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An individual's migration path shape should affect its fitness, because patchily distributed features (e.g. prey) are encountered more often on straight than tortuous paths. We hypothesized that *Crotalus viridis viridis* (Rafinesque, 1818) with straighter migration paths should have better body condition, because they encounter prey patches more frequently, and higher migration mortality, because they also encounter predators and hazardous human land uses more frequently, than individuals with tortuous paths. If true, then a straighter path should be favoured when the benefit (resource acquisition) outweighs the cost (mortality risk). Humans pose a significant mortality risk for migrants; thus the cost of straight-line movement should increase relative to the benefit in more human-dominated landscapes, favouring more tortuous movements. We tested these hypotheses using data on the body condition, mortality, and migration movements of 25 female rattlesnakes in one human-dominated and one semi-natural landscape. As hypothesized, we found better body condition and higher migration mortality for snakes with straighter migration paths, and that snakes followed more tortuous paths in the human-dominated landscape. Although selection for tortuous movements may reduce rates of migration mortality in human-dominated landscapes, this may ultimately contribute to population declines if poorer body condition reduces overwinter survival or reproductive success.

Keywords *Crotalus viridis viridis*; body condition; foraging success; human land use; migration; mortality; natural selection; path shape; prairie rattlesnake

Introduction

Migration, i.e. the seasonal movement of individuals between geographically distinct habitat regions, can be beneficial for individuals and populations. Proposed benefits of migration include the ability to track seasonal changes in resource availability, avoid seasonal peaks in competition and predation within part of their range, and exploit habitats that are optimal for different activities (e.g. breeding versus overwintering; Alerstam et al. 2003; Brönmark et al. 2008; Holt and Fryxell 2011). In migratory snake populations, seasonal movement between hibernacula and breeding and summer foraging grounds is beneficial because it allows snakes to locate mates and acquire the food resources necessary for successful breeding, growth, and overwintering (Duvall et al. 1990; Duvall and Schuett 1997).

Migratory rattlesnakes feed and mate during migration (King and Duvall 1990), thus their behaviour during migration influences how frequently they encounter prey and mates. Theory suggests that straight or near-straight migration movements optimize the frequency of encounters with patchily distributed resources, like food or mates (Duvall et al. 1997; Zollner and Lima 1999; Bartoń et al. 2009). This is supported by empirical study, showing that mate location (and thus mating success) was higher for male prairie rattlesnakes (*Crotalus viridis viridis* (Rafinesque, 1818)) that made straighter movements (Duvall and Schuett 1997). This is because individuals making straighter movements cover more novel ground, and avoid repeatedly searching for resources at the same sites. Thus, we hypothesize that snakes making straighter migration movements should also encounter resource patches more frequently than snakes with tortuous migration paths.

Although straighter migration paths could potentially benefit snakes, allowing for greater rates of resource acquisition, this behaviour is not without risk. The risk of mortality during migration may be high, because these movements expose snakes to predators, humans, and

hazardous land uses such as agriculture and roads (Bonnet et al. 1999). Humans and human land uses can cause particularly high rates of snake mortality. For example, roads have been shown to be a major source of mortality for snakes: one study reported that 70% of the snake deaths were associated with roads, and mortality rates were particularly high for snakes making long-distance movements (Bonnet et al. 1999). Humans also intentionally kill snakes. One study estimated that 37% of venomous snakes encountered by people were intentionally killed (Whitaker and Shine 2000). Persecution has been identified as a major threat to a number of threatened and endangered snake species (e.g. eastern hog-nosed snake [*Heterodon platirhinos* Latreille, 1801] and Massasauga rattlesnake [*Sistrurus catenatus* (Rafinesque, 1818)]; COSEWIC 2007; COSEWIC 2012).

Straighter migration paths likely exacerbate the risk of migration mortality. This is because, in addition to increasing rates of interaction with patchily distributed mates and prey, it should increase rates of encounter with patchily distributed predators, humans, and human land uses. Thus, snakes with straighter migration paths should have a greater risk of mortality than snakes with tortuous migration paths.

