête à l'étude de l'influence des perturbations et des barrières paysagères sur les motifs de déplacement et les migrations naturels. Le crotale de l'Ouest (*Crotalus oreganus* Holbrook, 1840) en Colombie-Britannique (Canada) est un petit prédateur migrateur qui effectue des déplacements printaniers de son aire d'hibernation à des lieux de chasse et d'accouplement estivaux, et les déplacements inverses à l'automne. De 2011 à 2016, nous avons examiné les changements des déplacements de la migration printanière de 27 crotales mâles en présence de clôtures d'atténuation et d'habitats perturbés. Les individus se déplaçant à travers des habitats perturbés ou interceptés par des clôtures d'atténuation étaient caractérisés par de plus courtes distances de migration et une plus faible sinuosité de leurs déplacements printaniers que les individus migrant à travers des habitats non perturbés. Plus précisément, les individus rencontrant une clôture durant leurs déplacements printaniers effectuaient des déplacements de migration de longueurs totales moins grandes et occupaient des domaines vitaux plus petits à l'échelle de la saison active. La distance totale de la migration printanière était aussi fortement associée à la distance parcourue par les individus avant qu'ils rencontrent une perturbation d'origine humaine pour la première fois. L'étude constitue une importante contribution aux connaissances sur l'influence possible des clôtures sur les motifs comportementaux normaux de petits vertébrés. [Traduit par la Rédaction]

**Mots-clés :** migration, *Crotalus oreganus*, perturbation, écologie des déplacements, clôtures pour la faune, crotale de l'Ouest.

## Introduction

How animals distribute themselves on the landscape is regulated by various factors, including habitat quality and availability, access to food, predator avoidance, and mate acquisition (DeGregorio et al. 2011; Christiansen et al. 2017). One notable and high-profile example of this process is migration. Migratory behaviour is the seasonal movement by individuals within a population (Wilcove et al. 1998; Naidoo et al. 2016; Martin et al. 2017) and is categorized by having a distinguishable objective with a

defined route. However, migration as a biological concept tends to be fluid and at times elusive, complicated by the variations seen in distances travelled, timing (annual to daily), and frequency within individual lifetimes (Hoare 2009).

Migration is critical for population persistence (Hoare 2009), allowing individuals to respond to seasonal changes in resource availability and exploit habitats beneficial or critical for different life history processes such as breeding, overwintering, and grazing or hunting prey (Alerstam et al. 2003). Therefore, interrup-

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**J.R. Maida.\*** Environmental Science Program, Thompson Rivers University, 805 TRU Way, Kamloops, BC V2C 0C8, Canada.

**C.A. Bishop.** Environment and Climate Change Canada, Science and Technology Branch, Wildlife Research Division, 5421 Robertson Road, Delta, BC V4K 3N2, Canada.

**K.W. Larsen.** Department of Natural Resource Science, Thompson Rivers University, 805 TRU Way, Kamloops, BC V2C 0C8, Canada.

**Corresponding author:** Jared R. Maida (email: [jaredmaida@gmail.com](mailto:jaredmaida@gmail.com)).

\*Present address: Canadian Wildlife Service, Environment and Climate Change Canada, 1238 Discovery Ave., Kelowna, BC V1V 1V9, Canada.

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tions to this behaviour can restrict individuals from acquiring resources, in turn impacting fitness and ultimately survival (Gubili et al. 2017). Understanding the patterns and implications of migration within wildlife populations may be a critical component of maintaining functional and connected landscapes (Epps et al. 2011; Naidoo et al. 2016) crucial for both species conservation and community–landscape preservation.

Due to increasing anthropogenic pressures and continued land-use transformations globally, the process of animal migration has been undergoing alterations in many different taxa (Wilcove et al. 1998; Dobson et al. 2010; Naidoo et al. 2016). The specific drivers of these changes vary across species, locale, and temporal scales, but the leading identifiable threats are the destruction of habitat, construction of physical barriers (e.g., dams and fences), animal exploitation, and climate change (Harris et al. 2009). Disturbed and fragmented areas typically exhibit ecological traits that differ from natural habitat, specifically altering resource composition, abundance, and access for animals (Shine et al. 2004). Furthermore, features and situations that present a barrier or restrict animal movement run the risk of fragmenting populations and presenting obstacles for individuals (Gubili et al. 2017). For example, weirs that fragment streams and tributaries prevent migratory trout (*Salmo trutta* Linnaeus, 1758) from reaching their spawning destinations (Gosset et al. 2006), and reindeer (*Rangifer tarandus tarandus* (Linnaeus, 1758)) avoid crossing parallel power lines and roads, reducing migration area and access to grazing habitat (Vistnes et al. 2004). Pink-footed Geese (*Anser brachyrhynchus* Baillon, 1884) that stage their migration within disturbed, human-influenced farmland habitat display relatively lower growth rates and reduced reproductive success (Madsen 1995).

Migrations involving long distances and the mass movement of animal aggregations tend to attract relatively more attention (e.g., wildebeest, Hopcraft et al. 2014; Pacific salmon, Kovach et al. 2015) compared with smaller scale, individual migrations such as those performed by many temperate amphibians and reptiles (Duvall et al. 1990; Chiszar et al. 2014; Yermokhin et al. 2015). However, human disturbance and landscape barriers may have a large and less visible impact on the seasonal movement of these animals despite smaller annual travel distances and the variation of spatial use on the landscape. Smaller migratory species with small-scale home ranges and movement patterns therefore may provide useful systems for investigating the implications of disturbance and barriers on natural migration behaviour.

Temperate snakes, particularly those at northern latitudes, undertake seasonal migrations between overwintering hibernacula to summer foraging and mating grounds (Landreth 1973; Duvall et al. 1990; Jørgensen et al. 2008; Chiszar et al. 2014; Gomez et al. 2015). These migrants typically exhibit three types of movement and behavioural patterns throughout the course of an active season: (i) spring migration away from hibernaculum; (ii) mid-summer movements within established hunting and mating grounds; and (iii) fall migration back to hibernaculum for overwintering. A number of factors have been posited to drive snake movements away from hibernacula, namely, the spatial separation between hibernacula and foraging–mating grounds, limited suitable habitat for hibernacula, reduced competition within a communal hibernacula community (Larsen 1987; Bauder et al. 2015), and the unequal dispersion of thermal habitat across the landscape (Huey 1991; Shine et al. 2004; Harvey 2015).

Spring migration can result in snakes travelling considerable distances from their hibernaculum while typically demonstrating linear pathways (Martino et al. 2012; Chiszar et al. 2014). These long and straight movements likely optimize encounter rates with irregularly distributed resources on the landscape such as prey and mates (Duvall and Schuett 1997; Duvall et al. 1997). Individual Prairie Rattlesnakes (*Crotalus viridis viridis* (Rafinesque, 1818)) provided with supplemental food had reduced movement frequencies and distance during spring migration (Duvall et al.

1990), suggesting a primary function of spring migration for this species was to locate and successfully hunt prey. However, detailed assessments of spring migration patterns in temperate climate snakes are rare.

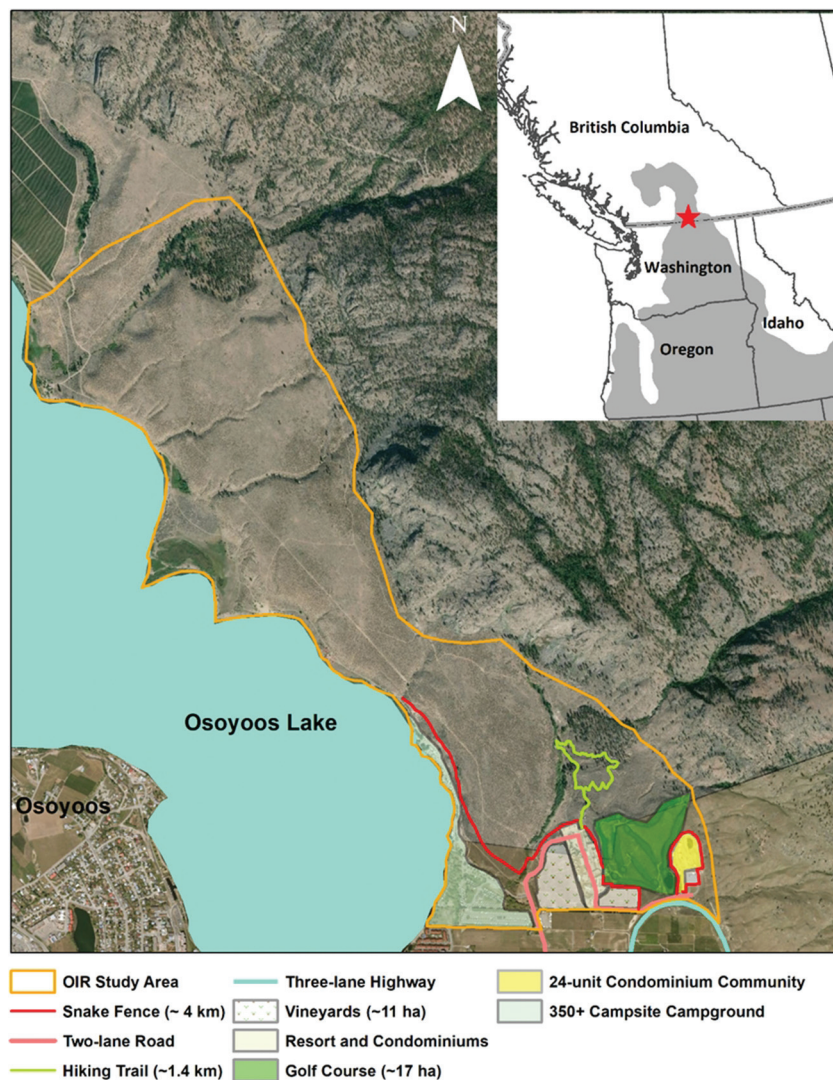
Migratory effects aside, the impacts of human disturbance, habitat loss, and habitat fragmentation on snake behaviour and movements are widely recognized (Parent and Weatherhead 2000; Shine et al. 2004; Breiningner et al. 2011; Lomas et al. 2019). For example, Eastern Indigo Snakes (*Drymarchon couperi* (Holbrook, 1842)) have smaller home ranges in fragmented landscapes in Florida (Breiningner et al. 2011), while Western Diamondback Rattlesnakes (*Crotalus atrox* Baird and Girard, 1853) and Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus* (Rafinesque-Schmaltz, 1818)) both move less frequently in disturbed, human-influenced habitats (Parent and Weatherhead 2000; Beale et al. 2016). Furthermore, Red-sided Garter Snakes (*Thamnophis sirtalis parietalis* (Say in James, 1823)) (Shine et al. 2004) and Eastern Hog-nose Snakes (*Heterodon platirhinos* Latreille, 1801) (Robson and Blouin-Demers 2013) appear to exhibit roadway avoidance. Prairie Rattlesnakes show more tortuous (i.e., crooked) movements and reduced body conditions in human-dominated landscapes (Martin et al. 2017).

