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Persistence of Northern Pacific Rattlesnakes masks the impact of human disturbance on weight and body condition

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Abstract

Species may remain present on developed landscapes over extended periods, suggesting viability, while in reality, populations may be indirectly affected in subtle and significant ways. We investigated indirect effects of human disturbance and habitat development on a population of the threatened Northern Pacific Rattlesnake *Crotalus oreganus oreganus* in British Columbia, Canada. We used mark-recapture ($n = 623$ males and non-gravid females, 2002–2011) and radio-telemetry ($n = 100$ males, $n = 4$ non-gravid females, 2004–2011) to examine weight, length, body condition, ecdysis and exposure risk in habitats of varying disturbance levels. Snakes in the most disturbed areas (<10 m to the nearest source of human activity or development) had lower weights and body condition, and they lost significantly more weight during the active season. Mean body condition of all snakes was stable or even increasing up to 2008 whereafter declines occurred in all categories, but particularly so for animals using disturbed habitat. Although there was some indication that ecdysis rates were affected by disturbance, we found no evidence that animals in disturbed habitat tended to be more exposed (i.e. distant from cover). Our findings indicate that there are consequences of occupying disturbed habitats, even though outward changes in behaviour or declines in density on the landscape are not detected.

Introduction

Habitat loss and alteration are among the greatest threats to wildlife (Wilcove *et al*., 1998; Gibbons *et al*., 2000; Hanski, 2005), with subsequent negative effects often being direct and tangible (e.g. Theobald, Miller & Hobbs, 1997; Tilman *et al*., 2001; Fahrig, 2007; Coristine & Kerr, 2011). These types of impacts may be relatively easily to determine, such as the complete loss of habitat and the immediate extirpation of a species from a location. However, indirect effects of habitat alteration may be equally serious yet less-easily detected. Animals may remain present in disturbed areas, but in smaller or declining numbers (Theobald *et al*., 1997) that will eventually lead to problems in recruitment and population stability (Burkey, 1995).

The indirect effects of habitat alteration on wildlife may be especially pervasive in areas near to or partially encompassed by urban development. Animals that continue to use urbanized landscapes likely are exposed to a suite of potential disturbances, including human presence (Burger, 2001, 2007), noise (Bowles, 1995), barriers to movement (Mader, 1984; Shine *et al*., 2004), increased predation (Pike *et al*., 2010), changes in prey density or composition (Jenkins & Peterson, 2005), increased disease (Theobald *et al*., 1997), and increased metabolic rates or stress levels (Gabrielsen & Smith, 1995). Despite this, animals may remain present through long-term site fidelity, mitigation (e.g. wildlife corridors, habitat patches) and/or immigration, implying population persistence and the absence of health impacts in the face of development.

Studies concerning the effects of disturbance on wildlife have mainly drawn attention to birds and mammals (Boyle & Samson, 1985; Burger, 2007), yet reptiles are experiencing worldwide population declines at rates that outpace most other vertebrates (Gibbons *et al*., 2000; Reading *et al*., 2010). Preventing these declines in the wake of increasing development is particularly challenging for feared species such as rattlesnakes. Despite stewardship programmes that seek increased tolerance of these animals, disturbance may still cause adverse effects. Many studies investigating disturbance on snakes do so in the context of snake–human encounters and examine snake behaviour only at the particular moment of contact (e.g. Burger, 2001). However, more lasting changes may have consequences for the individual or population. Behavioural changes due to human disturbance in a park setting have been noted in rattlesnakes (Parent & Weatherhead, 2000), as well as lower body condition, slower growth, reduced fecundity and less-viable offspring in disturbed landscapes (Jenkins *et al.*, 2009). Body size, condition and changes to growth will, in turn, affect overwinter survival and selection (Ashton, 2001), resulting in adverse changes in population demographics that could destabilize rattlesnake populations. All told, enabling rattlesnakes to persist in areas of development in the long-term, even along the periphery, represents a challenging management goal. Few long-term studies on snakes are available, especially in the context of human disturbance. We aim to contribute to the understanding of the effects of disturbance on the long-term viability of snake populations.