If straighter migration paths have both benefits and costs for the individual, then we expect selection for straighter migration paths when the benefit (resource acquisition) outweighs the cost (mortality risk), and tortuous migration paths when the cost outweighs the benefit. This cost/benefit ratio should depend on the level of human land use, because humans pose significant mortality risks for snakes (as introduced above). When human presence in a landscape is low, the benefits of straighter migration paths should be greater than its risks, favouring straighter migration paths. In contrast, in human-dominated landscapes the costs of encountering humans and human land uses when making straighter migration movements should exceed the benefits of

this behaviour. When this occurs, natural selection should favour tortuous migration paths, even if this is at the expense of potential foraging or mating success.

In this study, we collected data on the body condition, mortality, and migration movements of non-gravid female prairie rattlesnakes in two landscapes with contrasting levels of human land use, to test the following predictions:

- (1) Individuals with straighter migration paths have better body condition than individuals with more tortuous migration paths upon return to hibernacula in the fall.
- (2) Individuals with straighter migration paths have higher probabilities of mortality during migration than individuals with more tortuous migration paths.
- (3) Migration paths are straighter in the semi-natural landscape than in the human-dominated landscape.

Materials and methods

Study species

The prairie rattlesnake occurs in the Great Plains ecoregion, and is associated with grass and shrub land cover types (Andrus 2002; Shipley et al. 2013). In the studied northern portion of the species' range (see *Study sites* below; Fig. 1a) populations overwinter communally in underground hibernacula. Hibernacula are usually located along rivers and in coulees, or at the transition between riparian and upland habitats (COSEWIC 2015). The prairie rattlesnake is seasonally migratory in this area of its range. Rattlesnakes emerge from hibernacula in the spring (late April–late May; Gannon and Secoy 1985; Andrus 2002), after which they typically migrate to summer foraging habitat or move to nearby natal den sites, and return to the same hibernacula to overwinter (mid–late September; Gannon and Secoy 1985; Andrus 2002; Shipley et al. 2013).

Male and non-gravid female prairie rattlesnakes have been reported to move up to 25 km from the den in a single season (Didiuk 1999), although maximum migration distances are more typically 10–15 km in northern populations (COSEWIC 2015). Gravid females have limited mobility and move much shorter distances to give birth at perennially-used natal den sites, typically located within 500 m of the hibernaculum (Jørgensen and Nicholson 2007). Prairie rattlesnakes feed during migration and during localized movements in the summer foraging grounds (King and Duvall 1990). Northern prairie rattlesnakes predominantly prey on small rodents (mainly *Lagurus curtatus* (Cope, 1868), *Microtus pennsylvanicus* (Ord, 1815), and *Perognathus fasciatus* Wied-Neuwied, 1839) and some passerine birds (Hill et al. 2001). They will also occasionally prey on larger-bodied ground squirrels (e.g. *Spermophilus richardsonii* (Sabine, 1822); Hill et al. 2001).

Study sites

We used radio-telemetry to track the movements of prairie rattlesnakes over two active seasons (April to October in 2004 and 2005), around two hibernacula within the South Saskatchewan River watershed near Medicine Hat, Alberta, Canada (Fig. 1b). Each hibernaculum was a network of interconnected subterranean fissures and mammal burrows, separate from other such networks, from which prairie rattlesnakes emerged and migrated in the spring, and to which they returned in the fall to overwinter. One hibernaculum (hereafter hibernaculum A) was surrounded primarily by native rangeland, with a relatively small area of crop agriculture and little human development in the form of oil and gas wells and associated infrastructure (hereafter the ‘semi-natural landscape’; Fig. 1b). The second hibernaculum (hibernaculum B) was located in a ‘human-dominated landscape’ with extensive crop agriculture, seeded pasture, residential development, and far less native rangeland cover than in the area around hibernaculum A (Fig.

1b). Summer foraging grounds were presumed to be separate for individuals from these two hibernacula, because the distance between hibernacula (28 km) was approximately twice the typical maximum migration distance for snakes in this region. We note that this assumption was supported by our radio-telemetry data: all radio-telemetry locations for individuals originating in the semi-natural landscape were at least 25 km from the locations of individuals from the human-dominated landscape.