Fencing infrastructure on the landscape is a common cause of habitat fragmentation (Jakes et al. 2018); however, it also is used to reduce direct impacts of disturbance to herpetofauna, including snakes (Colley et al. 2017; Markle et al. 2017). Fencing is used to restrict snake access or movement into a specific area (Gregory 2007) or deflect snake movement away from certain areas and (or) towards favourable habitat (Willson and Gibbons 2009) and can be very effective at reducing human–snake encounters in residential areas or roadways (Colley et al. 2017). However, fencing still constitutes a physical barrier obstructing natural movement patterns and behaviour that may have consequences for individuals (i.e., mortality; Ferronato et al. 2014; Eye et al. 2018). The effects on spring migration patterns and movements of snakes by fencing, or other anthropogenic barriers, have not been adequately assessed.

The Western Rattlesnake (*Crotalus oreganus* Holbrook, 1840), listed as “Threatened” in Canada (COSEWIC 2015), exists at the northern limits of its range in southern British Columbia (B.C.) (Gomez et al. 2015; Lomas et al. 2015; Maida et al. 2018). The primary threats to Western Rattlesnakes are habitat loss, fragmentation, road mortality, and human persecution (Maida et al. 2018; Winton et al. 2018). Rattlesnakes in B.C. occupy hibernacula between October and April (Macartney and Gregory 1988; Brown et al. 2009; Maida et al. 2017) and can move up to 4 km away from their overwintering habitat during the active season (Harvey 2015). Within B.C., this snake resides in semi-arid valley bottoms that are subjected to increasing human development due to some of the fastest rates of human population growth in Canada (Statistics Canada 2014; Lomas et al. 2015). Due to strong fidelity to hibernacula, summer foraging grounds, and migration corridors (Brown et al. 2009; Gomez et al. 2015), these animals appear to lack the behavioural plasticity to adjust movement patterns and spatial distributions to avoid new development or other land-use changes, similar to that documented for Eastern Diamondback Rattlesnakes (*Crotalus adamanteus* Palisot de Beauvois, 1799) (Waldron et al. 2013).

Lomas et al (2015, 2019) found that rattlesnakes frequenting disturbed habitats demonstrated lower body conditions, smaller home ranges, and shorter range lengths at the extreme southern portion of their range in Canada. At that same study site, we investigated how human disturbance and fragmented landscapes altered rattlesnake spring migration patterns. Specifically, the main purpose of this study was to determine and quantify the shifts in spring migratory behaviour by individual rattlesnakes encountering mitigative fencing for the first time. We predicted that migrating rattlesnakes encountering barriers (both fencing

**Fig. 1.** Map of study site (indicated in orange) near Osoyoos, B.C., Canada. The northern and eastern portions remained undeveloped with developed areas concentrated to the southern and western portions of the study site. A condominium community and associated snake fence is located at the southeastern corner of the study site. Inset shows the northern extent of the Western Rattlesnake (*Crotalus oreganus*) range within the Pacific Northwest region, with the Osoyoos study site indicated by a star (map imaging: Esri, Digital Globe, GeoEye, Earthstar Geographics, CNES/Airbus, DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).



and landscape) in the spring would have shorter spring migration distances, shorter migration duration, and more sinuous movements compared with those migrating through undisturbed habitats. Further, we also predicted that alterations to spring migration would impact rattlesnake home-range parameters and, following Lomas et al. (2015), influence body characteristics over the course of the active season.

## Materials and methods

### Study site

We used radiotelemetry to track Western Rattlesnakes between 2011 and 2016 on the Osoyoos Indian Reserve (OIR) near Osoyoos, B.C., Canada (119.4°W, 49.28°N). The 450 ha area (Fig. 1) was mainly comprised of low-elevation (300–400 m) arid shrub–steppe habitat characterized by big sagebrush (*Artemisia tridentata* Nutt.), antelope bitterbrush (*Purshia tridentata* (Pursh) DC.), and native grasses (see Brown et al. 2009; Lomas et al. 2015; Maida 2018). The

site was bordered by Osoyoos Lake to the west and by open ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) forests and rocky slopes to the east that contained rattlesnake communal hibernacula at elevations of ~500–650 m (Maida et al. 2017). Hibernacula on our study site ranged between ~280 and 1880 m from human disturbance.

The study site contained drastic habitat quality contrasts, from heavily developed and fragmented portions to those in near-pristine condition with minimal human involvement or habitat fragmentation (Fig. 1; Supplementary Fig. S1<sup>4</sup>). Intensive human activity and development was primarily situated in the southern portion of the study area and was targeted towards tourism, including a golf course, winery and vineyards, cultural centre, walking trails, and a large campground and condominium resort with associated roads and parking lots. To reduce negative human–snake conflicts, ~4 km of snake exclusion fence surrounded most of the resort, parking lots, and roadways, as well as the camp-

<sup>4</sup>Supplementary figures and table are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0110>.



**Fig. 2.** Condominium community and construction with surrounding mitigative wooden snake fence structure. Colour version online.



ground (Eye et al. 2018). The northern and eastern portions of the study had limited human influence and lacked any landscape alterations or disturbance.

In the study site, rattlesnakes demonstrate two main spring movement patterns and orientations: (i) move west and down-slope into the valley bottom or (ii) move east into the higher elevation forest (Lomas 2013; J.R. Maida, personal observation). In this study, we focus on the animals moving from their hibernaculum into the valley bottoms in both the southern and northern portions of the study site.

In 2012, construction began on a condominium community located between the east edge of the golf course and the mountain slopes bordering the study site. As of 2016, the community had 24 units constructed (Fig. 1), and the construction lasted the duration of the study through 2016. To minimize human–snake conflict, a permanent drift fence (Fig. 2) was built surrounding the ~4 ha community to limit snake access into the community and to redirect snakes into neighbouring habitats. A fence ~0.9 m tall composed of galvanized mesh hardware cloth with 0.6 cm openings was buried approximately 15 cm under the surface (for further detail on the entire snake fence structure on the OIR study site, see Eye et al. 2018). The fence was supported by wooden posts and top and bottom rails. Based on previous research and the location of the new development and fence (well within 400 m of some hibernaculum; Fig. 1), rattlesnakes embarking on spring migration into the valley bottom were expected to encounter the fence early in their annual spring migration.

#### Radiotelemetry

We radio-tracked only adult males due to the extreme variations in movement patterns exhibited by females of different reproductive status (Macartney and Gregory, 1988). In each year, we captured snakes during egress (April–May) at or near hibernacula for transmitter implantation. We transported the animals to a nearby veterinary clinic for surgical implantation of radio transmitters (SB-2; Holohil Systems Ltd., Carp, Ontario, Canada). Surgical procedures followed Reinert and Cundall (1982) and pharmaceutical procedures followed Brown et al. (2009). Transmitters weigh-

ing, on average, 2.5% of total body mass (range: 1.6%–3.7%) were implanted into the coelomic cavity. Animals were held in captivity for 24–48 h following surgery to allow recovery and rehydration before being released at their original capture location.

We located each telemetered snake approximately every 2–3 days throughout the entire active season (April–October). In doing so, we tracked snakes from hibernacula in the spring, throughout the summer season, and then back to hibernacula in the fall (ingress), unless mortality and (or) transmitter failure occurred. To track individuals, we used a three-element yagi antenna and a portable radiotelemetric receiver (TRX-1000S; Wildlife Materials Inc., Murphysboro, Illinois, USA) and we recorded the Universal Transverse Mercator (UTM) coordinates of each location using a MobileMapper 6 device (Magellan Professional Inc., Santa Clara, California, USA). We briefly recaptured and inspected each snake approximately once per month to monitor health and ensure that the surgical incision was healing appropriately; during these “checkups,” we documented snout–vent length (SVL; in centimetres) and mass (in grams). Apart from that, care was taken to collect location data of animals from 2 to 5 m away to limit disruption and changes in snake behaviour. All rattlesnake handling, transportation, and surgical protocols were reviewed and approved by the Thompson Rivers Animal Care Committee.

#### Spring migration parameters

We calculated a series of metrics to quantify rattlesnake spring migration on our study site. We identified outbound spring migration as ending when movements away from hibernaculum became <50 m between consecutive locations and (or) 4 days spanned between movements (Lomas et al. 2019). We assessed spring migration distance (MD) as the total straight-line distance between the start of migration (hibernaculum) and the end (start of summer foraging). Spring migration path length (MPL) was the total sum distance of each consecutive movement event until the end of spring migration. We calculated spring migration path sinuosity (MPS) as  $MPL/MD$ , creating a ratio ranging between 0 and 1, with values approaching 1 indicating straighter movements and values approaching 0 equating to more crooked and random

movements (Saumure et al. 2010; Martin et al. 2017). Distance to nearest source of disturbance (DTD) was the total straight-line distance from each individual's starting point in the spring (hibernacula) to the first confirmed contact with human disturbance, with this being a golf course fairway, snake fence, roadway, or walking trails. Rattlesnakes from the same hibernacula contained dissimilar migration routes and corridors and may have come into first contact with a disturbance at different times. Therefore, snakes from the same hibernacula often had different DTD values. Spring migration duration (DAYS) was calculated from the first move away from hibernacula in the spring until the end of migration movements and the beginning of the summer foraging season. We analyzed and calculated MD, MPL, and DTD using the measuring tool in Garmin Basecamp version 4.6.2 (Garmin International, Inc., Olathe, Kansas, USA; [www.garmin.com/en-CA/software/basecamp/](http://www.garmin.com/en-CA/software/basecamp/)).