In British Columbia, Canada, the Northern Pacific Rattlesnake *Crotalus oreganus oreganus* occurs at its northern limits within semi-arid grassland valley bottoms. The distribution of this animal thus coincides closely with areas subject to increased human development (COSEWIC, 2004). Efforts to conserve these animals in the wake of disturbance to their natural habitat generally rely upon the continued presence of the animals as an indicator of success. However, we have a weak understanding of whether this accurately reflects 'successful' conservation of the species, and whether more indirect effects of development on the animals may be present.

We used radio-telemetry for 8 years along with a 10-year mark-recapture dataset to test for indirect effects on a population of Northern Pacific Rattlesnakes living within a gradient of disturbance. We examined body condition, weight change, ecdysis (shedding) rate and exposure risk of the snakes. Disturbance levels ranged from heavily developed sites through to unaltered habitat. We predicted that as the level of disturbance increased, body condition and weight changes would be adversely affected, along with ecdysis (being a reflection of snake growth; Jenkins *et al.*, 2009). Changes in the exposure of the animals from cover objects were expected to reflect an increased tendency to relocate and/or seek refuge when in suboptimal (developed) habitat. Such behavioural changes can interfere with biological processes such as thermoregulation and consume valuable energy stores, causing negative effects on snake condition and growth (Beaupre, 1995).

Materials and methods

Study area

Our study was conducted on the Osoyoos Indian Reserve (latitude 49°N, longitude 119°W) near the US–Canada border in the extreme southern Okanagan valley of British Columbia, Canada. Our primary study area (*c.* 350 ha) was in low elevation (elevation 500 m) habitat characterized by Antelope Brush *Purshia tridentata*, Big Sagebrush *Artemisia tridentata* and grasses. The site was bordered to the north and east by mountain slopes dominated by Ponderosa Pine stands *Pinus ponderosa*; above *c.* 600 m elevated dry Douglas-fir *Pseudotsuga menziesii* forests become more prominent (Lloyd *et al.*, 1990).

Landscape development and human activity were concentrated in the southern and western fringes of the study area. Development included a large-scale visitors' facility, interpretive walking trails, condominiums, golf course, winery, vineyards, campground, associated roads and parking lots, and a two-lane highway. These facilities result in tens of thousands of visitors annually (C. Stringam, pers. comm.; www.nkmipdesert.com). In contrast to this area, the northern and eastern portions of the study area had restricted human access and no land development. All rattlesnakes in the area used denning sites located on the rocky mountainsides. Ensuring that rattlesnakes and other local fauna persist on the landscape has been a long-standing objective of developers and operators in the area. Activities include educational programmes advocating tolerance and a minimalist intervention policy for 'problem snakes' (i.e. only short-distance relocations permitted).

Mark-recapture

Rattlesnakes were captured at dens as they emerged in the spring by active or incidental searches, or through reported sightings. We measured body weight using an electronic balance or Pesola scale, and determined sex by probing for hemipenal pouches. We measured snout–vent length (SVL) electronically from photos with SigmaScan Pro 5 (Systat Software Inc., 2011) or ImageJ version 1.45s (Rasband, 2011), and/or by hand with a measuring tape while the animal's head was held in a restraining tube. A Wilcoxon signed-rank test on 35 snakes measured through both methods revealed no significant differences in lengths [$P = 0.08$; $\bar{x}$ cm ± 1 SE: 70.5 ± 1.90 (electronic), 70.9 ± 1.86 (by hand)]. Snakes were implanted with a sterile passive integrated transponder tag (Biomark Model TX1411SSL; Biomark, Boise, ID, USA). The base rattle segment was dabbed with acrylic paint to monitor ecdysis (see below). Snakes were released at their point of capture 4–24 h after capture, although snakes captured near roads or campsites were released a maximum of 50 m away to minimize danger to the animal and people (Brown, Bishop & Brooks, 2009). Neonates and juveniles of less than 35 cm SVL were removed from the dataset due to an inability to permanently tag or rattle-code these smaller animals, and a lack of knowledge on basic natural history such as side fidelity and movement ecology.

