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# Movement Ecology of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) in Response to Disturbance

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Abstract: Anthropogenic disturbances often present novel habitat features to which the members of an existing population must adapt. We examined the effects of disturbance and habitat fragmentation on the movements of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) from 2006 through 2012 in southern British Columbia, Canada. We radio-tracked 44 adult male rattlesnakes through shrub-steppe, grassland, and dry forest habitats that varied from highly disturbed and fragmented to near pristine with little human interaction. Sources of disturbance were primarily associated with tourism (golf course, campground, hiking trails, roads, parking lots, vineyards, condominium complex). After accounting for interyear variation and daily temperature, rattlesnakes in undisturbed areas had larger home ranges (100% minimal convex polygon) and longer home-range lengths compared to individuals frequenting minimally to highly disturbed areas. Contrary to our predictions, snakes in highly disturbed sites did not move greater total distances, display elevated movement frequencies, higher movement rates, and/or more convoluted movement patterns.

**Key words:** Behavior; British Columbia; Conservation; Home range; Human disturbance; Telemetry

The degree to which populations are affected by landscape alteration and human development will depend largely on the ability of individuals to navigate fragmented habitat and respond to disturbances (Webb and Shine 1997). Changes to movement patterns triggered by disturbance might represent additional costs and risks for individuals (Murphy and Curatolo 1987). Furthermore, particular species whose movements and migrations are restricted to predetermined or traditional migration corridors, such as some northern snakes, might be more at risk to landscape disturbance (Berger 2004). For example, both Harvey (2015) and Martin et al. (2017) found that rattlesnakes (*Crotalus oreganus* and *C. viridis*, respectively) with more linear and longer migration routes had higher body condition (greater mass per unit body length) than individuals with more sinuous migration paths. However, animals in the former study that moved straighter, longer distances in human-dominated landscapes also were more susceptible to anthropogenic mortality.

Snakes also might alter their movements and behavior in human-disturbed areas because of a reduction in resources, and potentially in response to the risk of mortality in fragmented and altered landscapes (Shine et al. 2004; Andrews and Gibbons 2005; Breininger et al. 2011). Eastern Indigo Snakes (*Drymarchon couperi*) in Florida had smaller home ranges in fragmented habitats (Breininger et al. 2011), and female Prairie Rattlesnakes (*Crotalus v. viridis*) exhibited more tortuous movements in human-dominated landscapes (Martin et al. 2017). Furthermore, during the mating season, Western Diamondback Rattlesnakes (*C. atrox*) exhibited higher movement frequencies in disturbed areas compared to undisturbed areas (Beale et al. 2016).

Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) in Canada are sensitive to human activities that contribute to habitat alteration and continued persecution, making this species designated as "threatened" at both the provincial and federal level (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2015). The dry southern-interior valleys that this species inhabits in British Columbia (BC) are experiencing rapid changes because of urban development, tourism, and agriculture (Okanagan Valley Economic Development Society 2013; McAllister et al. 2016; Maida et al. 2018). Rattlesnakes must make seasonal movements between two important resources: winter refugia and summer foraging grounds. Winter denning sites must be safe and suitable for the climate, and foraging areas must contain sufficient prey to support the individuals using a given den. When the habitats within a home range are altered, a snake experiences higher risk and energy expenditure as it moves between the two resources, when compared to individuals representing populations in less disturbed habitats (Gregory et al. 1987). Recovery from the impacts of habitat loss, both anthropogenic and natural (Maida et al. 2017), is made even more difficult because of the characteristics associated with the northern periphery of the species' range, namely, low juvenile survivorship, slow juvenile growth, delayed sexual maturity, and infrequent parturition (Macartney and Gregory 1988).

Previous studies have identified consequences of human disturbance on Northern Pacific Rattlesnakes. In Idaho, Jenkins et al. (2009) found lower body condition, slower growth rates, and lower fecundity among snakes occupying disturbed areas. Further north in BC, Lomas et al. (2015) showed that rattlesnake body condition was negatively associated with human presence and disturbance. Using data collected coincidentally with the Lomas et al. (2015) study, we herein examine movement and behavior parameters of rattlesnakes in relation to the degree of disturbance occurring within the home ranges occupied by snakes during

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the active season. The biological parameters we measured were (1) the sizes and attributes of snake home ranges, and (2) movement patterns by snakes within those home ranges. Disturbance took the form of anthropogenic barriers and the conversion of natural habitat into roads, condominiums, hiking trails, a campground, and a golf course. We predicted that rattlesnakes in more disturbed areas would have smaller home-range sizes, travel shorter maximum distances from hibernacula, have greater movement rates and total distances moved, and more convoluted movement patterns when compared to snakes living in natural habitats without human contact.

## Materials and Methods

### Study Area

We conducted our study on the Osoyoos Indian Reserve (OIR; 49°2′57.09″N, 119°26′51.38″W; in all cases, datum WGS84) in the southern Okanagan Valley of BC, Canada. The 450-ha study area was located 3 km east of the town center of Osoyoos, BC, and 4 km north of the Canada–US border. The study area was situated in low elevation (~400 m) habitat dominantly characterized by Antelope Bitterbrush (*Purshia tridentata*), Big Sagebrush (*Artemisia tridentata*) and grasses, although there was also a linear riparian area within the center of the study site. The site was bordered to the north and east by mountain slopes dominated by open Ponderosa Pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) stands, and to the west by Osoyoos Lake (Fig. 1).