### Home-range parameters

For the entire active season, we estimated rattlesnake home ranges using the 100% minimum convex polygon (MCP). The MCP method creates a polygon around the outermost points plotted on a map, including 100% of the individual's telemetric locations. We chose the MCP method to maximize comparisons with existing literature on snake activity studies, including many studies at the northern extent of our species' range (Brown et al. 2009; Holding et al. 2014; Harvey 2015; Lomas et al. 2019). This method also has been suggested to best reflect herpetofauna home-range size (Row and Blouin-Demers 2006; Shipley et al. 2013; MacGowan et al. 2017). The core area of use within each snake's home range was calculated using 50% fixed-kernel (KD) isopleths (Tiebout and Cary 1987; Lomas et al. 2019). For this calculation, we used an ad hoc method to select the appropriate smoothing factor ( $h_{\text{ad hoc}}$ ) to prevent over- or under-smoothing (Berger and Gese 2007). We decreased the reference bandwidth ( $h_{\text{ref}}$ ) by 0.1 until we found the home-range estimate that included all telemetric locations and represented the smallest continuous polygon with no lacuna (Berger and Gese 2007; Kie 2013; Bauder et al. 2015), and we then used the outputs from the 50% isopleths from those estimates. We calculated both 100% MCP and 50% fixed-kernel isopleths using the Home Range Tools (HRT) extension (Rodgers et al. 2007) in ArcGIS version 10.2.2 ([www.esri.com](http://www.esri.com)).

### Body condition and growth

We calculated body condition index scores for each telemetered rattlesnake by using the residuals from a log-transformed regression between mass and SVL (cf. Parent and Weatherhead 2000; Taylor et al. 2005; Shipley et al. 2013; Lomas et al. 2015). A positive residual value indicated that the mass for an individual snake was higher than predicted by its SVL, and vice versa. We considered mass, SVL, and body condition data collected near the end of each active season to reflect summer foraging success and health. To this end, we used August measurements because not all snakes were successfully captured late in the active season (September–October).

To determine individual growth, we used a modification of Brody's formula to standardize instantaneous growth over the active season for each telemetered rattlesnake (Brody 1945; Maida et al. 2018):

$$\Delta\text{GR} = \frac{(\log_e \text{SVL}_2 - \log_e \text{SVL}_1)}{(t_2 - t_1)/167}$$

In this equation,  $\log_e$  is the natural base of the logarithm,  $\text{SVL}_1$  is the individual size at the beginning of the active season (April–May),  $\text{SVL}_2$  is the individual size at the end of the active season (August),  $t_1$  is the date of first capture, and  $t_2$  is the date at second (last) capture. Based on previous radiotelemetric studies at this

study site, the estimated active season for rattlesnakes is approximately 1 April – 15 September (Brown et al. 2009; Lomas et al. 2019). Therefore, the constant (167) in the equation represents, in days, the estimated length of the active season or “growth season” (cf. Maida et al. 2018). We assumed that no growth occurred during hibernation (King et al. 2016).

### Quantifying migration groups

We assigned telemetered rattlesnakes into one of three distinct categories based on their spring migration experience: Individuals in the FENCE category encountered the condominium snake fence during their spring migration, while DSTB snakes encountered other forms of disturbance (i.e., a hiking trail, golf course fairway, or road) during migration but did not contact the snake fence. Lastly, UN snakes were individuals in the northern portion of the study site that did not encounter any type of disturbance during migration or throughout the entire active season. For these snakes, we simply used the distance from the individual hibernacula to the nearest source of human disturbance to quantify DTD.

### Prey population monitoring

To account for the potential influence that prey abundance has on rattlesnake movement and behaviour, small mammals were live-trapped on the study site to monitor the prey base population for rattlesnakes from 2012 to 2016. Sampling was performed once per year (end of June – early July) over four trapping grids. Fixed grid locations were used each year to encompass the main land-use types on the landscape. To this end, a single grid was established on the golf course (in the shrub–steppe between fairways), in a vineyard, in undisturbed shrub–steppe, and on the toe slope of the eastern mountains (“Hillside,” below hibernacula locations) (for grid locations, see Supplementary Fig. S1).<sup>1</sup> Each grid was sampled using Longworth-style traps (Little Critter Live Traps, Rogers Manufacturing, West Kelowna, B.C., Canada) set up in a 6 × 6 grid (36 traps in total) spaced 15 m apart, and each trap was covered with a board (~15 cm × 30 cm) to protect it from sun and rain (Larsen et al. 2007). Three baiting nights were followed by three trapping nights. Traps were baited with a piece of apple (source of water) along with rolled oats and sunflower seeds and were provided with synthetic bedding for warmth. During trapping nights, traps were baited and armed immediately prior to sunset and then checked the following morning starting at sunrise (~0500). Captured small mammals were identified to species, sexed, ear-tagged (Monel #1; Kent Scientific Corporation, Torrington, Connecticut, USA), and released immediately at the point of capture.

Due to low capture rates, mark–recapture models could not be fitted, so we used counts (i.e., number of unique individuals captured within the 3 days) to represent small-mammal population density within each grid (Torre et al. 2016). We assumed that the uncaptured proportion of the small-mammal population is constant and that individual counts within the grids would yield a representative density estimate (Slade and Blair 2000; Torre et al. 2016).

### Statistical analysis

We used R version 3.4.3 (R Core Team 2017) to perform all statistical analysis. We log-transformed migration distance (MD), 100% MCP, and 50% KD to meet assumptions of normality. We used univariate one-way ANOVA to compare each migration and home-range parameter, as well as end-of-year body condition and instantaneous growth between the three migration categories. We used Tukey's honestly significant difference (HSD) test for post hoc comparisons. We also used linear regressions to investigate the relationship between migration and home-range attributes and the distance to nearest source of disturbance. Data on telemetered snakes were used only if the animals were tracked for

the entire spring migration (started at or near hibernacula) and for more than 75% of the active season or they had provided at least 20 locations (Lomas et al. 2019). However, due to mortality and (or) transmitter failure, not all snakes were tracked for the entire active season. Given strong site fidelity to hibernacula (Maida et al. 2017), for animals not successfully tracked back to their hibernacula, we used the location of their spring hibernacula as the predicted end point in home-range calculations (note that every snake tracked during this study for an entire active season returned to the same hibernacula from which it originated). Considering that GPS error was typically  $\pm 5$  m, we assigned consecutive locations that were  $<10$  m apart as identical, i.e., representing no movement. All statistical interpretation was guided by  $\alpha = 0.05$  and all means reported include  $\pm 1$  SE.

## Results

A total of 78 adult male rattlesnakes were equipped with radio transmitters. Of those, 27 individual rattlesnakes (FENCE,  $n = 7$ ; DSTB,  $n = 10$ ; UN,  $n = 10$ ) were tracked for their entire spring migration (starting at or near hibernaculum) and for more than 75% of the active season, each furnishing more than 20 location points. No snakes from 2013 met these criteria and were thus excluded in our analysis (telemetry started in June of that year). Four snakes tracked for their entire spring migration did not provide data through the entire active season due to road mortality ( $n = 1$ ), predation ( $n = 1$ ), and transmitter failure or unknown ( $n = 2$ ). Both spring migration ( $F_{[2,24]} = 0.056$ ,  $P = 0.95$ ) and entire active season ( $F_{[2,24]} = 0.30$ ,  $P = 0.74$ ) sampling effort (number of telemetric locations) did not differ across the three spring migration categories. During their spring migration, rattlesnakes in disturbed habitats encountered a fence, a hiking trail, or a golf course fairway. These individuals also encountered roads, vineyards, fencing, fairways, and hiking trails throughout the rest of the active summer period.

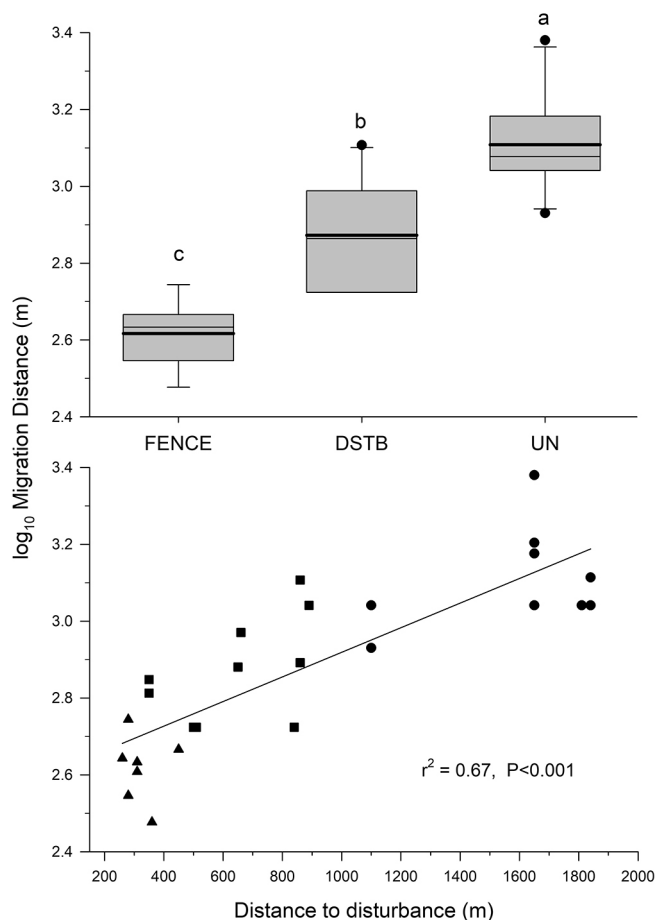
### Migration parameters

Sampling effort did not influence spring migration distance (MD;  $F_{[1,25]} = 0.10$ ,  $P = 0.75$ ), spring migration path length (MPL;  $F_{[1,25]} = 2.53$ ,  $P = 0.12$ ), or spring migration path sinuosity (MPS;  $F_{[1,25]} = 2.96$ ,  $P = 0.09$ ) estimates. Mean ( $\pm 1$  SE) MD within our sample was  $892.6 \pm 92.1$  m (FENCE,  $421 \pm 30.8$  m; DSTB,  $780 \pm 80.8$  m; UN,  $1335 \pm 137.0$  m), and there was a significant relationship with distance to disturbance (DTD;  $F_{[1,25]} = 58.7$ ,  $P < 0.001$ ). Log-transformed MD differed significantly between categories ( $F_{[2,24]} = 34.78$ ,  $P < 0.001$ ; Fig. 3), with snakes in the UN category displaying significantly greater MD lengths than both FENCE and DSTB categories (FENCE,  $P < 0.001$ ; DSTB,  $P < 0.001$ ). In addition, snakes in the FENCE category had shorter MD lengths than snakes in the DSTB category ( $P < 0.001$ ).