Prairie rattlesnake capture

We included only non-gravid, adult female prairie rattlesnakes in this study. We excluded gravid females because they do not make long-distance movements during the active season, instead residing in protected natal den sites until giving birth in late summer (Graves and Duvall 1993). We excluded males because this simplified our classification of observed movements (as either migratory or localized within the foraging grounds): in addition to migration and foraging movements, males engage in mate-searching movements during the active season (King and Duvall 1990).

Trapping occurred during spring emergence (late April to early May) in 2004 and 2005. We erected drift fences around each hibernaculum. At hibernaculum A, 15 m of drift fence was erected, surrounding the emergence holes, and two funnel traps were used along the fence line to trap emerging rattlesnakes. At hibernaculum B, 125 m of drift fence was erected upslope from the network of burrows, and three funnel traps were used to trap emerging rattlesnakes. We measured the mass (g) and snout-to-vent length (SVL; cm) of each captured female at emergence, and upon its return to the den at the end of the active season (when possible).

Radio-telemetry transmitter implantation

Captured females were immediately transported to the Calgary Zoo Animal Health Centre where qualified veterinary personnel implanted each snake with a passive integrated transponder (PIT) tag (Avid) and a radio-telemetry transmitter (Model SB-2; Holohil Systems Ltd., Ontario, Canada). The transmitters were lighter and smaller than a typical prey item (5 g, 1.0%–2.3% of the mass of the snake), and were implanted in the coelomic cavity where they would not obstruct the passage of prey through the digestive system. Snakes were given antibacterial treatment (trimethoprim-sulfa, 30 mg/kg) and analgesics (meloxicam, 0.1 mg/kg, butorphanol, 1 mg/kg) prior to transmitter implantation, and were anaesthetised with intravenous propofol (6 mg/kg) followed by isoflurane (2–3% with oxygen 1 L/min) and nitrous oxide (500 mL/min). They received intracoelomic fluids post-operatively (50 mL/kg) to ensure hydration, and were monitored in a controlled environment for 24 hours before being released at the hibernaculum where they had been captured.

All surgical and handling procedures were approved and permitted under the University of Calgary, Certification of Animal Care #BI2004-024 (2004–2006), Alberta Sustainable Resource Development Collection Licences #118 (2004–2005) and #20372 (2005–2006), and Alberta Sustainable Resource Development Research Permits #15383 (2004–2005) and #20390 (2005–2006). For additional details of these methods, see Jørgensen et al. (2008).

Radio-telemetry

The locations of snakes were monitored daily during the active season, or as weather and accessibility permitted, using radio signals to locate them. We recorded the Universal Transverse Mercator coordinates (UTM zone 12; NAD83) with a Garmin 12XL Global Positioning System unit (Garmin Ltd., Canton of Schaffhausen, Switzerland) each time the snake moved (i.e. its current location differed from its previous one). The minimum interval between recorded

locations was 12 hours. Each transmitter-equipped female was tracked until it returned to the den at the end of the active season, or until it died.

Data preparation

The movement path of each prairie rattlesnake was classified into an outbound migration component (characterized by movement away from its hibernaculum in the spring), a foraging habitat use component (characterized by localized movements within the foraging habitat), and an inbound migration component (with movement in fall towards its hibernaculum). We identified the end of outbound migration as the point of maximum net displacement from the first recorded location at or near the hibernaculum.

We used data points for the outbound migration path of each individual to measure migration path shape as the path sinuosity index, calculated as the net displacement distance/total path length (e.g. Saumure et al. 2010). This measure of path shape ranges from zero (random walk) to one (perfectly straight). We used only the outbound migration component because (a) we were interested in migration movements rather than movements within the summer foraging grounds, and (b) not all tracked individuals survived to return to the hibernaculum in the fall.

We calculated a body condition index (BCI) for each individual from fall mass and SVL measurements. BCI was estimated as the residual from a linear regression of the fall mass against the fall SVL, where a more positive residual indicates a better body condition (i.e. greater mass than predicted for its body length; Wayne and Mason 2008). We focused our analysis on fall body condition because condition of a female upon return to the den is what determines whether it has the stored tissue resources necessary to survive winter hibernation (Shine et al. 2001) and become gravid in the following season (Gregory 2006). Additionally, we assumed that a snake's fall body condition reflects its summer foraging success. To test this assumption, we evaluated the

correlation between the fall BCI and the change in mass over the active season (fall mass measurement – spring mass measurement).