Distinct contrasts in development and human activity were present within the study site. The northern and eastern portions of the area had restricted access with no anthropogenic features or interruptions on the landscape. In the southern and western portions along the lakefront, however, development was widespread and targeted toward tourism, producing a landscape that was highly fragmented within these portions of our study area (Fig. 1). In 2006, development and human activity included a golf course, winery, vineyards, campground, an interpretative center, walking paths/trails, parking lots, and roads along with a two-lane highway bordering the south end of the study area. Construction of a large-scale resort including hotels and condominiums and ~4 km of snake exclusion fencing was ongoing until 2008. Visitors to these attractions number in the tens of thousands annually, yet rattlesnakes remain present in the area. All rattlesnakes within the developed and undeveloped portions of the study site use communal hibernacula (Brown et al. 2009; Lomas et al. 2015; Maida et al. 2017) located within the eastern rocky mountainsides at approximately 450–650-m elevation (see Lomas 2013 for more study site details).

### Radio Telemetry

From 2006 through 2012, we radio-tracked 44 adult male rattlesnakes between April and October. Rattlesnakes were captured as they emerged from hibernacula in the spring (April–May), and by incidental encounters during the active season. Procedures for snake body measurements (snout–vent length [SVL] and body mass) and implantation of a passive integrated transponder (PIT) followed methods in Lomas et al. (2015). Only adult males were selected for telemetry because female rattlesnakes may restrict their movements, or otherwise alter their behavior, if gravid (Macartney and Gregory 1988). Animals were transported to a nearby veterinary clinic and implanted with radio-transmitters (Holohil Systems Ltd., SB-2T 5.0 g or SI-2T 9.0 g) following Reinert and Cundall (1982) with modifications by Reinert (1992), and pharmaceutical procedures following Brown et al. (2009). We kept individual rattlesnakes in captivity for 24–48 hr following surgery to monitor recovery and rehydration before releasing them at their capture site. Transmitters weighed on average 2.2% of total body weight (range = 1.0–3.8%) and were removed at the end of the active season prior to hibernation or at the end of transmitter battery life (approximately 12 mo for SB-2T, and 24 mo for SI-2T).

In each year, we located each snake at minimum of every 2–3 d during the active season, with the exception of 2007, when snakes were located approximately once per week. We briefly recaptured snakes every 1–2 mo to measure subject length and body mass, and ensure that the surgery site showed no sign of infection. Otherwise, we restricted our presence near the animals to a minimum of 2-m distance, to avoid triggering movement or other defensive behavior.

### Quantifying Disturbance

As detailed in Lomas et al. (2015), we subdivided the study area using a disturbance rating (DR) system similar to that previously used by Parent and Weatherhead (2000). Different sections of the study area were assigned a priori on a DR scale of 0–4 based on distance ($D$) to the nearest source of human disturbance (i.e., $D > 200$ m = DR0; 100 m $< D > 200$ m = DR1; 50 m $< D > 100$ m = DR2; 10 $< D > 50$ m = DR3; $D < 10$ m = DR4). Essentially, DR0 sections had restricted public access and zero land development (e.g., northern section of study site; Fig. 1), whereas DR4 sections represented drastically transformed landscapes with continuous human presence (e.g., southern section of study site including campground, residential areas, and golf course; Fig. 1). We reassessed assignment of DRs prior to the active season each year to account for any new development and changes on the landscape. Finally, we assigned each telemetered snake its own DR based on the DR section of the study site that contained ≥50% of its home range (area) during a given year.

### Home-Range Parameters

We calculated a series of parameters to investigate rattlesnake home-range attributes. We used minimum convex polygon (MCP) and kernel density (KD) to calculate home-range size. Core area size, range length, and maximum distance traveled from hibernacula also were determined. We calculated all home-range parameters using data from the entire active season (April–October).

We analyzed all spatial data in GIS software ArcView v3.2 and ArcMap v10.0 (Esri, Redlands, CA) using the animal movement analysis extension (Hooge and Eichenlaub 1997). To facilitate comparisons with other snake populations and herpetofauna in the literature, and to take into account patterns of temporal and spatial selection, we used both 100% MCP and 95% KD estimators to calculate home-range sizes (Brown et al. 2009; Bauder et al. 2015; Smith et al. 2015; MacGowan et al. 2017). We used a least-squares cross-