Mean ( $\pm 1$  SE) MPL was  $1443.8 \pm 87.4$  m, and there was a significant relationship between MPL and DTD ( $F_{[1,25]} = 14.1$ ,  $P < 0.001$ ). Rattlesnakes within the UN category ( $1714.1 \pm 148.6$  m) contained significantly longer MPL than individuals in the FENCE category ( $1056 \pm 142.9$  m,  $P = 0.005$ ).

The mean ( $\pm 1$  SE) migration path sinuosity index (MPS) for all snakes in our study was  $0.60 \pm 0.04$ , and there was a significant correlation between this measurement and DTD ( $F_{[1,25]} = 23.1$ ,  $P < 0.001$ ; Fig. 4). Furthermore, MPS differed significantly between the three migration groups ( $F_{[2,24]} = 13.62$ ,  $P < 0.001$ ), with the UN category MPS ( $0.78 \pm 0.003$ ) being significantly straighter than both the FENCE and DSTB categories (FENCE,  $0.43 \pm 0.04$ ,  $P < 0.001$ ; DSTB,  $0.55 \pm 0.06$ ,  $P = 0.004$ ). Mean values indicate that the FENCE category migration path was more tortuous than straight, whereas the DSTB category sinuosity index indicated slightly more straight than crooked, and UN snakes had almost completely straight migration movements. Furthermore, the lowest sinuosity index value for snakes in the UN category was 0.54 (range, 0.54–0.89),

Fig. 3. (Top) Comparison of log-transformed migration distance (MD) between the three migration categories. Means with different letters indicate a significant difference at  $\alpha = 0.05$ . (Bottom) The relationship between log-transformed migration distance and distance to disturbance of male Western Rattlesnakes (*Crotalus oreganus*) near Osoyoos, B.C., Canada. Sample sizes: FENCE,  $n = 7$ ; DSTB,  $n = 10$ ; and UN,  $n = 10$ . Individuals in the FENCE category encountered the condominium snake fence during their spring migration, while DSTB snakes encountered other forms of disturbance. Thirdly, UN snakes were individuals in the northern portion of the study site that did not encounter any type of disturbance during spring migration or throughout the entire active season. Data from the FENCE category are represented by triangles, data from the DSTB category are represented by squares, and data from the UN category are represented by circles.



compared with the highest sinuosity index values registered in the FENCE category (0.53; range, 0.28–0.53).

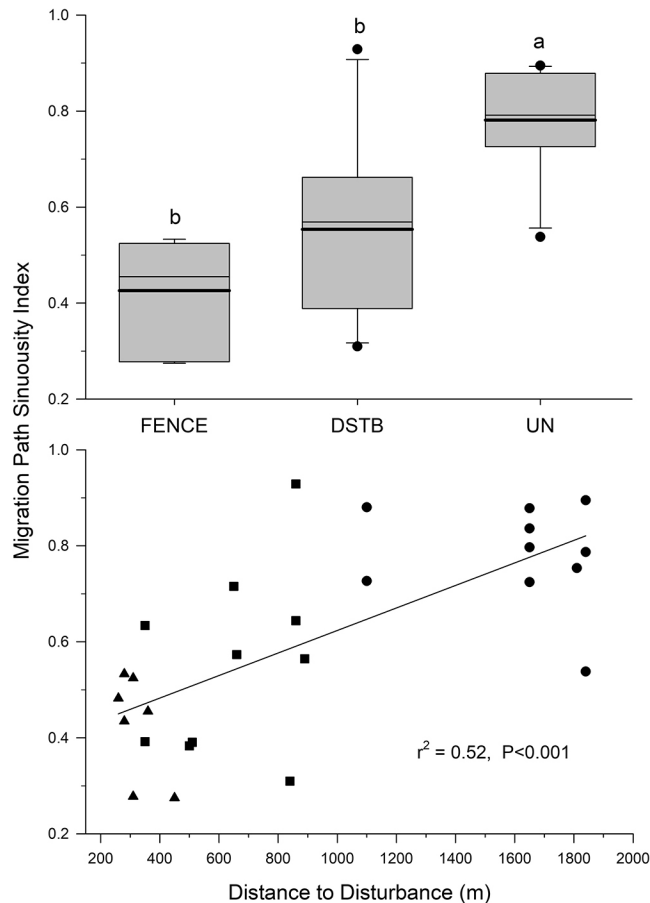
The mean ( $\pm 1$  SE) spring migration duration (DAYS) for our sample was  $41 \pm 2.4$  days, and there was no relationship between DAYS and DTD ( $F_{[1,25]} = 0.1$ ,  $P = 0.48$ ). Moreover, there was no difference in DAYS between the three groups ( $F_{[2,24]} = 0.09$ ,  $P = 0.91$ ), and there was no relationship in MD (the length of the individual's migration) and DAYS ( $F_{[1,25]} = 0.03$ ,  $P = 0.87$ ).

### Home-range parameters

Rattlesnake MCP home-range sizes varied from 4.4 to 103 ha (FENCE,  $10.1 \pm 1.4$  ha; DSTB,  $21.1 \pm 2.9$  ha; UN,  $36.8 \pm 8.2$  ha) in our study site, and there was a significant relationship between rattlesnake log-transformed home-range size and both DTD and MD (DTD,  $F_{[1,25]} = 23.3$ ,  $P < 0.001$ ; MD,  $F_{[1,25]} = 51.66$ ,  $P < 0.001$ ). Log-transformed home-range size differed significantly between the three migration categories ( $F_{[2,24]} = 9.50$ ,  $P < 0.001$ ; Fig. 5), with the



**Fig. 4.** (Top) Comparison of migration path sinuosity (MPS) between the three migration categories. Means with different letters indicate a significant difference at  $\alpha = 0.05$ . (Bottom) The relationship between spring migration sinuosity and the initial spring distance travelled to disturbance of male Western Rattlesnakes (*Crotalus oreganus*) near Osoyoos, B.C., Canada (for category definitions, see the caption of Fig. 3).

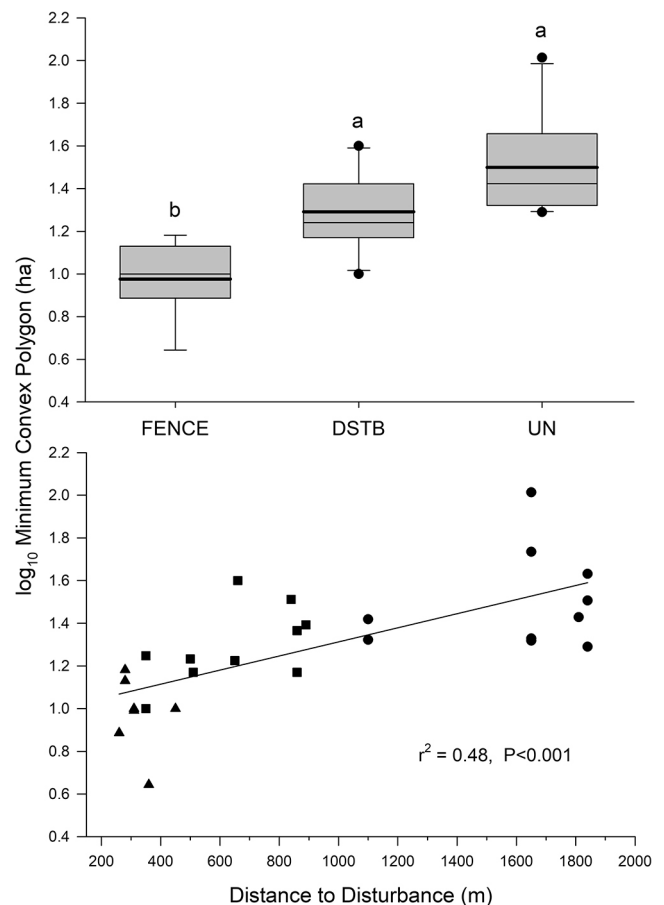


FENCE category home range being significantly smaller than both DSTB and UN categories (DSTB,  $P = 0.02$ ; UN,  $P < 0.001$ ). Furthermore, rattlesnake home ranges in the FENCE category only extended, on average,  $106.9 \pm 39.4$  m (range, 0–205 m) beyond the fencing structure (distance away from hibernacula). Mean ( $\pm 1$  SE) core area of use on our study site was  $8.9 \pm 1.63$  ha (FENCE,  $2.7 \pm 0.4$  ha; DSTB,  $7.4 \pm 0.8$  ha; UN,  $13.9 \pm 10.2$  ha), and log-transformed core area was significantly related to rattlesnake spring migration DTD ( $F_{[1,25]} = 23.9$ ,  $P < 0.001$ ). Log-transformed core area of use differed significantly between the three groups ( $F_{[2,24]} = 18.3$ ,  $P < 0.001$ ), where the FENCE group core area was significantly lower than DSTB and UN categories (DSTB,  $P = 0.002$ ; UN,  $P < 0.001$ ). Lastly, snakes with larger home ranges (MCP) contained larger core areas ( $F_{[1,25]} = 137.5$ ,  $P < 0.001$ ).

#### Body characteristics and growth

The mean ( $\pm 1$  SE) initial spring mass of telemetered snakes was  $209.5 \pm 8.7$  g, and mean ( $\pm 1$  SE) SVL was  $66.8 \pm 1.3$  cm; mass was strongly associated with SVL ( $F_{[1,25]} = 43.49$ ,  $R^2 = 0.65$ ,  $P < 0.001$ ). The range of SVL in our sample of snakes was 54.5–78.5 cm, reflecting the bulk of male rattlesnake sizes at our study site (Supplementary Fig. S2).<sup>1</sup> From captures in 2011–2016 ( $n = 489$ ), male rattlesnakes larger than 78.5 cm SVL represented 6.7% of total male captures. Furthermore, Maida et al. (2018) estimated asymptotic SVL at this site as 73.4 cm SVL for the entire population.

**Fig. 5.** (Top) Comparison of log-transformed minimum convex polygon (MCP) home-range estimates between the three migratory categories. Means with different letters indicate a significant difference at  $\alpha = 0.05$ . (Bottom) The relationship between log-transformed MCP and the initial spring distance travelled to disturbance of male Western Rattlesnakes (*Crotalus oreganus*) near Osoyoos, B.C., Canada (for category definitions, see the caption of Fig. 3).