Data analysis

We used multi-model inference to determine the level of support for relationships between BCI and path sinuosity, when controlling for the study landscape (semi-natural or human-dominated) and year of radio-telemetry tracking (2004 or 2005). We used the small-sample Akaike Information Criterion (AICc) to compare eight candidate models relating BCI to all combinations of the three predictors, plus the null (intercept-only) model, using linear regression. We squared path sinuosity to satisfy assumptions of linear regression. We then calculated the model-averaged regression coefficient and 95% unconditional confidence interval (95% CI) for each predictor. Our hypothesis would be supported if this 95% CI for the BCI-sinuosity relationship did not cross zero, and BCI were higher for individuals with straighter migration paths (i.e. sinuosity index values closer to one).

We used multi-model inference to determine the level of support for relationships between the probability of migration mortality, and path sinuosity, study landscape, and year, as described above, except that here we used logistic regression. Our hypothesis would be supported if the 95% CI for the mortality-sinuosity relationship did not cross zero, and the probability of mortality was higher for individuals with straighter migration paths.

Finally, we used multi-model inference to determine the level of support for relationships between (path sinuosity²) and the study landscape and sampling year, as described above, using linear regression. Our hypothesis would be supported if the 95% CI for the sinuosity-landscape relationship did not cross zero, and paths were straighter in the semi-natural landscape than in the

human-dominated landscape. All statistical analyses were conducted in R (R Core Team 2015), using the ‘MuMIn’ package (Bartoń 2014).

Results

We tracked 25 non-gravid female rattlesnakes, 10 in the semi-natural landscape (3 in 2004, 7 in 2005) and 15 in the human-dominated landscape (8 in 2004, 7 in 2005; Table 1). The number of radio-telemetry locations used to estimate path sinuosity varied among individuals (mean = 40, range 18–68), as did the average time between these locations (Table 1). Path sinuosity values calculated for the outbound migration path ranged from 0.17 (highly tortuous) to 0.96 (nearly straight; e.g. Fig. 2). These values were not affected by the number of radio-telemetry locations or the time between locations ($r = -0.28$, $P = 0.17$ and $r = -0.10$, $P = 0.63$, respectively). BCI was calculated for each of the 18 individuals for which fall mass and SVL measurements were collected, as the residuals from the positive mass-SVL relationship ($r^2 = 0.79$). Fall BCI was strongly correlated with the accumulation of mass over the active season ($r = 0.74$, $P < 0.001$), supporting our assumption that fall BCI reflects the individual’s summer foraging success. Twenty percent (5 / 25) of tracked individuals died during migration.

Body condition and the probability of migration mortality varied with path sinuosity as expected. Individuals with straighter paths (i.e. sinuosity index values closer to one) had higher BCI than individuals with more tortuous paths (Fig. 3a, Supplementary Table S1¹). The positive relationship between path sinuosity and BCI was supported by multi-model inference (its 95% CI did not cross zero). The probability of migration mortality also tended to be higher for individuals with straighter migration paths (Fig. 3b, Supplementary Table S2¹). Although multi-model inference suggested weak support for this relationship (the 95% CI calculated from the candidate

model set crossed zero), the two most supported models included an effect of path sinuosity on the probability of mortality.

Path sinuosity was different in the two study landscapes. Migration paths were straighter in the semi-natural landscape than in the human-dominated landscape (Fig. 4, Supplementary Table S3¹). This relationship between sinuosity and the landscape context was supported by multi-model inference (its 95% CI did not cross zero).

Discussion

Female prairie rattlesnakes with straighter migration paths had better fall body condition. We infer this is because snakes with straighter migration movements encounter prey more frequently than snakes with tortuous migration paths. The strong, positive correlation between the fall body condition and change in mass over the summer was consistent with this inference. Previous research showed that male prairie rattlesnakes that make straighter migration movements locate mates more frequently (Duvall and Schuett 1997). Taken together, these studies suggest that straighter migration movements are beneficial for prairie rattlesnakes, increasing both foraging and mating success.