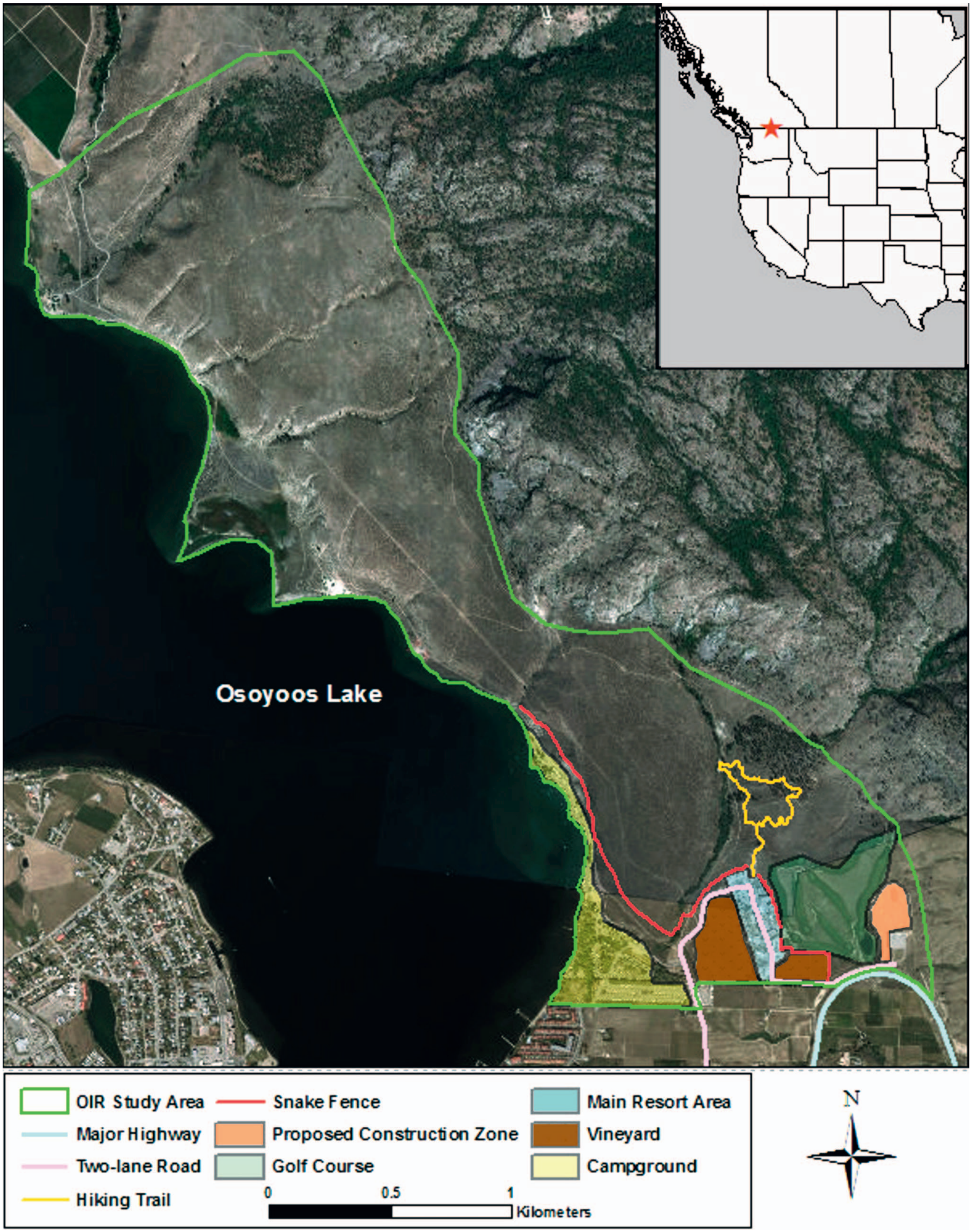

FIG. 1.—Map of the Osoyoos Indian Reserve (OIR) study site (indicated in green), near Osoyoos, BC, Canada (inset shows site location within North America). All developed areas occurred in the southern and western portions of the OIR, whereas the northern and eastern portions were undeveloped. All development and infrastructure was completed by 2008. Included on the map is a proposed condominium construction site set to begin in 2013 (poststudy), as well as the township of Osoyoos (lower left).

validation (LSCV) method to calculate the smoothing factor (*h*) for both 95 and 50% KDs (Worton 1989; Seaman and Powell 1996; Row and Blouin-Demers 2006), and 50% KD values as estimates of core area (CA; Tiebout and Cary 1987). Range length (RL) is the longest straight line that is completely contained within the home range of a snake (Roth and Greene 2006; Rouse 2006), whereas the maximum distance from hibernacula (MDH) is the maximum Euclidean distance between a snake's hibernaculum and any tracked location. We measured RL and MDH using the ArcView v3.2 extension Longest Straight Line v1.3a (Jenness 2007). We expected that for many snakes, RL would equal the maximum distance traveled from their hibernaculum (MDH; depending on range shape).

Some subjects initially were captured away from their hibernaculum in the spring. Because of the strong fidelity of these snakes to specific hibernacula (Macartney et al. 1990; Brown et al. 2009), we assumed the hibernaculum used by an individual snake in the subsequent autumn also had served as the starting point for that snake's movement earlier in spring, and we thus used this point for applicable range calculations.