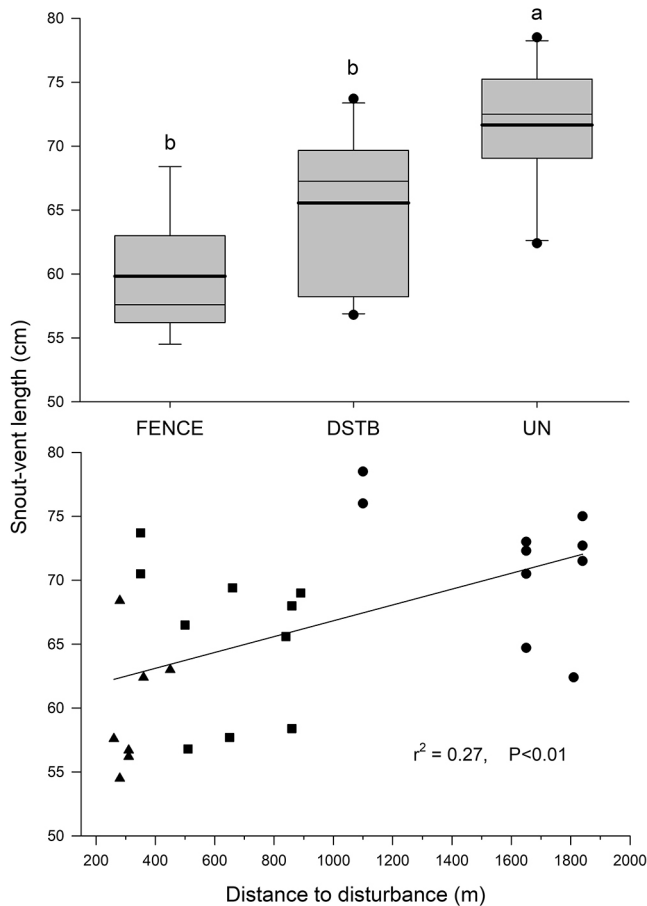


Undisturbed snakes (UN,  $71.7 \pm 1.5$  cm) were longer than both FENCE ( $59.8 \pm 1.8$  cm,  $P < 0.001$ ) and DSTB snakes ( $65.6 \pm 1.9$  cm,  $P = 0.04$ ; Fig. 6), and there was a positive, significant relationship between rattlesnake size (SVL) and DTD ( $F_{[1,25]} = 9.7$ ,  $P = 0.004$ ; i.e., smaller snakes travelled shorter distances to first encounter disturbance than bigger snakes). Due to snake mortality and transmitter failure, size and mass data were not recorded on two snakes within our sample in the month of August, resulting in a body characteristics sample size of 25 individuals (FENCE,  $n = 6$ ; DSTB,  $n = 10$ ; UN,  $n = 9$ ).

There was no significant relationship between DTD and end-of-year body condition ( $F_{[1,23]} = 0.58$ ,  $P = 0.46$ ), and body condition did not differ between the three migration categories ( $F_{[2,22]} = 0.19$ ,  $P = 0.83$ ). A post hoc analysis showed that the observed power for this test was 11% ( $f = 0.18$ , power  $(1 - \beta) = 0.11$ ). Given the variances in the samples, to achieve reasonable power ( $>0.80$ ) in the analysis, the total sample size between the three migration groups would require  $\approx 303$  individuals. Rattlesnakes with higher end-of-year body condition had both larger home ranges and core areas of use (home range,  $F_{[1,23]} = 7.5$ ,  $P = 0.01$ ; core area,  $F_{[1,23]} = 5.0$ ,  $P = 0.04$ ).

Not surprisingly, smaller snakes grew at a faster rate than larger snakes ( $F_{[1,23]} = 5.5$ ,  $P = 0.02$ ), but instantaneous growth did not appear to differ between the three migration categories ( $F_{[2,22]} =$

**Fig. 6.** (Top) Comparison of spring snout–vent length (SVL) between the three migration categories. Means with different letters indicate a significant difference at  $\alpha = 0.05$ . (Bottom) The relationship between spring SVL and initial spring distance travelled to disturbance of male Western Rattlesnakes (*Crotalus oreganus*) near Osoyoos, B.C., Canada (for category definitions, see the caption of Fig. 3).



1.17,  $P = 0.33$ ; Fig. 7). Post hoc power for this analysis was 35% ( $f = 0.39$ , power  $(1 - \beta) = 0.35$ ), and to obtain a power estimate  $> 0.80$  would require 69 individuals in the analysis. Furthermore, there was no significant relationship between instantaneous growth and DTD ( $F_{[1,23]} = 0.86$ ,  $P = 0.36$ ). Overall, a Pearson's correlation matrix showed no significant correlations between each spring migration parameter (MD, TPL, DTD, DAYS, and MPS) with either rattlesnake end-of-year body condition or instantaneous growth (Supplementary Table S1).<sup>1</sup>

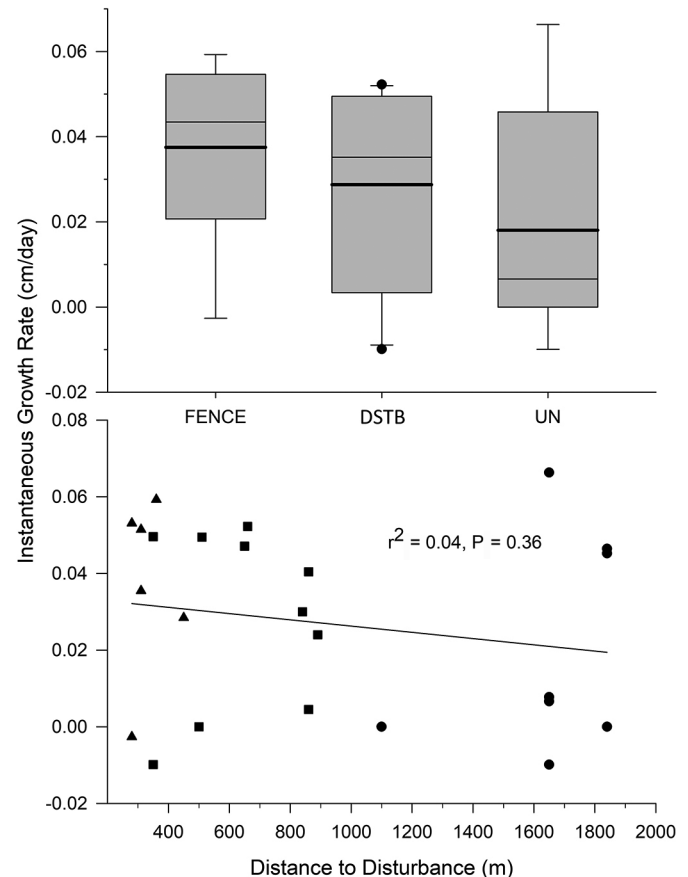
### Prey population monitoring

Over the 2160 trap-nights conducted during 2012–2016, only two species of small mammals were captured: Great Basin pocket mice (*Perognathus parvus* (Peale, 1848)) were the prominent species, with 179 animals caught (97.2% of total), compared with five individual deer mice (*Peromyscus maniculatus* (Wagner, 1845)). This equated to a mean annual population density of 16.4 animals·ha<sup>-1</sup> (range, 10.7–26.3 animals·ha<sup>-1</sup>; Table 1) across the study area. Furthermore, small-mammal density appeared homogenous across the landscape (Table 1), with no significant differences in capture numbers occurring between the grids ( $F_{[3,16]} = 1.03$ ,  $P = 0.41$ ).

### Discussion

To our knowledge, this is the first detailed study investigating rattlesnake spring migration in relation to human disturbance. More specifically, this is the first study addressing how fence bar-

**Fig. 7.** (Top) Comparison of instantaneous growth rates between the three migration categories. Sample sizes: FENCE,  $n = 6$ ; DSTB,  $n = 10$ ; and UN,  $n = 9$ . (Bottom) The relationship between instantaneous growth rates and the initial spring distance travelled to disturbance of male Western Rattlesnakes (*Crotalus oreganus*) near Osoyoos, B.C., Canada (for category definitions, see the caption of Fig. 3).



**Table 1.** Small-mammal population density estimates (animals·ha<sup>-1</sup>) of trapping grids within the Western Rattlesnake (*Crotalus oreganus*) study area near Osoyoos, B.C., Canada, from 2012 to 2016.

Year	Golf			Mean
	Hillside	course	Vineyard	
2012	10.7	3.6	25.0	10.7
2013	28.6	0.0	5.4	10.7
2014	23.2	35.7	19.6	26.3
2015	30.4	8.9	21.4	18.3
2016	14.3	7.1	23.2	16.1
Mean	21.4	11.1	18.9	16.4

**Note:** Small mammals represented within the population include Great Basin pocket mice (*Perognathus parvus*) and deer mice (*Peromyscus maniculatus*).

riers affect rattlesnake spring migratory behaviour and the consequences for summer home ranges and body characteristics. We observed a strong correlation between distance travelled to disturbance with all our spring migration metrics, home-range estimates, and animal body size (SVL). We found that disturbed and fragmented habitats had a strong, consistent influence on rattlesnake spring migration distance and migration sinuosity compared with snakes migrating through undisturbed landscapes during the spring. Furthermore, encountering the fence structure during spring migration had a significant influence on rattlesnake migration distance, as well as home range and core area



size, compared with snakes in disturbed areas that did not encounter the fencing structure.

We acknowledge that physical construction was taking place on site during all or part of our study and the potential proximate impacts on snakes moving through adjacent habitat or along the fencing structure. Tremors created from the use of heavy machinery may have negative impacts on animals such as snakes that use vibrations as a source of communication and sensory input (Hartline 1971; Hill 2001; Lovich and Ennen 2017); however, we did not have the equipment or expertise to measure and quantify the potential vibration intensity from the construction zone.

Interestingly, variations in spring migration distance and path length did not correlate with migration durations within the three categories; in other words, the migration duration of individuals migrating shorter distances in disturbed areas was not significantly shorter (different) than that of individuals migrating further distances in undisturbed landscapes. In addition, there did not appear to be a clear, consistent relationship between the animals' body characteristics and the spring migration metrics considered in this study.