Radio-telemetry

We transported snakes to a nearby veterinary clinic for the surgical intracoelomic implantation of radio transmitters (SB-2T 5.0 g or SI-2T 9.0 g; Holohil Systems Ltd., Carp, ON, Canada) following the procedures described by Reinert & Cundall (1982) and Reinert (1992). Pharmaceutical procedures followed Brown *et al.* (2009). Transmitters weighed, on average, 2.10% of total body weight (range: 0.97–3.81%).

We surgically removed transmitters at the end of the battery life (*c.* 12 months for SB-2T and 24 months for SI-2T). We only used adult male rattlesnakes because of the inherent difficulty in assessing body weight fluctuations and behavioural changes in adult females due to their triennial reproductive schedules (Macartney & Gregory, 1988). In addition, the impact of implantation and removal in females may have had questionable effects on reproductive success.

We located each snake at least every 2–3 days during the active season (approximately April–October). Care was taken to pinpoint the animals from at least 2 m away without triggering any noticeable response. If snakes were disturbed, the data were excluded from behavioural (exposure) analyses.

Quantifying disturbance

We identified categories of snakes based on the different degrees of disturbed habitat where the animals were captured. Because our long-term mark-recapture dataset provided larger samples, we were able to follow a procedure similar to Parent & Weatherhead (2000) and assign animals to disturbance ratings (DR) for each of 17 sections within the study area. These sections were identified *a priori* using naturally occurring or anthropogenic boundaries that also took into account general foraging and movement areas of telemetered snakes. The sections were assigned a DR ranging from 0 to 4 on the basis of the distance (m) to the nearest source of human activity or development. The five DR categories were designated as follows: DR0 > 200 m, 200 m > DR1 > 100 m, 100 m > DR2 > 50 m, 50 m > DR3 > 10 m, DR4 < 10 m. The DR0 category thus represented completely undeveloped areas, and DR4 represented the most drastically transformed landscapes and heavily frequented regions (e.g. campground, residential sites). Each snake in the dataset was assigned a DR category based on the section where at least 50% of their recaptures were located, and only if they had been captured at least twice within that DR. This process was repeated within each year of the study (i.e. the DR for a section could change between years according to new development). Over the lifetime of our study, the propensity for snakes to encounter disturbance increased in tandem with property development and visitor numbers. However, the core developed areas and sources of disturbance were present for the entire duration of the study. Additionally, the re-assignment of DR categories took yearly variations into account, since distances to disturbance sources were reassessed annually.

The original objective of our telemetry work was to focus on snakes living in extreme habitats (i.e. either heavily disturbed habitat or natural areas), and this bias created insufficient samples for applying the DR system to our sample of radio-tracked snakes. We instead used a coarser system, assigning telemetered animals to 'disturbed-site' or 'undisturbed-site' categories (greater than 50% of telemetry observations located ≤100 m or ≥200 m from disturbance, respectively). We also designated a third category of snakes termed 'mountain', being those animals that moved into the higher-elevation forests above the grassland valley bottom. Although the snakes in this third category could have been classified as 'undisturbed site', we separated them as they foraged in a unique biogeoclimatic zone and were noted *a posteriori* to be noticeably larger than snakes living at lower elevations.

Variation in weight, length and body condition

We compared the relationship between rattlesnake weight and SVL among disturbance categories and years with analysis of covariance. We $\log_{10}$-transformed weight and SVL values to meet assumptions of normality. We removed snakes with discernible food items in their stomachs from analyses, and if a snake was captured more than once in the same year, we used only one set of measurements (drawn at random) in the analysis to avoid pseudoreplication (Coates *et al*., 2009). For the body condition analysis, we followed Parent & Weatherhead (2000), Shine *et al*. (2001) and Brown *et al*. (2009) by using residuals from a regression between weight and SVL as an index of body condition. Differences and interactions in the body condition scores between disturbance categories and years were tested using analysis of variance (ANOVA).

Percent weight change for individual snakes in the three disturbance categories (disturbed site, undisturbed site and mountain) over the active season was calculated using weight data collected at dens during spring egress (April/May) and the subsequent autumn ingress (September/October). Overwinter weight changes were calculated in an analogous fashion (from autumn ingress to the following spring egress). To investigate for effects of carrying a transmitter, we also compared the results for telemetered snakes to those snakes monitored solely through mark-recapture. We $\log_{10}$-transformed percent changes in weight to achieve normality and used ANOVA to compare across categories, with area, year and an interaction term as factors.