### Movement Parameters

In addition to investigating home-range attributes, we examined specific parameters of snake movement within those home ranges, including: total distance moved (TDM), movement frequency (MF), mean distance between consecutive locations (MED), mean movement rate (MMR), and fractal dimension (FD). Total distance moved (TDM) is the sum of Euclidean distances between sequential locations, and represents the minimum distance moved. Movement frequency (MF) is the proportion of tracking events that revealed a movement greater than 10 m. Mean distance between consecutive locations (MED) is standardized to sequential locations pairs in a set time frame (24–72 h). Mean movement rate (MMR) is the mean distance (m) moved per day; we measured the distance traveled between two consecutive locations, divided by the number of days between, measured across all sequential pairs of tracking events (Diffendorfer et al. 2005). Fractal dimension (FD) is an estimate of tortuosity, or crookedness, of a movement path. We calculated FD of subject movement using the program FractalMean estimator within the program Fractal v5.20 (Nams 1996). This index ranges between 1 (straight path) to 2 (a path so tortuous as to completely cover a plane; Nams 1996, 2006).

To account for seasonal weather patterns, and migratory movements of subjects to and from hibernacula, we focused on the part of the active season where snakes had left the rocky hillsides and reached their summer foraging grounds. To do this, we first divided the entire active season (April–October) into three stages: (i) egress (from hibernacula to foraging grounds), (ii) summer foraging, and (iii) ingress (from summer foraging grounds to hibernacula). On account of the environmental variability among years, we delineated each stage based on subject movement rather than date. We designated the egress stage as ending and the foraging stage as starting after the movements by a snake became more truncated. Specifically, movements of $<50$ m between subsequent locations and/or 4 d spanned between movements away from hibernaculum marked the end of egress. Subsequently, we considered the foraging season ending and ingress starting when snakes began making movements of $>50$ m towards their hibernaculum. We included snakes that were not tracked for a full active season in the movement analysis if their data spanned at least the summer foraging season.

Periods of mating and ecdysis might influence snake movement patterns (Gibbons and Semlitsch 1987; Gillingham 1987). The cryptic behavior of snakes and our protocol of minimal disturbance on individuals made it untenable to consistently identify periods of ecdysis or mating events for each snake in each year. Separate analyses did not detect differences in shedding frequency or timing among male Northern Pacific Rattlesnakes in this region (Macartney et al. 1990; Lomas et al. 2015), giving us confidence that ecdysis variation among snakes would not bias our analyses of movement parameters.

### Temperature Effects

We used logistic regression to investigate whether DR combined with local maximum daily temperature (°C) influenced the probability of a snake making a movement. Using a binary response variable (no movement vs. movement), we fit a regression using a generalized linear model function (GLM; Crawley 2007). We used Wald's $\chi^2$ statistic to assess the association of variables (maximum daily temperature and DR) with snake movement. We used temperature data from the National Climate Data and Information Archive for the weather station located in the town of Osoyoos, approximately 2 km south of the OIR study site (49°1′41.85″N, 119°26′27.57″W; Environment Canada 2012). We analyzed temperature effects for the summer foraging season only, and standardized data by using only those locations recorded up to 48 hr apart. We pooled all years in the analysis.

### Statistical Considerations

We performed all analyses using R v2.12.1 (R Development Core Team 2011). We tested all data (home-range attributes and movement parameters) for normality by visual examination of histograms and bar-and-whisker plots of residuals against fitted values, and the Kolmogorov-Smirnov goodness-of-fit test (Zar 1999). We tested homogeneity of variances among DR categories and year using the Fligner-Killeen test (Conover et al. 1981; Crawley 2007). We used univariate two-factor analyses of variance (ANOVA) to compare each home-range attribute and movement parameter (foraging season only) between DRs and years. Tukey's honestly significant difference (HSD) test was used for post hoc multiple comparisons (Crawley 2007). Individuals were only included in analyses if they were tracked for more than 75% of the active season, more than 110 d, or 20 fixes. We treated consecutive locations $<10$ m apart as identical (i.e., movement $= 0$ m), given that the accuracy of our GPS unit was ±5 m. Data from multiple seasons (for those snakes tracked $>1$ yr; $n = 8$) were treated as independent because simulations have shown that this produces unbiased results in cases where intrasubject variance $\geq$ between-subject variance (Leger and Didrichsons 1994). As applied here, the variation of differences in range and movement parameters across seasons demonstrated by an individual animal were similar to (or larger than) the variation among all of the animals observed within a single season (see Pearson et al. 2005). We verified this pattern by comparing variances using an $F$-test, following Crawley (2007). Our data met these assumptions; therefore we treated home-range attributes and movement parameters calculated for each snake in each season as independent. For all statistical analyses, we used a Type I error rate of $\alpha = 0.05$, and report all means ±1 SE.

## RESULTS

Of the 44 male rattlesnakes that we followed over the course of our study, we tracked 7 subjects for 2 successive active seasons, and 1 individual for 3 successive active seasons, providing 53 rattlesnake spatial data sets. Because of predation ($n = 5$), road mortality ($n = 1$), human persecution ($n = 1$), transmitter failures ($n = 4$), and timing of capture, not all snakes were tracked for a full season. Although snakes did use areas within our study site having the a priori designation of DR4, no snake had ≥50% of its home range within DR4. Therefore, our analyses and results include DR0–DR3 only, with individual snakes who utilized DR4 habitats during the active season represented within the DR3 samples.