On our study site, there were two general types of barriers on the landscape interrupting rattlesnake spring migration: physical (fence) and permeable "landscape" barriers (golf course and hiking trails), and both appeared to influence rattlesnake spring migration. Snakes and other reptiles avoid or alter their behaviour along open areas, including hiking trails and golf course fairways (Parent and Weatherhead 2000; Andrews and Gibbons 2005; Goode 2010). In Arizona, Gila Monsters (*Heloderma suspectum* Cope, 1869) tended to avoid golf course fairways, while Tiger Rattlesnake (*Crotalus tigris* Kennicott, 1859) home-range size and shape was altered in golf course habitats (Goode 2010). Furthermore, Massachusetts Rattlesnakes and Western Diamondback Rattlesnakes exhibit a reduction in movement frequency within areas of high human use (Parent and Weatherhead 2000; Beale et al. 2016), including hiking trails. The scale of our analysis was insufficient to determine if rattlesnakes avoided golf course fairways and hiking trails; however, reductions in spring migration distances, total migration path lengths, and path sinuosity (more crooked movements) in these "habitats" suggest the animals altered their spring migration behaviour compared with individuals in areas lacking human involvement and landscape disturbance. Shorter, more tortuous movements may be a behavioural response to perceived threats or predator avoidance caused by human influence and landscape alterations and may help decrease the probability of encountering predators and (or) humans (Martin et al. 2017).

Encountering the snake fence appeared to have a large influence on rattlesnake spring migration, specifically migration distance, migration path length, and migration sinuosity compared with individuals migrating in undisturbed habitats. Furthermore, individuals encountering the fence had greatly reduced spring migration distances compared with all other snakes in our study (including both disturbed and undisturbed). Previous studies (see above) show avoidance of open areas associated with landscape disturbance; however, individuals still have the ability to cross these features. Animals encountering barriers such as a golf course fairway or hiking trails face trade-offs between the costs of crossing these impedances versus moving around them (Beyer et al. 2016). On the other hand, individuals encountering a fence do not have this option and must either halt movement or circumnavigate the barrier. Having alternative movement options when encountering an impediment (golf course and (or) hiking trails) or a nonpermeable barrier (fence) appears to strongly influence the total distance that a rattlesnake travels during its spring migration on our study site. Furthermore, rattlesnakes exhibit a high level of fidelity to various areas and (or) habitats throughout their life history (hibernacula, corridors, summer foraging areas). Adult rattlesnakes contain high spatial and site fidelity on the landscape and are not likely to redistribute themselves (Waldron et al. 2013).

A novel obstruction such as the fencing structure likely impedes access to areas used in previous years. Again, in response to this, individuals may or may not attempt to skirt the barrier (decreasing path sinuosity and (or) distance moved).

Overall, the home-range patterns and sizes that we observed appear to be similar to those previously reported from rattlesnakes at our study site and in other areas at the northern extent of the species' range (B.C.). Harvey (2015) found that MCP home ranges in undisturbed habitats throughout B.C. ranged from 1.5 to 184.7 ha (mean = 52 ha). Furthermore, at the Osoyoos study site, Brown et al. (2009) calculated average rattlesnake MCP to be 25.1 ha and Lomas et al. (2019) calculated MCP home ranges at 20.0 ha. Previously, Macartney (1985) determined that den population home ranges (estimated size of area used by individual dens) averaged 26.0–122.3 ha in a study area approximately 140 km north of our study site. However, despite the similarities to previous studies, we found differences in home-range sizes based on rattlesnake spring migration tactics and disturbances encountered during migration.

Using a disturbance rating (DR) system (Parent and Weatherhead 2000), Lomas et al. (2019) found that rattlesnakes in the undisturbed areas of our study site had larger home ranges than animals within minimally to highly disturbed areas. We found similar trends; however, interactions with the fencing structure during spring migration had a drastic influence on rattlesnake summer home-range size and core areas of use compared with both undisturbed and disturbed snakes. Regardless of disturbance, our results further indicate that home-range size was strongly associated with the length of an individual's spring migration distance, and with respect to disturbance, rattlesnake home-range size decreased in closer proximity to disturbance (shorter DTD = shorter MD). Similarly, Mojave Desert Tortoise (*Gopherus agassizii* (Cooper, 1861)) home ranges decreased with proximity to roads and mitigative roadside fencing (Peaden et al. 2017). The authors inferred this may have been a result of road avoidance or increased resources along roadsides (water runoff or forbs). Based on anecdotal observations of vegetation and resources adjacent to the construction site and snake fence, this does not appear to be the case in our study, and changes to home-range size likely result from the interaction and behavioural shifts in migration of individuals in response to the barrier fencing structure.

Growth and body condition are the two of the most common metrics used to quantify rattlesnake physiology, health, and individual or population success (Moore et al. 2000; Jenkins et al. 2009; Lomas et al. 2015; King et al. 2016). One of the primary functions of spring migration in rattlesnakes appears to be finding habitats with food (Duvall et al. 1990). Prairie Rattlesnakes with straighter, longer range lengths had higher end-of-year body condition (Martin et al. 2017), and increased body condition in male Timber Rattlesnakes (*Crotalus horridus* Linnaeus, 1758) allowed individuals to allocate more time to finding mates than hunting (Lind and Beaupre 2015). In support of this, we found that individuals with higher body conditions at the end of the active season maintained larger home ranges and larger core areas. Being a sit-and-wait ambush predator, we infer that larger home ranges and core areas, regardless of habitat quality, likely reflect more time for rattlesnakes to search for mates during the summer months, rather than hunting. However, we surprisingly did not notice any trends or differences in end-of-year body condition over the three migration categories. The lack of a significant difference and the large sample size required (303 individuals) to achieve statistical power suggests that body condition index scores may not be appropriate metrics for gauging the physiological impacts of barriers to rattlesnake migration in our study area.

Our observations of rattlesnakes being shorter (SVL) when living closer to disturbance (i.e., travelling shorter distances) mirrors previous observations by Lomas et al. (2015) at our study site;

similar trends also were noticed in a Western Rattlesnake population south of our study site in Idaho (rattlesnakes living in disturbed areas were smaller; Jenkins et al. 2009). Furthermore, similar trends have been observed in other snake species such as urban-living Dugites (*Pseudonaja affinis* Günther, 1872) being smaller than non-urban individuals in Australia (Wolfe et al. 2018). Typical snake growth rates involve a highly correlated, linear, negative relationship between size and growth (i.e., smaller snakes grow faster than larger snakes; cf. Macartney et al. 1990; King et al. 2016; Dreslik et al. 2017; Maida et al. 2018). With mean SVL of snakes in disturbed areas (both fence and disturbed categories) being significantly smaller than undisturbed snakes and estimated population asymptotic SVL, we would expect to find an increased rate of growth in snakes encountering fencing and disturbance during the spring compared with snakes in the undisturbed category, but this was not the case in our study. However, due to the lack of power in the analysis, further investigation on the impacts on growth (and body condition) based on rattlesnake spring movements may be required.

There now is considerable evidence that rattlesnakes occupying disturbed areas of our study site are both smaller and move shorter distances than snakes within undisturbed areas (Lomas et al. 2015; Lomas et al. 2019; this study). Due to the significant variation in life history that rattlesnakes (and other species) show between populations and along latitudinal gradients (Putman et al. 2013; Waldron et al. 2013; Maida et al. 2018), there may be several potential drivers behind this phenomenon. Rattlesnakes show high site fidelity to migration corridors and home ranges (Gomez et al. 2015; Waldron et al. 2013), but as telemetry tends to involve larger animals (to facilitate surgical implants), we do not know for certain if ontogenetic shifts in migration accompany growth. Still, at this time, it appears unlikely that snakes reaching relatively large body sizes would begin to displace smaller snakes in more optimal habitat. One plausible explanation for the relationship between habitat quality and body size is that larger snakes are more likely to be killed in highly disturbed and fragmented habitats, therefore becoming under-represented in those landscapes (or even possibly being selected against). Data testing this hypothesis are difficult to obtain, although another recent study indicates that size is not strongly linked to road mortality (Winton 2018). Regardless, it is apparent that habitat condition is related to snake movement in our study area (specifically when individuals are tasked with navigating barriers). This likely restricts the ability of individual rattlesnakes to exploit resources on the landscape such as variation in prey abundance.

A previous analysis of road-killed rattlesnakes from the broader region of the south Okanagan reported a relatively large suite of mammalian prey species (nine prey species identified with the most common being deer mice; cf. McAllister et al. 2016). In contrast, our study site appears to support only two microtine mammal species, deer mice and Great Basin pocket mice, and in relatively low densities. The homogenous array of low densities and a low species diversity of prey across our study site suggests that the ability of rattlesnakes to successfully find prey may be of significance at our study site. However, the similarity in prey density estimates between the grids in both natural landscapes and disturbed areas (i.e., golf course, vineyard) suggests that prey abundance does not appear to be a likely contributor to changes in spring movements and home ranges observed in rattlesnakes at this study site.

## Conclusion

Small-scale migrants such as rattlesnakes are extremely useful for assessing landscape connectivity and implications of long-term disturbance and barriers. Overall, spring migration and behaviour of these animals appear to be very much impacted by human disturbance, including interactions with associated mitigative fencing. Similar to the effects of disturbance on rattlesnake

body condition outlined by Lomas et al. (2015), these effects are not readily apparent when rattlesnakes remain persistent on the landscape. Furthermore, this study does not show the ultimate implications of these impacts (i.e., fecundity, population viability). Fencing is becoming a very important conservation tool for reducing the direct impacts of road mortality and other negative consequences of human interactions with snakes and animals from multiple taxonomic groups; however, fencing also needs to be considered as a disturbance in itself and documentation of shifts in animal behaviour and ecology due to fencing structures has been widely unreported to date. Therefore, the implementation of wildlife mitigation fencing should not be the end point for population monitoring. Once barriers are established, efforts need to focus on how local fauna are indirectly affected as a means to inform the future use of these important mitigation structures.