Alternatively, the observed BCI-sinuosity relationship could occur because fall body condition is positively correlated with spring body condition, and individuals with better spring condition are the ones able to make long, straight migration movements (Southwood and Avens 2010). However, supplementary analyses did not support this explanation. Spring body condition was not significantly related to fall body condition (Supplementary Fig. S1¹). Additionally, spring body condition was only weakly related to the migration path shape (Supplementary Fig. S2, Table S4¹).

The better fall body condition of individuals with straighter paths was also not explained by the landscape context (semi-natural or human-dominated). Although migration paths were straighter in the semi-natural landscape, this landscape context would only explain the observed BCI-sinuosity relationship if body condition was also better in the semi-natural landscape than the human-dominated one. This is the opposite of what we observed (Fig. 3a). Thus, the most likely explanation is that straighter migration paths led to better fall body condition because of increased foraging success during migration.

Although straighter migration movements can benefit snakes, our results also suggest that this migration behaviour may increase the risk of mortality. We note that statistical support for this relationship was weak relative to the relationship between body condition and path shape. Nevertheless, the direction of effect of path shape on the probability of mortality was consistent with our expectation that snakes moving in straighter lines have higher mortality risk because they are more likely to encounter predators, humans, and human land uses during migration. Three of the five deaths recorded in this study were attributable to human causes (two were killed by raptors, two by agricultural equipment in cultivated fields, and one was killed on a road).

It was surprising that road mortality was not more prevalent in our study, given that roads are a significant source of snake mortality (Bonnet et al. 1999; Row et al. 2007; Quintero-Ángel et al. 2012; Weyer et al. 2014). The low road mortality rates we observed may, at least in part, be explained by the observed differences in migration behaviour in the two study landscapes. More tortuous movements in the human-dominated landscape – where risk of road mortality was extreme – could have reduced actual road mortality rates. This is because, all else being equal, a snake that makes more tortuous movements is less likely to encounter a road than a snake that makes straighter movements. In support of this, Weyer et al. (2014) found eight times more prairie rattlesnakes on a road near the hibernacula in the semi-natural landscape than on the road

near the hibernacula in the human-dominated landscape. Actual road mortality rates relative to other sources of mortality (e.g. predation) could also have been underestimated because our sample size (of five mortality events) was too small to reliably estimate the population-level mortality risks from different sources.

If straighter migration paths have both benefits and costs for individuals, as our results suggest, then we expect selection for straighter migration paths when benefits outweigh the costs, and tortuous migration paths when costs outweigh the benefits. In particular, we hypothesized that encountering humans and human land uses should increase the cost/benefit ratio of straight-line migration, because they pose significant mortality risks for snakes. Our results supported this hypothesis: migration paths of female prairie rattlesnakes were straighter in the semi-natural landscape relative to the human-dominated landscape. This may explain why all prairie rattlesnakes radio-tracked in an urban setting made highly tortuous seasonal movements (Andrus 2002).

Fall body condition tended to be higher in the human-dominated landscape (Fig. 3a). Previous studies suggest that rattlesnakes cease migration when they encounter a source of rodent prey (Duvall et al. 1990; King and Duvall 1990). Thus, one might speculate that migration paths were more tortuous in the human-dominated landscape because snakes only make long, straight migration movements when food is scarce, and food resources were more abundant in the human-dominated landscape. However, we suggest this explanation is unlikely for two reasons. First, if snakes ceased migration earlier in the human-dominated landscape, we would expect the cumulative distance moved during the active season (from emergence to return to the den) would be shorter in the human-dominated landscape than in the semi-natural landscape. We found no difference in cumulative migration distances between landscapes (Supplementary Fig. S3¹). Second, if individuals making tortuous movements in the human-dominated landscape ceased

migration because they found ample prey, we would expect them to have similar, or better, body condition than those making straighter, long-distance migration movements. This is because individuals making tortuous movements should spend more time foraging, and less time migrating, than those making straighter movements. In contrast, individuals with straight migration paths had better body condition than those with tortuous paths (Fig. 3a).