Ecdysis

We recorded the frequency of ecdysis (shedding rate) of telemetered snakes by determining the number of such events per year (identified by the appearance of new, unpainted rattle segments). Snakes with broken distal rattle segments were excluded from the analysis. We then compared the shedding frequencies of snakes between the three habitat categories (undisturbed site, disturbed site and mountain).

Exposure

At each telemetry location within all DRs, we scored the percent of body exposed (i.e. not under cover) on a scale of 0–5 based on visual observation (0 = 0% exposed (not visible); 1 = 1–24%; 2 = 25–49%; 3 = 50–74%; 4 = 75–99%; 5 = 100%). To account for the potential effects of temperature on snake exposure, we classified each snake telemetry point as cool (<22.9°C), warm (≥22.9 and ≤31.4°C) or hot (>31.4°C) following the 25 and 75% quartile divisions of all substrate temperatures measured at the tracked locations (range: 6.2–47.0°C) (Parent & Weatherhead, 2000).

We used snakes as the sample unit (instead of radio-locations) to avoid problems of non-independence (Aebischer, Robertson & Kenward, 1993). The mean exposure score of individual snakes was calculated from a minimum of three observations collected within each substrate temperature and area combination (e.g. hot, disturbed; see Parent & Weatherhead, 2000). We then used these averages as the response variable in a two-factor ANOVA with substrate temperature class (cool, warm or hot) and area (undisturbed site and disturbed site) as treatments.

Statistical considerations

All analyses were performed using R version 2.12.1 (R Development Core Team, 2011). Statistical interpretation was guided by $\alpha = 0.05$. Tukey's honestly significant difference test was used for post-hoc multiple comparisons (Crawley, 2007).

Results

Snake captures and radio-telemetry

We processed 1850 rattlesnakes from 2002 to 2011 through mark-recapture. After accounting for age, gravidity and multiple recaptures, we used 623 adult males and non-gravid females in the body condition analyses ($n = 66$ in DR0; $n = 105$ in DR1; $n = 116$ in DR2; $n = 140$ in DR3; and $n = 196$ in DR4). From 2004 to 2011, we radio-tracked 104 rattlesnakes ($n = 100$ males, $n = 4$ non-gravid females). Of these, we tracked 25 for 2 years, resulting in 129 full or partial seasons. Due to mortality and transmitter failures, we did not track all snakes for a full season.

Variation in weight, length and body condition

Snakes in the DR0 category generally were heavier and longer than in other DRs (Fig. 1a,b). Overall, ANOVA showed a significant effect on weight by DR category, year and the interaction (DR: $F_{4,581} = 8.77$, $P < 0.0001$; year: $F_{9,581} = 7.67$, $P < 0.0001$; DR × year: $F_{27,581} = 1.62$, $P = 0.02$). For SVL, similar results were found (DR: $F_{4,581} = 10.03$, $P < 0.0001$; year: $F_{9,581} = 3.15$, $P = 0.001$; DR × year: $F_{27,581} = 1.76$, $P = 0.01$). The interaction between DR and year reflects that the numbers of snakes in all DRs were not represented evenly throughout the study years.

Overall, there was a very strong relationship between rattlesnake weight and SVL ($r^2 = 0.78$, $F_{1,621} = 2210$, $P < 0.0001$; Fig. 2). Snakes in the most disturbed areas weighed