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## References

- Alerstam, T., Hedenström, A., and Åkesson, S. 2003. Long-distance migration: evolution and determinants. *Oikos*, **103**(2): 247–260. doi:10.1034/j.1600-0706.2003.12559.x.
- Andrews, K.M., and Gibbons, J.W. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia*, **2005**(4): 772–782. doi:10.1643/0045-8511(2005)005[0772:HDHISM]2.0.CO;2.
- Bauder, J.M., Akenson, H., and Peterson, C.R. 2015. Movement patterns of prairie rattlesnakes (*Crotalus v. viridis*) across a mountainous landscape in a designated wilderness area. *J. Herpetol.* **49**(3): 377–387. doi:10.1670/13-153.
- Beale, M., Poulin, S., Ivanyi, C., and Blouin-Demers, G. 2016. Anthropogenic disturbance affects movement and increases concealment in western diamondback rattlesnakes (*Crotalus atrox*). *J. Herpetol.* **50**(2): 216–221. doi:10.1670/14-112.
- Berger, K.M., and Gese, E.M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* **76**(6): 1075–1085. doi:10.1111/j.1365-2656.2007.01287.x. PMID:17922704.
- Beyer, H.L., Gurarie, E., Börger, L., Panzacchi, M., Basille, M., Herfindal, I., et al. 2016. 'You shall not pass!': Quantifying barrier permeability and proximity avoidance by animals. *J. Anim. Ecol.* **85**(1): 43–53. doi:10.1111/1365-2656.12275. PMID:25056207.
- Breininger, D.R., Bolt, M.R., Legare, M.L., Drese, J.H., and Stolen, E.D. 2011. Factors influencing home-range sizes of eastern indigo snakes in central Florida. *J. Herpetol.* **45**(4): 484–490. doi:10.1670/10-176.1.
- Brody, S. 1945. Bioenergetics and growth with specific reference to the energetic efficiency complex in domestic animals. Reinhold Publishing Corporation, New York.
- Brown, J.R., Bishop, C.A., and Brooks, R.J. 2009. Effectiveness of short-distance translocation and its effects on western rattlesnakes. *J. Wildl. Manage.* **73**(3): 419–425. doi:10.2193/2007-558.
- Chiszar, D., Shipley, B.K., Smith, H.M., Fitzgerald, K., and Saviola, A.J. 2014. Straightness-of-path during and after vernal migration in prairie rattlesnakes, *Crotalus viridis*, in eastern Colorado. *Herpetol. Notes*, **7**: 425–436.
- Christiansen, F., Esteban, N., Mortimer, J.A., Dujon, A.M., and Hays, G.C. 2017. Diel and seasonal patterns in activity and home range size of Green Turtles on their foraging grounds revealed by extended Fastloc-GPS tracking. *Mar. Biol.* **164**: 10. doi:10.1007/s00227-016-3048-y.



- Colley, M., Lougheed, S.C., Otterbein, K., and Litzgus, J.D. 2017. Mitigation reduces road mortality of a threatened rattlesnake. *Wildl. Res.* **44**(1): 48–59. doi:10.1071/WR16130.
- COSEWIC. 2015. COSEWIC assessment and status report on the western rattlesnake *Crotalus oreganus* in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ont. Available from <https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry.html>.
- DeGregorio, B.A., Manning, J.V., Bieser, N., and Kingsbury, B.A. 2011. The spatial ecology of the eastern massasauga (*Sistrurus c. catenatus*) in northern Michigan. *Herpetologica*, **67**(1): 71–79. doi:10.1655/09-049R1.1.
- Dobson, A.P., Borner, M., Sinclair, A.R.E., Hudson, P.J., Anderson, T.M., Bigurube, G., et al. 2010. Road will ruin Serengeti. *Nature*, **467**: 272–273. doi:10.1038/467272a. PMID:20844519.
- Dreslik, M.J., Shepard, D.B., Baker, S.J., Jellen, B.C., and Phillips, C.A. 2017. Body size, growth and sexual dimorphism in the eastern massasauga (*Sistrurus catenatus*). In *The biology of rattlesnakes II*. Edited by M.J. Dreslik, W.K. Hayes, S.J. Beaupre, and S.P. Mackessy. ECO Herpetological Publishing and Distribution, Rodeo, N.M. pp. 65–77.
- Duvall, D., and Schuett, G.W. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. *Anim. Behav.* **54**(2): 329–334. doi:10.1006/anbe.1996.0418. PMID:9268464.
- Duvall, D., Goode, M.J., Hayers, W.K., Leonhardt, J.K., and Brown, D.G. 1990. Prairie rattlesnake vernal migration: field experimental analyses and survival value. *Natl. Geogr. Res.* **6**(4): 457–469.
- Duvall, D., Chiszar, D., Mintzer, R.A., and Roster, N.O. 1997. Experimental simulation in behavioral ecology: a multimedia approach with the spatial searching simulation Rattlesnake®. *Exp. Biol. Online*, **2**(16): 1. doi:10.1007/s00898-997-0016-5.
- Epps, C.W., Mutayoba, B.M., Gwin, L., and Brashares, J.S. 2011. An empirical evaluation of the African elephant as a focal species for connectivity planning in east Africa. *Divers. Distrib.* **17**(4): 603–612. doi:10.1111/j.1472-4642.2011.00773.x.
- Eye, D.M., Maida, J.R., McKibbin, O.M., Larsen, K.W., and Bishop, C.A. 2018. Snake mortality and cover board effectiveness along exclusion fencing in British Columbia, Canada. *Can. Field-Nat.* **132**(1): 30–35. doi:10.22621/cfn.v132i1.2031.
- Ferronato, B.O., Roe, J.H., and Georges, A. 2014. Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions. *J. Nat. Conserv.* **22**(6): 577–585. doi:10.1016/j.jnc.2014.08.014.
- Gomez, L., Larsen, K.W., and Gregory, P.T. 2015. Contrasting patterns of migration and habitat use in neighboring rattlesnake populations. *J. Herpetol.* **49**(3): 371–376. doi:10.1670/13-138.
- Goode, M. 2010. Population and community responses of reptiles to golf courses. *USGA Green Section Record*, **48**: 28–31.
- Gregory, P.T. 2007. Biology and conservation of a cold-climate snake fauna. In *Ecology, conservation and status of reptiles in Canada*. Edited by C. Sebrun and C.A. Bishop. Society for the Study of Amphibian and Reptiles, Salt Lake City, Utah. pp. 41–56.
- Gosset, C., Rives, J., and Labonne, J. 2006. Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). *Ecol. Freshw. Fish*, **15**(3): 247–254. doi:10.1111/j.1600-0633.2006.00144.x.
- Gubili, C., Mariani, S., Weckworth, B.V., Galpern, P., McDevitt, A.D., Hebblewhite, M., et al. 2017. Environmental and anthropogenic drivers of connectivity patterns: a basis for prioritizing conservation efforts for threatened populations. *Evol. Appl.* **10**(2): 199–211. doi:10.1111/eva.12443. PMID:28127396.
- Harris, G., Thirgood, S., Hopcraft, J.G.C., Crooms, J.P.G.M., and Berger, J. 2009. Global decline in aggregated migrations of large mammals. *Endanger. Species Res.* **7**: 55–76. doi:10.3354/esr00173.
- Hartline, P.H. 1971. Physiological basis for detection of sound and vibration in snakes. *J. Exp. Biol.* **54**: 349–371. PMID:5553415.
- Harvey, J.A. 2015. Thermal influences on summer habitat use by western rattlesnakes (*Crotalus oreganus*) in British Columbia. M.Sc. thesis, Department of Science, Thompson Rivers University, Kamloops, B.C.
- Hill, P.S.M. 2001. Vibration and animal communication: a review. *Integr. Comp. Biol.* **41**(5): 1135–1142. doi:10.1093/icb/41.5.1135.
- Hoare, B. 2009. Animal migration: Remarkable journeys in the wild. University of California Press, Oakland, Calif.
- Holding, M.L., Frazier, J.A., Dorr, S.W., Henningsen, S.N., Moore, I.T., and Taylor, E.N. 2014. Physiological and behavioral effects of repeated handling and short-distance translocations on free-ranging northern Pacific rattlesnakes (*Crotalus oreganus oreganus*). *J. Herpetol.* **48**(2): 233–239. doi:10.1670/11-314.
- Hopcraft, J.G.C., Morales, J.M., Beyer, H.L., Borner, M., Mwangomo, E., Sinclair, A.R.E., et al. 2014. Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecol. Monogr.* **84**(3): 355–372. doi:10.1890/13-1446.1.
- Huey, R.B. 1991. Physiological consequences of habitat selection. *Am. Nat.* **137**: 91–115.
- Jakes, A.F., Jones, P.F., Paige, L.C., Seidler, R.G., and Huijser, M.P. 2018. A fence runs through it: a call for greater attention to the influence of fences on wildlife and ecosystems. *Biol. Conserv.* **227**: 310–318. doi:10.1016/j.biocon.2018.09.026.
- Jenkins, C.L., Peterson, C.R., Doering, S.C., and Cobb, V.A. 2009. Microgeographic variation in reproductive characteristics among western rattlesnake (*Crotalus oreganus*) populations. *Copeia*, **2009**: 774–780. doi:10.1643/CE-07-277.
- Jørgensen, D., Guyer, C., Smith, L.L., and Schuett, G.W. 2008. Movements, migrations, and mechanisms: a review of radiotelemetry studies of prairie (*Crotalus v. viridis*) and western (*Crotalus oreganus*) rattlesnakes. In *The biology of rattlesnakes*. Edited by W.K. Hayes, K.R. Beamant, M.D. Cardwell, and S.P. Bush. Loma Linda University Press, Loma Linda, Calif. pp. 303–316.
- Kie, J.G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Anim. Biotelem.* **1**: 13. doi:10.1186/2050-3385-1-13.
- King, R.B., Stanford, K.M., Jones, P.C., and Bekker, K. 2016. Size matters: Individual variation in ectotherm growth and asymptotic size. *PLoS ONE*, **11**(1): e0146299. doi:10.1371/journal.pone.0146299. PMID:26730712.
- Kovach, R.P., Ellison, S.C., Pyare, S., and Tallmon, S.A. 2015. Temporal patterns in adult salmon migration timing across southeast Alaska. *Glob. Change Biol.* **21**(5): 1821–1833. doi:10.1111/gcb.12829.
- Landreth, H.F. 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. *Copeia*, **1973**: 26–31. doi:10.2307/1442353.
- Larsen, K.W. 1987. Movements and behavior of migratory garter snakes, *Thamnophis sirtalis*. *Can. J. Zool.* **65**(9): 2241–2247. doi:10.1139/z87-339.
- Larsen, K.W., Adams, I.T., and Haughland, D.L. 2007. Small mammal communities in a pyrogenic habitat mosaic. *Int. J. Wildl. Fire*, **16**(6): 728–740. doi:10.1071/WF05106.
- Lind, C.M., and Beaupre, S.J. 2015. Male snakes allocate time and energy according to individual energetic status: body condition, steroid hormones, and reproductive behavior in timber rattlesnakes, *Crotalus horridus*. *Physiol. Biochem. Zool.* **88**(6): 624–633. doi:10.1086/683058. PMID:26658410.
- Lomas, E.V. 2013. Effects of disturbance on the northern Pacific rattlesnake (*Crotalus oreganus oreganus*) in British Columbia. M.Sc. thesis, Department of Science, Thompson Rivers University, Kamloops, B.C.
- Lomas, E., Larsen, K.W., and Bishop, C.A. 2015. Persistence of northern Pacific rattlesnakes masks the impact of human disturbance on weight and body condition. *Anim. Conserv.* **18**(6): 548–556. doi:10.1111/acv.12208.
- Lomas, E., Bishop, C.A., Maida, J.R., and Larsen, K.W. 2019. Movement ecology of the northern Pacific rattlesnake (*Crotalus oreganus oreganus*) in response to disturbance. *Herpetologica*, **75**(2): 153–161. doi:10.1655/D-17-00060.
- Lovich, J.E., and Ennen, J.R. 2017. Reptiles and amphibians. In *Wildlife and wind farms, conflicts and solutions*. Edited by R.M. Perrow. Pelagic Publishing, Exeter, U.K. pp. 97–118.
- Macartney, J.M. 1985. The ecology of the Northern Pacific Rattlesnake, *Crotalus viridis oreganus*, in British Columbia. M.Sc. thesis, University of Victoria, Victoria, B.C.
- Macartney, J.M., and Gregory, P.T. 1988. Reproductive biology of female rattlesnakes (*Crotalus viridis*) in British Columbia. *Copeia*, **1988**: 47–57. doi:10.2307/1445921.
- Macartney, J.M., Gregory, P.T., and Charland, M.B. 1990. Growth and sexual maturity of the western rattlesnake, *Crotalus viridis*, in British Columbia. *Copeia*, **1990**: 528–542. doi:10.2307/1446356.
- MacGowan, B.J., Currylow, A.F.T., and MacNeil, J.E. 2017. Short-term responses of timber rattlesnakes (*Crotalus horridus*) to even-aged timber harvests in Indiana. *For. Ecol. Manage.* **387**: 30–36. doi:10.1016/j.foreco.2016.05.026.
- Madsen, J. 1995. Impacts of disturbance on migratory waterfowl. *Int. J. Avian Sci.* **137**(Suppl. 1): S67–S74. doi:10.1111/j.1474-919X.1995.tb08459.x.
- Maida, J.R. 2018. Impact of fencing and development on western rattlesnake (*Crotalus oreganus*) spring movements in British Columbia. M.Sc. thesis, Department of Science, Thompson Rivers University, Kamloops, B.C.
- Maida, J., Larsen, K., Hooper, C., and Bishop, C.A. 2017. *Crotalus oreganus* (western rattlesnake) mortality. *Herpetol. Rev.* **48**: 487.
- Maida, J.R., Kirk, D.A., McKibbin, O., Row, J.R., Larsen, K.W., Stringam, C., and Bishop, C.A. 2018. Population estimate, survivorship and generation time of the northern Pacific rattlesnake (*Crotalus o. oreganus*) at its northern-most range. *Herpetol. Conserv. Biol.* **13**(3): 662–672.
- Markle, C.E., Gillingwater, S.D., Levick, R., and Chow-Fraser, P. 2017. The true cost of partial fencing: evaluating strategies to reduce reptile road mortality. *Wildl. Soc. Bull.* **41**(2): 342–350. doi:10.1002/wsb.767.
- Martin, A.E., Jørgensen, D., and Gates, C.C. 2017. Costs and benefits of straight versus tortuous migration paths for prairie rattlesnakes (*Crotalus viridis viridis*) in seminatural and human-dominated landscapes. *Can. J. Zool.* **95**(12): 921–928. doi:10.1139/cjz-2017-0031.
- Martino, J.A., Poulin, R.G., Parker, D.L., and Somers, C.M. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. *J. Wildl. Manage.* **76**(4): 759–767. doi:10.1002/jwmg.313.
- McAllister, J.M., Maida, J.R., Dyer, O., and Larsen, K.W. 2016. Diet of roadkilled western rattlesnakes (*Crotalus oreganus*) and gophersnakes (*Pituophis catenifer*) in southern British Columbia. *Northwest. Nat.* **97**(3): 181–189. doi:10.1898/NWN15-25.1.
- Moore, I.T., Lerner, J.P., Lerner, D.T., and Mason, R.T. 2000. Relationships between annual cycles of testosterone, corticosterone, and body condition in male red-spotted garter snakes, *Thamnophis sirtalis concinnus*. *Physiol. Biochem. Zool.* **73**(3): 307–312. doi:10.1086/316748. PMID:10893170.
- Naidoo, R., Chase, M.J., Beytell, P., Du Preez, P., Landen, K., Stuart-Hill, G., and Taylor, R. 2016. A newly discovered wildlife migration in Namibia and