Although we inferred that increasing human land use favours selection for more tortuous migration behaviours, migration movement paths may also be, at least in part, the product of individual responses to human landscape features. When a snake encounters roads or cultivated fields it may change direction to avoid these surfaces, resulting in more tortuous migration paths in the human-dominated landscape. A study of the behavioural responses of a related rattlesnake species (*Crotalus horridus* Linnaeus, 1758) to roads found that approximately 80% of snakes avoided the road surface (Andrews and Gibbons 2005). However, in our study rattlesnakes were observed crossing roads, cultivated fields, and other human-dominated areas with no evidence of avoidance behaviour, although this behaviour was not quantified in a way that allowed for analysis. Future study is needed to determine the role of avoidance behaviour in prairie rattlesnake migration. This may be particularly revealing in this system, where it is apparent that some rattlesnakes continue to make straight or near-straight migration movements despite encounters with human land uses (Fig. 2c), while other rattlesnakes engage in highly tortuous movements throughout the active season without encountering any apparent human modifications to the landscape (Fig. 2d).

Conclusions

Our findings suggest that risks associated with human land use can drive selection for migration behaviours that reduce the chance of encountering humans or human land uses. In

particular, snakes may make more tortuous migration movements in a human-dominated landscape because this behaviour reduces the risk of mortality from human persecution and encounters with high-risk human-associated landscape features like roads and cultivation. Our results further suggest that rattlesnakes make more tortuous migration movements in a human-dominated landscape, even though this is at the expense of their foraging success.

These results have implications for our understanding of human impacts on wildlife populations. In the short-term, tortuous migration movements may reduce rates of population decline in human-dominated landscapes because this behaviour should reduce rates of direct human-caused migration mortality. However, poorer foraging success resulting from this same behaviour may ultimately contribute to population declines if (a) poorer foraging success results in a decrease in overwinter survival, frequency of reproduction, and/or reproductive success, and (b) population persistence depends on these factors. This may be the case for some taxonomic groups, including snakes. Empirical studies suggest that rates of snake reproduction increase with prey availability and female body condition, supporting the idea that reproduction depends on foraging success (Aubret et al. 2002; Reading 2004; Taylor et al. 2005). Population viability analysis for the eastern Massasauga rattlesnake suggests that its viability is strongly dependent on the proportion of females reproducing and brood size (Miller 2005). Thus if a wildlife population's viability is dependent on these factors, changes in migration path shape in human-dominated landscapes may contribute to its decline.

Our results also highlight how important it is to account for within-species behavioural variability in the conservation decision-making process. In the case of the prairie rattlesnake, assuming the 'typical' migration behaviour, i.e. straight or near-straight migration paths, fails to represent the actual behaviour of the most at-risk populations, i.e. those in human-dominated landscapes. This assumption could lead to selection of suboptimal conservation actions for the

population. For example, conservation actions targeted at reducing road mortality 10 km from the hibernaculum may be ineffective if the population has already adopted behaviours that keep them close to the den. This shows how a failure to incorporate within-species behavioural variability into the conservation decision-making process could result in implementation of suboptimal conservation actions for the most at-risk populations of a target species.

Footnotes

¹ Supplementary material, Tables S1–S4 and Figs. S1–S3, is available with the article through the journal Web site.

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Figure captions

Fig. 1. The (a) range of prairie rattlesnakes (*Crotalus viridis viridis*) in North America (derived from IUCN (2016) spatial data), and (b) location of hibernaculum A in a semi-natural landscape, and hibernaculum B in a human-dominated landscape, near Medicine Hat, Alberta, Canada.

UTM coordinates of the study area are given in the figure margins (UTM Zone 12N).

Fig. 2. Example migration paths of tracked prairie rattlesnakes (*Crotalus viridis viridis*) in the semi-natural landscape (a, b) and human-dominated landscape (c, d). Inset graphs show the displacement of each individual relative to its den over time. UTM coordinates are given in the figure margins (UTM Zone 12N).

Fig. 3. (a) Relationships between the female prairie rattlesnake (*Crotalus viridis viridis*) body condition index (BCI; $n = 18$) and its path sinuosity index (net displacement distance/total path length for the outbound migration path), landscape (semi-natural or human-dominated), and year of radio-telemetry tracking (2004 or 2005). Positive coefficients indicate better body condition for individuals with straighter paths, in the human-dominated landscape, or in 2005. The inset figure shows the relationship between the BCI of each rattlesnake and path sinuosity in the semi-natural landscape (light triangles) and human-dominated landscape (dark circles). (b)

Relationships between migration mortality ($n = 25$) and its path sinuosity, landscape, and sampling year. Positive coefficients indicate higher probabilities of migration mortality for individuals with straighter paths, in the human-dominated landscape, or in 2005. The inset figure shows the relationship between the migration outcome (0 = survive, 1 = die) of each rattlesnake

and path sinuosity in the semi-natural landscape (light triangles) and human-dominated landscape (dark circles).