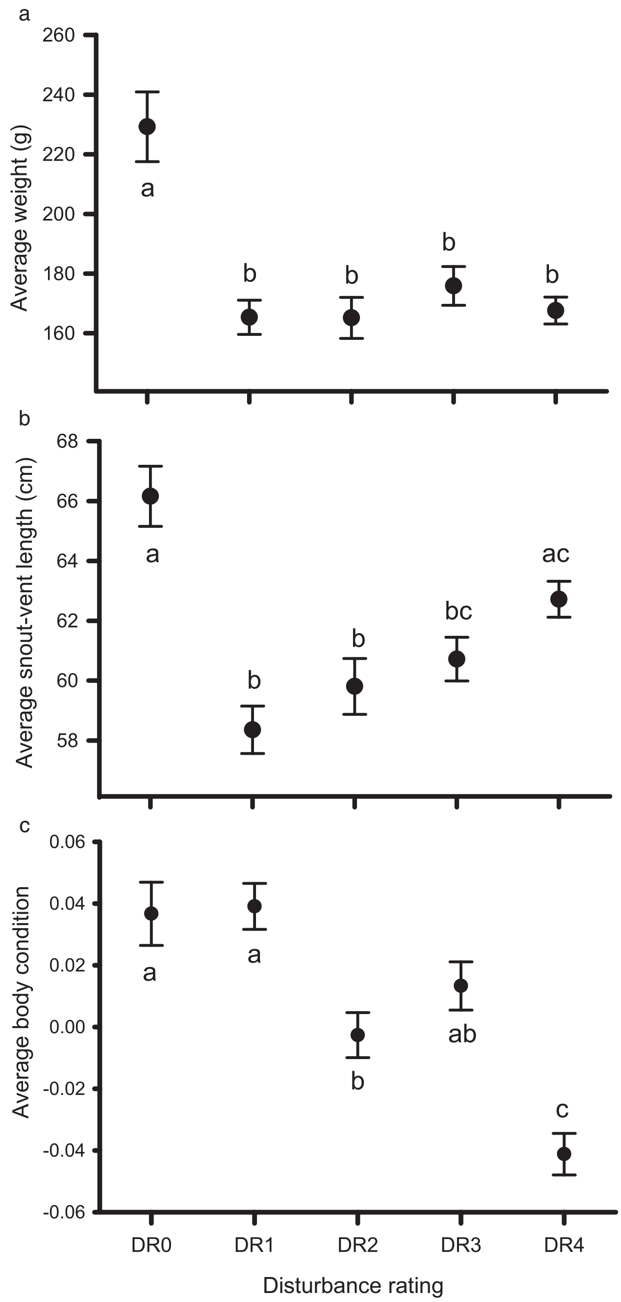

Figure 1 Comparison across disturbance rating categories of the average weight (a), snout–vent length (b) and body condition score (c) of male and non-gravid female Northern Pacific Rattlesnakes *Crotalus oreganus oreganus* captured at Osoyoos, British Columbia from 2002 to 2011. The disturbance rating (DR) is based on distance (m) to the nearest source of disturbance, that is, DR0 > 200 m, 200 m > DR1 > 100 m, 100 m > DR2 > 50 m, 50 m > DR3 > 10 m, DR4 < 10 m. Body condition scores were derived from the residuals of a regression of weight on snout–vent length (see Fig. 2). Sample sizes for the DR categories are 66, 105, 116, 140 and 196, respectively. Means with different letters indicate a significant difference at $\alpha = 0.05$.

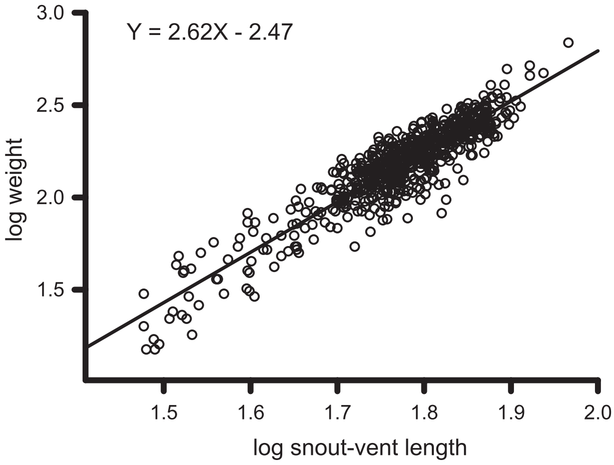

Figure 2 Linear relationship (r^2 = 0.78) between log(weight) (g) and log(snout–vent length) (cm) for male and non-gravid female Northern Pacific Rattlesnakes *Crotalus oreganus oreganus* captured in Osoyoos, British Columbia, between 2002 and 2011. Residuals from this relationship were used to compare body condition between snakes in different disturbance categories.