- Botswana is the longest in Africa. *Oryx*, **50**(1): 138–146. doi:10.1017/S0030605314000222.
- Parent, C., and Weatherhead, P.J. 2000. Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance. *Oecologia*, **125**(2): 170–178. doi:10.1007/s004420000442. PMID: 24595828.
- Peadar, J.M., Nowakowski, A.J., Tuberville, T.D., Buhlmann, K.A., and Todd, B.D. 2017. Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. *Biol. Conserv.* **214**: 13–22. doi:10.1016/j.biocon.2017.07.022.
- Putman, B.J., Lind, C., and Taylor, E.N. 2013. Does size matter? Factors influencing the spatial ecology of northern Pacific rattlesnakes (*Crotalus oreganus oreganus*) in central California. *Copeia*, **2013**: 485–492.
- R Core Team. 2017. R: a language and environment for statistical computing. Version 3.4.3. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.r-project.org/>.
- Reinert, H.K., and Cundall, D. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia*, **1982**: 702–705. doi:10.2307/1444674.
- Robson, L.E., and Blouin-Demers, G. 2013. Eastern hognose snakes (*Heterodon platirhinos*) avoid crossing paved roads, but not unpaved roads. *Copeia*, **2013**: 507–511. doi:10.1643/CE-12-033.
- Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L., and Kie, J.G. 2007. HRT: Home range tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystems Research, Thunder Bay, Ont.
- Row, J.R., and Blouin-Demers, G. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia*, **2006**: 797–802. doi:10.1643/0045-8511(2006)6[797:KANAE0]2.0.CO;2.
- Saumure, R.A., Herman, T.B., and Titman, R.D. 2010. Effects of patch size and habitat structure on the movements of adult male wood turtles, *Glyptemys insculpta*. *Herpetol. Conserv. Biol.* **5**(3): 403–413.
- Shine, R., Lemaster, M., Wall, M., Langkilde, T., and Mason, R. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). *Ecol. Soc.* **9**(1): 9.
- Shipley, B.K., Chiszar, D., Fitzgerald, K.T., and Saviola, A.J. 2013. Spatial ecology of prairie rattlesnake (*Crotalus viridis*) associated with black-tailed prairie dog (*Cynomys ludovicianus*) colonies in Colorado. *Herpetol. Conserv. Biol.* **8**(1): 240–250.
- Slade, N.A., and Blair, S.M. 2000. An empirical test of using counts of individuals captured as indices of population size. *J. Mammal.* **81**(4): 1035–1045. doi:10.1644/1545-1542(2000)081<1035:AETOU>2.0.CO;2.
- Statistics Canada. 2014. Canada's population estimates: Subprovincial areas, July 1, 2014. Available from [www.statcan.gc.ca](http://www.statcan.gc.ca).
- Taylor, E.N., Malawy, M.A., Browning, D.M., Lemar, S.V., and DeNardo, D.F. 2005. Effects of food supplementation on the physiological ecology of female western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia*, **144**(2): 206–213. doi:10.1007/s00442-005-0056-x. PMID:15800735.
- Tiebout, H.M., and Cary, J.R. 1987. Dynamic spatial ecology of the water snake, *Nerodia sipedon*. *Copeia*, **1987**: 1–18. doi:10.2307/1446031.
- Torre, I., Freixas, L., Arrizabalaga, A., and Diaz, M. 2016. The efficiency of two widely used commercial live-traps to develop monitoring protocols for small mammal biodiversity. *Ecol. Indic.* **66**: 481–487. doi:10.1016/j.ecolind.2016.02.017.
- Vistnes, I., Nellemann, C., Jordhøy, P., and Strand, O. 2004. Effects of infrastructure on migration and range use of wild reindeer. *J. Wildl. Manage.* **68**(1): 101–108. doi:10.2193/0022-541X(2004)068[0101:EOIOMA]2.0.CO;2.
- Waldron, J.L., Welch, S.M., Bennett, S.H., Kalinowsky, W.G., and Mousseau, T.A. 2013. Life history constraints contribute to the vulnerability of a declining North American rattlesnake. *Biol. Conserv.* **159**: 530–538. doi:10.1016/j.biocon.2012.11.021.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., and Losos, E. 1998. Quantifying threats to imperiled species in the United States. *BioScience*, **48**(8): 607–615. doi:10.2307/1313420.
- Willson, J.D., and Gibbons, J.W. 2009. Drift fences, cover boards and other traps. In *Amphibian ecology and conservation: a handbook of techniques*. Edited by K. Dodd Jr. Oxford University Press, New York. pp. 229–245.
- Winton, S.A. 2018. Impact of road mortality on the Western Rattlesnake (*Crotalus oreganus*) in British Columbia. M.Sc. thesis, Department of Science, Thompson Rivers University, Kamloops, B.C.
- Winton, S.A., Taylor, R., Bishop, C.A., and Larsen, K.W. 2018. Estimating actual versus detected road mortality rates for a northern viper. *Global Ecol. Conserv.* **16**: e00476. doi:10.1016/j.gecco.2018.e00476.
- Wolfe, A.K., Bateman, P.W., and Fleming, P.A. 2018. Does urbanization influence the diet of a large snake? *Curr. Zool.* **64**(3): 311–318. doi:10.1093/cz/zox039. PMID:30402072.
- Yermokhin, M.V., Tabachishin, V.G., and Ivanov, C.A. 2015. Spawning migration phenology of the spadefoot toad *Pelobates fuscus* (Pelobatidae, Amphibia) in the valley of the Medveditsa River (Saratov oblast). *Biol. Bull.* **42**(10): 931–936. doi:10.1134/S1062359015100040.