Sampling effort (number of locations [$F_{3,40} = 1.53$, $P = 0.22$] and length of season [$F_{3,40} = 0.86$, $P = 0.47$]) did not differ across DRs. The average body mass of rattlesnakes at initial capture was 250.5 ± 42.2 g, and average SVL was 71.7 ± 5.3 cm. These measurements did not differ among the DR categories (SVL: $F_{3,40} = 1.53$, $P = 0.22$; mass: $F_{3,40} = 0.94$, $P = 0.43$).

### Home-Range Parameters

We calculated home-range parameters on 38 rattlesnake spatial data sets ($n = 14$ in DR0, $n = 7$ in DR1, $n = 5$ in DR2, and $n = 12$ in DR3) from 2006 through 2012 ($n = 10$ in 2006, $n = 0$ in 2007, $n = 2$ in 2008, $n = 1$ in 2009, $n = 5$ in 2010, $n = 13$ in 2011, $n = 7$ in 2012). Three of six parameters that we tested differed significantly between DR categories, and all other effects were similar (Table 1). Measurements of home-range size (MCP) differed according to DR category ($P < 0.04$; Table 1), with a Tukey's HSD post hoc test indicating that individuals in DR0 had larger home ranges than those subjects occupying other DR categories ($P < 0.05$ in all cases, whereas all other pairwise comparisons were $P > 0.09$; Fig. 2). In contrast, the 95% kernel density home-range estimates were similar among DRs (Table 1; Fig. 2). Snakes in the different DR categories showed a difference in CA values (50% kernel density), with Tukey's HSD tests indicating that snakes in the DR1 category had higher CA values than those in DR2 areas ($P = 0.01$; all other pairwise comparisons $P > 0.13$; Fig. 3). The estimates of RL differed, with Tukey's HSD tests indicating that subjects in DR0 areas had greater RL values than those in DR2 ($P < 0.01$) and DR3 ($P = 0.03$; Fig. 3). The majority of subjects (79%) had similar estimates of RL and MDH (Table 1).

### Movement Parameters

We calculated movement parameters on 47 rattlesnake spatial data sets across disturbance ratings ($n = 19$ in DR0, $n = 8$ in DR1, $n = 5$ in DR2, $n = 15$ in DR3) from 2006 through 2012 ($n = 11$ in 2006, $n = 2$ in 2007, $n = 4$ in 2008, $n = 1$ in 2009, $n = 5$ in 2010, $n = 16$ in 2011, $n = 8$ in 2012).

TABLE 1.—Values for home-range parameters of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, BC, Canada, and results of analyses of variance assessing differences in these parameters ($n = 38$ spatial data sets) as a function of disturbance rating (DR), study year, and interaction effects. Statistically significant $P$ values are indicated in bold.

| Home-range parameters | $\bar{x}$ ± SE | Variable | Statistic | $P$ |
|---|---|---|---|---|
| 100% minimum convex polygon | 20.3 ± 12.1 ha | DR | $F_{3,25} = 3.20$ | **0.04** |
| | | Year | $F_{5,25} = 0.65$ | 0.67 |
| | | DR × Year | $F_{4,25} = 0.92$ | 0.47 |
| 95% kernel density | 23.7 ± 14.5 ha | DR | $F_{3,25} = 2.73$ | 0.07 |
| | | Year | $F_{5,25} = 1.79$ | 0.15 |
| | | DR × Year | $F_{4,25} = 0.92$ | 0.47 |
| Core area | 4.1 ± 2.9 ha | DR | $F_{3,25} = 3.81$ | **0.02** |
| | | Year | $F_{5,25} = 2.53$ | 0.05 |
| | | DR × Year | $F_{4,25} = 1.50$ | 0.23 |
| Range length | 976.2 ± 297 m | DR | $F_{3,25} = 6.08$ | **<0.01** |
| | | Year | $F_{5,25} = 1.08$ | 0.40 |
| | | DR × Year | $F_{4,25} = 1.52$ | 0.23 |
| Maximum distance traveled from hibernacula | 960 ± 318 m | DR | $F_{3,36} = 2.78$ | 0.06 |
| | | Year | $F_{6,36} = 1.10$ | 0.38 |
| | | DR × Year | $F_{7,36} = 1.32$ | 0.27 |

No significant effects of DR, year, or their interaction were detected for four of the five movement parameters (Table 2). The exception was MMR, where a Tukey's HSD post hoc test indicated that subjects in the DR2 areas had lower values than those in all other DRs ($P < 0.04$ in all cases). Furthermore, MMR values in 2006 were higher than in 2011 ($P = 0.03$; all other pairwise comparisons $P > 0.26$). Overall, rattlesnake movement paths were more linear than crooked (i.e., FD was closer to 1 than 2; Table 2).

### Temperature Effects

Both full and partial season data sets from all years were used in the temperature analyses, with a total sample size of 750 movement events. Overall, maximum daily temperature was associated with the probability that a snake would undertake a movement (Wald's $\chi^2 = 7.6$, df = 1, $P < 0.01$) and there was an effect of DR on movement (Wald's $\chi^2 = 13.7$, df = 3, $P < 0.01$) but no discernable trend across DR categories.