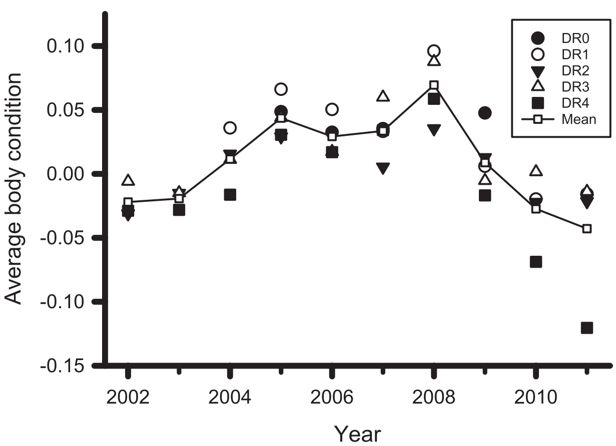

Figure 3 Trends in body condition scores for male and non-gravid female Northern Pacific Rattlesnakes *Crotalus oreganus oreganus* captured within different disturbance rating (DR) categories in Osoyoos, British Columbia between 2002 and 2011. See Fig. 1 caption for the descriptions of DR categories and sample sizes.

relatively less for their lengths (Fig. 1c; DR: $F_{4,581} = 22.7$, $P < 0.0001$; year: $F_{9,581} = 10.9$, $P < 0.0001$; DR × year: $F_{27,581} = 1.14$, $P = 0.29$). The average body condition of all snakes was stable or even increasing up to 2008 when declines were seen in all categories of snakes, but particularly so for animals in DR4 (Fig. 3).

Within the telemetry sample, snakes in the disturbed-site category lost weight over the active season versus gains by animals in the two other groups ($F_{3,70} = 6.15$, $P < 0.001$; Fig. 4). No year effect was noted ($F_{5,70} = 2.10$, $P = 0.08$). The post-hoc tests verified that disturbed-site snakes were significantly different from undisturbed-site snakes ($P = 0.02$) and mountain snakes ($P = 0.001$), and the weight loss of

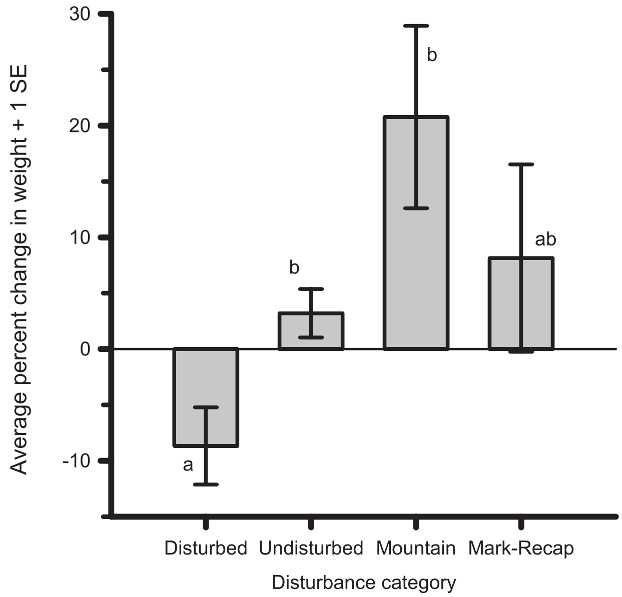

Figure 4 Comparison of percent change in body weight in telemetered Northern Pacific Rattlesnakes *Crotalus oreganus oreganus* in different disturbance categories, over the active period between the emergence and return to hibernation in Osoyoos, British Columbia (2004–2011). Snakes in this analysis were classified as disturbed (*n* = 17) if 50% or more of the telemetry observations occurred ≤100 m from disturbance, and undisturbed (*n* = 43) when the same proportion of observations were ≥200 m from disturbance. Mountain snakes (*n* = 6) were those snakes that left the lower valley habitat and used upland, forested habitat. Also shown for reference are animals monitored solely through mark-recapture (*n* = 13). Significant differences between the categories are indicated by different lowercase letters.

snakes tracked by mark-recapture was not different from that recorded for the telemetered snakes ($P = 0.28$; Fig. 4). Overwinter weight loss was not significantly different between any of the categories of snakes ($F_{12,24} = 1.03$, $P = 0.45$).