Fig. 4. Relationships between the female prairie rattlesnake (*Crotalus viridis viridis*) path sinuosity index (net displacement distance/total path length for the outbound migration path; $n = 25$) and the landscape (semi-natural or human-dominated) and year of radio-telemetry tracking (2004 or 2005). Positive coefficients indicate straighter migration paths for individuals in the human-dominated landscape or in 2005. The inset figure shows the path sinuosity of each rattlesnake in the semi-natural landscape (light triangles) and human-dominated landscape (dark circles).

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Fig. 1. The (a) range of prairie rattlesnakes (*Crotalus viridis viridis*) in North America (derived from IUCN (2016) spatial data), and (b) location of hibernaculum A in a semi-natural landscape, and hibernaculum B in a human-dominated landscape, near Medicine Hat, Alberta, Canada. UTM coordinates of the study area are given in the figure margins (UTM Zone 12N).

120x79mm (300 x 300 DPI)

Fig. 2. Example migration paths of tracked prairie rattlesnakes (*Crotalus viridis viridis*) in the semi-natural landscape (a, b) and human-dominated landscape (c, d). Inset graphs show the displacement of each individual relative to its den over time. UTM coordinates are given in the figure margins (UTM Zone 12N).

169x158mm (300 x 300 DPI)

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144x244mm (300 x 300 DPI)

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Table 1. Data collected during our field study of the movements of non-gravid female prairie rattlesnakes (*Crotalus viridis viridis*) near Medicine Hat, Alberta, Canada; each row represents data collected for one of the 25 radio-telemetry tracked snakes.

Landscape	Year	<i>n</i> *	Relocation interval, days†	Sinuosity	Body condition index	Migration outcome
A	2004	68	1.72 (0.64–7.02)	0.19	---	survived
A	2004	48	1.28 (0.72–3.93)	0.88	7.71	survived
A	2004	43	1.81 (0.72–8.18)	0.95	48.66	survived
A	2005	36	2.83 (0.94–11.00)	0.74	-52.44	survived
A	2005	31	2.77 (0.92–11.05)	0.75	1.71	survived
A	2005	19	3.38 (1.07–10.98)	0.78	-129.82	survived
A	2005	24	2.16 (0.70–11.52)	0.83	---	died
A	2005	40	2.95 (0.90–10.98)	0.88	-64.62	survived
A	2005	34	3.12 (1.11–10.99)	0.93	-36.09	survived
A	2005	21	2.39 (1.00–10.96)	0.96	---	died
B	2004	55	1.43 (0.70–3.93)	0.30	56.32	survived
B	2004	60	1.34 (0.73–5.08)	0.38	-107.34	survived
B	2004	54	1.34 (0.59–3.89)	0.47	---	survived
B	2004	40	1.31 (0.73–2.93)	0.48	---	survived
B	2004	47	1.39 (0.70–6.97)	0.74	-33.00	survived
B	2004	45	1.28 (0.60–3.64)	0.78	---	died
B	2004	63	1.34 (0.69–5.20)	0.78	90.87	died
B	2004	63	1.29 (0.50–3.89)	0.81	177.25	survived

B	2005	47	2.59 (0.65–7.12)	0.17	-42.70	survived
B	2005	39	2.56 (0.98–11.00)	0.33	31.36	survived
B	2005	18	8.19 (0.64–25.83)	0.40	-33.32	survived
B	2005	28	2.60 (0.70–7.91)	0.53	31.94	survived
B	2005	27	2.54 (0.85–7.89)	0.62	-26.82	survived
B	2005	24	2.09 (0.64–5.89)	0.70	---	died
B	2005	31	2.27 (0.83–7.78)	0.83	80.33	survived

* The number of radio-telemetry locations used to estimate path sinuosity, i.e. locations

representing animals' movements along the outbound migration path.

† Mean number of days between radio-telemetry locations used to estimate path sinuosity, with the range in brackets.