The strongest relationship between temperature and movement was observed in DR2, where snakes were more likely to make a movement during warmer temperatures than cooler temperatures ($P = 0.04$). This relationship was different compared to that in lower DRs, where probability of movement was much less associated with temperature (Fig. 4). A difference in the relationships was observed between DR0 and DR2 ($P = 0.02$). Regardless of temperature, subjects in DR0 had a higher probability of having moved within a 48-h period than those snakes in DR1 ($P < 0.001$) and DR3 ($P < 0.01$; Fig. 4).

## DISCUSSION

Contrary to our predictions, male *Crotalus o. oreganus* in disturbed areas within OIR did not display consistent changes or trends in movement parameters. Home ranges and range lengths were larger for subjects occupying and moving through natural areas (DR0) compared to both slightly and severely disturbed areas within our study site. In the northern portions of the OIR study area, rattlesnakes were able to move throughout the active season without coming into contact with any unnatural landscape features

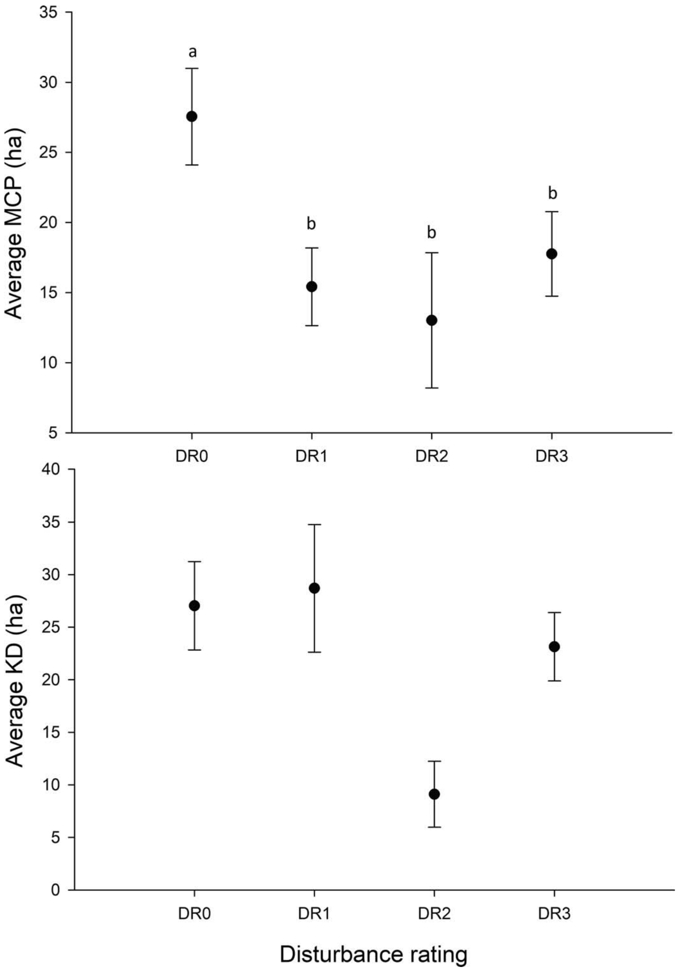

FIG. 2.—Mean ± 1 SE of 100% minimum convex polygon (MCP) and 95% kernel density (KD) home-range estimates (ha) over the active season of male Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) within areas having different disturbance ratings (DR) near Osoyoos, BC, Canada, between 2006–2012. Sample sizes for the DRs are DR0 ($n = 14$), DR1 ($n = 7$), DR2 ($n = 5$), and DR3 ($n = 12$). Statistically distinct mean values ($P < 0.05$) are indicated with different superscript letters.