Ecdysis

We had 73 cases where shedding rates of telemetered snakes were reliably documented over an active season. In all cases, animals shed at least once, with only 15 instances of ecdysis occurring twice in the same year. All of these cases were in the undisturbed-site (13/47) or mountain (2/8) categories, compared with 0/18 for snakes in the disturbed-site category ($G_2 = 9.7$, $P = 0.08$).

Exposure

We used data from 82 rattlesnakes in the exposure analyses, with an average of over 46 observations per snake. The mean exposure of rattlesnakes varied significantly with substrate temperature ($F_{2,269} = 28.58$, $P < 0.0001$), but not between disturbance categories ($F_{1,269} = 0.37$, $P = 0.54$).

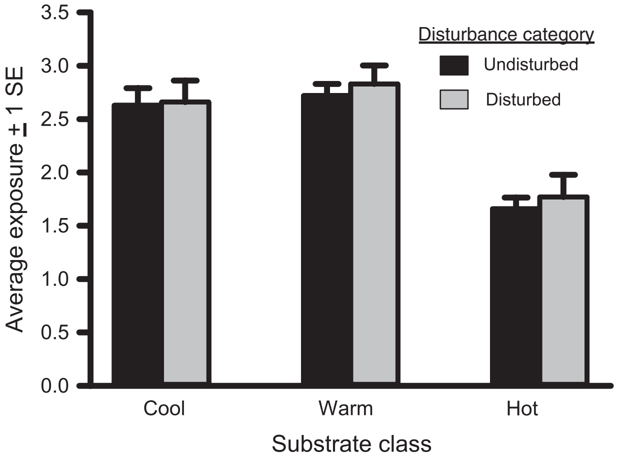

Figure 5 Exposure of telemetered Northern Pacific Rattlesnakes *Crotalus oreganus oreganus* (males and non-gravid females) according to substrate temperature and habitat disturbance categories in Osoyoos, British Columbia, between 2004 and 2011. Substrate temperature categories were cool (<22°C), warm (≥22.9 and ≤31.4°C) and hot (>31.4°C). Exposure values are averages derived from the score assigned to an animal each time it was observed.

Pairwise comparisons showed that animals were more concealed when on hot substrates ($P < 0.0001$ in all cases; Fig. 5).

Discussion

We found that indirect disturbance (as measured herein) had a consistent negative effect on body characteristics (body condition, weight gain) of the animals. There was a suggestion that the frequency of ecdysis was influenced by habitat, but contrary to our prediction, snakes in disturbed habitat did not appear more exposed from cover. Overall, our data indicate that there are consequences of occupying disturbed habitat, even though outward changes in the behaviour or the continued presence of animals on the landscape may not be detectable.

Few studies have examined the effects of human disturbance on rattlesnakes, and differences in how ‘disturbance’ is measured complicate interpretation. For example, Parent & Weatherhead (2000) found no difference in body condition between Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) occupying disturbed and undisturbed locations. Their study occurred within a provincial park where ‘disturbance’ (campgrounds, hiking trails) was not akin to that in urban or rural landscapes, or in our study area. The authors also indicated the degree that their study animals associated with either category of habitat was not well known, whereas in our study, we used repeated observations to assign habitat type (further, rattlesnakes in BC are known to exhibit high fidelity to summer foraging locations, see Brown, 2006; Lomas, 2013; Gomez *et al*., 2014). In habitat conditions more similar to our study area, rattlesnakes (*C. oreganus*) in Idaho disturbed by livestock and wildfire had lower body condition (Jenkins *et al*., 2009). These animals were shorter, grew slower, had lower fecundity and the offspring were shorter and had lower body condition than those in other populations. In that study, snakes from disturbed sites also underwent ecdysis less often, something our data suggest less conclusively [rattlesnakes in extreme northern areas shed less often (Macartney, 1985), making it relatively difficult to detect changes in ecdysis rates]. To improve our ability to categorize levels of human disturbance across studies (and predict impacts), it may be prudent to adopt quantitative parameters such as those used to measure natural disturbances (e.g. severity, intensity; see Kulakowski & Veblen, 2007). This approach would improve our ability to detect patterns of responses through a future meta-review of studies on this and related taxa.

The changes in snake weight and body condition that we detected in disturbed habitats were striking, as were the large differences in snake size between the most highly disturbed and least disturbed areas. We hypothesize that multiple factors may be at play: larger size may result from greater cumulative growth (perhaps due to higher prey availability – see below), as well as a longer lifespan owing to a lack of mortality from anthopogenic effects (e.g. roadkill often was observed in disturbed areas). Although the overwinter weight losses we recorded (2.5–10%) are consistent with those reported for these species elsewhere in this region (2.3–20.0%; Macartney, 1985), to our knowledge, weight loss over the active season has not been clearly shown for northern snakes, with the possible exception of weight loss during gestation or through desiccation immediately before or after hibernation (e.g. rattlesnakes; Macartney, 1985). However, our work did not reveal any blatant shifts in exposure risk that could be related to suboptimal weight gain. Possible benefits from lessening exposure or altering other behaviour(s) in response to disturbance are not worth the costs of reduced activity (Lima & Dill, 1990). Other mechanisms may be at work, such as changes in prey availability (Jenkins & Peterson, 2005), or more specifically, declines of small mammal populations in disturbed areas (McGee, 1982; Parmenter & MacMahon, 1983; Sullivan & Sullivan, 2006). The hypothesis that prey availability impacts snakes using disturbed habitat is supported by the fact our ‘mountain’ snakes using more vegetated forested habitat had higher body condition and weight gains. Monitoring prey abundance across different habitat types along with experimental, *in situ* manipulations of food intake will be necessary to determine the relationship between feeding rates and levels of disturbance (e.g. Taylor *et al*., 2005).

Indirect effects such as those demonstrated herein (reduced weight gains, poor body condition) become highly significant if they ultimately impact survival, recruitment and population stability. Our current estimate of mean annual survival in the study population (all DRs combined) is ≈70% (Kirk *et al*., 2013) but as with most animal populations, precise recruitment and population trends are lacking, much less survivorship estimates within disturbance categories. Delayed sexual maturity, long inter-birth intervals and low juvenile growth rates have been noted in BC rattlesnakes (Macartney, 1985; Didiuk, Macartney & Gregory, 2004), so poor body condition, weight gain and low densities likely would affect population age and genetic structure, and exacerbate declines (Bertram, Larsen & Surgenor, 2001; Didiuk *et al*., 2004). It is important to note that a decline in fitness (an individual trait) does not automatically signal a decline in population size, and long-term population growth data still remain crucial to conservation assessments. It is also important to recognize that this study collected data on one segment of the population that was relatively mobile, while other groups within the same population (e.g. reproducing females) may be even more prone to the effects of disturbance (Macartney & Gregory, 1988).

Extirpation is not necessarily abrupt, especially for long-lived animals (like rattlesnakes; Klauber, 1972) where declines in abundance may take many years to detect, even if monitoring protocols are in place. Further, density of wildlife (much less detection) has been long recognized as an imperfect indicator of habitat suitability (Van Horne, 1983), but this canon often is relaxed in the assessment of landscape development or management actions, and detections become heavily relied upon as an indicator of sustainable practices. Our study provides strong evidence that the continued presence of a species on a landscape does not reflect completely successful management efforts. Even if animals recognize differences in habitat quality (Clark & Shutler, 1999), declines in populations following habitat degradation may be tempered by individuals demonstrating lifetime fidelity to particular areas, possibly even influencing habitat selection by their offspring through habitat imprinting and familiarity (Davis, 2008; Dixson *et al*., 2014). Clearly, indirect effects of development on wildlife need to be further examined, such that management practices may be tailored more effectively (e.g. Sato *et al*., 2014), while more accurate and detailed data are collected as part of ongoing impact assessments.

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