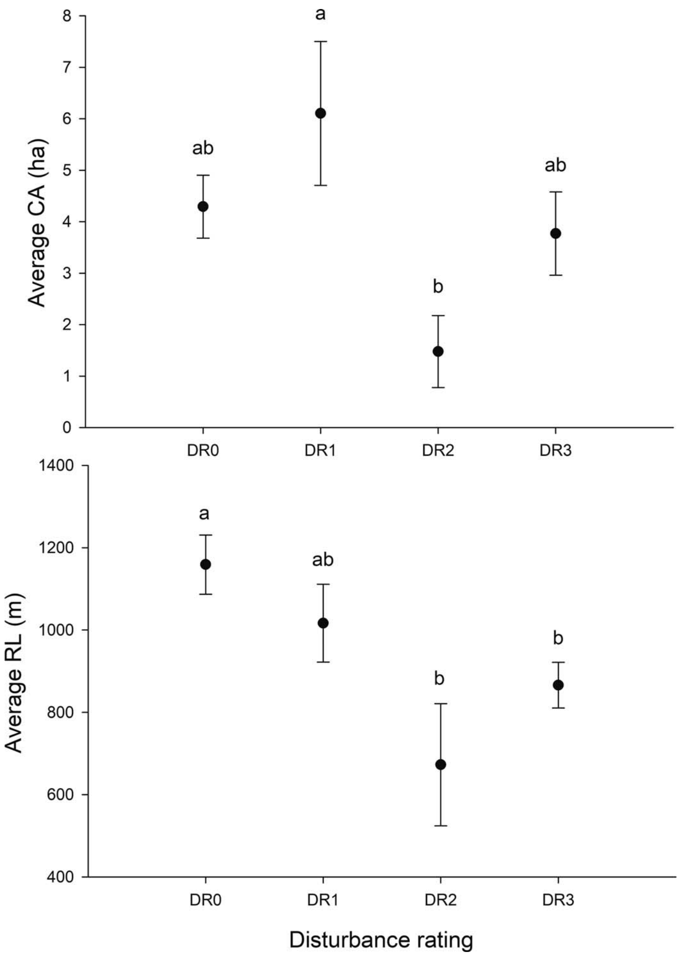

FIG. 3.—Mean ± 1 SE of core area (CA) and range length (RL) over the active season of male Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) within areas having different disturbance ratings (DR) near Osoyoos, BC, Canada, between 2006–2012. Sample sizes for the DRs are DR0 ($n = 14$), DR1 ($n = 7$), DR2 ($n = 5$), and DR3 ($n = 12$). Statistically distinct mean values ($P < 0.05$) are indicated with different superscript letters.

and barriers. Conversely, rattlesnakes in disturbed sites were more likely to experience contact with humans and/or anthropogenic structures including roads, golf course fairways, vineyards, buildings, snake fencing, or hiking trails. Although some of these barriers are permeable (excluding fencing and buildings), all types can restrict or alter natural snake movements, and none provide cover or refuge habitat in close proximity to human activities (Eye et al. 2018). Previous studies have suggested that snakes avoid open areas such as roads and trails (Weatherhead and Prior 1992; Shine et al. 2004; Clark et al. 2010; Robson and Blouin-Demers 2013). Conversely, snakes in our study area experiencing an absence of unnatural barriers or altered habitat appeared to move more freely across the landscape, which corresponds with increased home-range sizes and range lengths in undisturbed areas. However, the differences in habitat quality as categorized by disturbance level appeared to exert little effect on more specific movement parameters within the home ranges.

The inconsistent relationship between disturbance intensity (our DR rating) and the small-scale movement parameters might be partially attributable to the fact that all, if not most, of our subjects had access to some undisturbed habitat even when occupying home ranges within or adjacent to disturbed areas (i.e., natural shrub steppe cover between golf course fairways; Fig. 1). These areas might have been large enough to allow some natural movements and behaviors. A comparable example of this pattern was documented in Northern Pinesnakes (*Pituophis m. melanoleucus*) where the spatial ecology of the subjects was similar in disturbed and undisturbed areas within a military base, likely attributable to the amount of natural habitat within disturbed areas (Smith et al. 2015).

The availability of prey can influence snake movement patterns and movement rates (Wasko and Sasa 2012), but did not appear to be a factor in our study. The principal prey for rattlesnakes at OIR are rodents (McAllister et al. 2016), but how this small mammal community responds to disturbance is variable. For example, golf courses (one of the primary disturbed landscape types at OIR) have a somewhat unique impact (Smith et al. 2008) because they fragment the landscape yet often contain pockets of natural habitat. Because irrigation provides a relatively constant supply of

TABLE 2.—Values for movement parameters of Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) near Osoyoos, BC, Canada, and results of analyses of variance assessing differences in these parameters ($n = 47$ spatial data sets) as a function of disturbance rating (DR), year, and interaction effects. Statistically significant *P* values are indicated in bold.

| Movement parameters | $\bar{x} \pm$ SE | Variable | Statistic | *P* |
|---|---|---|---|---|
| Total distance moved | 2837.0 ± 1099.4 m | DR | $F_{3,30} = 1.37$ | 0.27 |
| | | Year | $F_{6,30} = 1.61$ | 0.18 |
| | | DR × Year | $F_{7,30} = 0.28$ | 0.96 |
| Movement frequency | 0.76 ± 0.12 | DR | $F_{3,29} = 2.91$ | 0.05 |
| | | Year | $F_{5,29} = 2.34$ | 0.08 |
| | | DR × Year | $F_{7,29} = 1.06$ | 0.42 |
| Mean movement rate | 35.4 ± 14.5 m/d | DR | $F_{3,30} = 4.35$ | **0.01** |
| | | Year | $F_{6,30} = 4.34$ | **<0.01** |
| | | DR × Year | $F_{7,30} = 0.73$ | 0.65 |
| Mean distance between consecutive locations | 110.9 ± 40.3 m | DR | $F_{3,30} = 1.06$ | 0.38 |
| | | Year | $F_{6,30} = 1.64$ | 0.17 |
| | | DR × Year | $F_{6,30} = 0.64$ | 0.70 |
| Fractal dimension | 1.3 ± 0.10 | DR | $F_{3,29} = 2.24$ | 0.11 |
| | | Year | $F_{5,29} = 0.45$ | 0.81 |
| | | DR × Year | $F_{7,29} = 2.10$ | 0.08 |

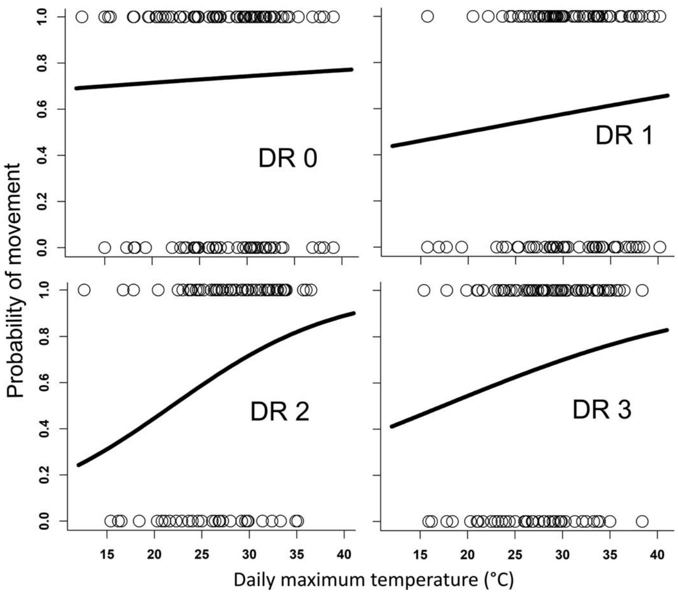

FIG. 4.—Movement probability of adult male Northern Pacific Rattlesnakes (*Crotalus o. oreganus*) in relation to maximum daily temperature (°C) for areas having different disturbance ratings (DR) near Osoyoos, BC, Canada, between 2006 and 2012. Points indicate frequency of occurrences of movement/no movement by temperature. Lines represent probabilities of predicted movement. See text for description of DR levels.

moisture, these habitats typically have increased productivity that leads to an increase in species richness and abundance compared to adjacent areas (Smith et al. 2008). Some reptile populations have benefited from golf courses because small mammal abundance generally is higher in those areas when compared to neighboring urban or rural landscapes (Hodgkison et al. 2007). Other types of human disturbance cause decreases in small mammal abundance (Sauvajot et al. 1998; Umestu and Pardini 2007). Small mammal live-trapping at OIR (2012 to present) has not detected any differences in small mammal species diversity or abundance across different habitat types (Maida 2018). Therefore, it is unlikely that prey availability across the landscape is exerting an effect on rattlesnake behavior and movements among habitats categorized as having different DRs.

Subjects within DR2 areas had consistently smaller core areas, smaller range lengths, and lower movement rates. A posteriori assessments of the DR2 areas indicated they were unique in containing some riparian habitat rather than the typical arid shrub-steppe and open pine forests found in the other DR areas. The riparian habitat contained substantial differences in shrub cover composition, and summer-long access to water, which could potentially affect movement patterns by rattlesnakes.

There was a strong association between the local maximum daily temperature and the probability that a subject would move. There was no noticeable trend in the relationship between maximum daily temperature and disturbance, other than a difference between undisturbed (DR0) areas and semidisturbed areas (DR2). Future studies might reveal a more pronounced effect of temperature in disturbed sites because snakes in disturbed areas have reduced access to cover, both quantitatively and qualitatively. This might mean that subjects must move in order to thermoregulate effectively during fluctuations in ambient temperature. We acknowledge that when assessing temperature, microclimate and topographic conditions will affect the conditions experienced by ectotherms like rattlesnakes (Lelièvre et al. 2010), and considerable discrepancies will exist between climate across local and microhabitat scales. Because microhabitat data were not collected, we cannot account for the role that microclimate plays in dictating snake movements according to patterns of disturbance documented in our study.

Despite the variation in size of the areas used by subjects occupying habitats within the OIR that had different DRs, the pattern of repeated interannual use of habitat features (e.g., movement corridors) and high site fidelity of male rattlesnakes (Sealy 2002; Travsky and Beauvais 2004; Brown 2006; Gomez et al. 2015) appears to hold true in our study. Timber Rattlesnakes (*C. horridus*) prior to, during, and after deforestation and logging operations did not exhibit short-term changes in behavior, movement patterns, activity areas, or home ranges (Reinert et al. 2011; MacGowan et al. 2017). As a type of disturbance, deforestation can create barriers on the landscape; however, in those studies the levels of disturbance did not appear to deter snakes from returning and utilizing those specific areas, which is similar to how rattlesnakes behaved at our study site.

Previous studies suggest that landscape disturbance, specifically that caused by urbanization and other anthropogenic alterations, can have negative, long-term impacts and consequences on snakes (Roe et al. 2006; Clark et al. 2010). Other studies suggest that rattlesnake populations, specifically those of Northern Pacific Rattlesnakes, might be resilient to disturbance and frequent interactions with humans (Brown et al. 2009; Holding et al. 2014). In contrast, Lomas et al. (2015) found a consistent negative trend in rattlesnake body condition as the level of disturbance (DR category) increased in occupied habitats. Those authors suggested that the persistence of the snakes in the area might be masking more indirect and negative effects from occupying a landscape with an intense pattern of human activity. Taken together, our results and those of Lomas et al. (2015) indicate that the body condition of rattlesnakes, their home-range sizes, and their movement characteristics within home ranges all need to be examined relative to the anthropogenic stressors, as well as the natural features available to individuals occupying that landscape.

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