Oecologia (2000) 125:170–178
DOI 10.1007/s004420000442

C. Parent · P.J. Weatherhead

Behavioral and life history responses of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to human disturbance

Received: 13 July 1999 / Accepted: 21 March 2000 / Published online: 27 June 2000
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Abstract Parks and nature reserves protect important natural habitats but also provide public opportunities for outdoor recreational activities that may have unintended negative effects on wildlife. We examined the response of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) to inadvertent disturbance by humans in Killbear Provincial Park, Ontario, Canada. Radio telemetry of 25 adult snakes over two active seasons revealed that, as disturbance increased, gravid females were less visible to observers, but the visibility of non-gravid females and males did not change. Mean distance moved per day decreased and mean time between moves greater than 10 m increased in gravid females, non-gravid females and males with increasing exposure to human disturbance. However, mark-recapture data revealed no differences in the condition or growth rates of snakes, or in the litter size of gravid females, between individuals captured in disturbed and undisturbed study areas. While it is possible that the behavioral responses we observed are not sufficient to have life history consequences, more detailed information on the exposure of individual snakes to human activity is necessary before the conclusion that disturbance is not detrimental to snakes can be accepted. Similarly, other potential negative effects of human disturbance not investigated here remain to be explored.

Key words Rattlesnakes · Human disturbance · Life history · Predator avoidance · Conservation ecology

C. Parent · P.J. Weatherhead
Department of Biology, Carleton University,
1125 Colonel By Drive, Ottawa, ON, K1S 5B6, Canada

Present address:
P. Weatherhead, Department of Natural Resources
and Environmental Sciences,
University of Illinois at Urbana-Champaign, Turner Hall,
1102 South Goodwin Ave., Urbana, IL 61801, USA

Introduction

Outdoor recreation and ecotourism are often considered benign because they involve the non-consumptive use of wilderness areas. However, the growing popularity of these activities has prompted increasing concern that human intrusion into natural habitats may have unintended negative effects on wildlife (Hammitt and Cole 1987; Boo 1990). Many animals respond to people as potential predators, and human avoidance may result in home range displacement (e.g., McLellan and Shackleton 1988), disruption of foraging (e.g., Gander and Ingold 1997) and reduced reproductive success (e.g., Safina and Burger 1983; Giese 1996). To date, most studies on the effects of human disturbance have focused on mammals and birds (Boyle and Samson 1985). However, reptiles might be especially vulnerable to human disturbance because their limited mobility restricts movement to less disturbed areas. In addition, ectothermy is a physiological constraint to behavioral avoidance of disturbance because reptiles are often tied to specific activity periods, habitats or retreat sites (Heatwole 1977; Pough 1983). In this paper we examine the effects of human disturbance on a population of eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) in a heavily used park in Ontario, Canada.

The eastern massasauga rattlesnake has suffered pronounced range contraction and fragmentation due to human destruction of both individuals and habitat, and the species is now considered endangered by most jurisdictions in which it is still found (Szymanski 1998). Of the four disjunct populations of eastern massasauga rattlesnakes remaining in Ontario, the largest two occur along the Bruce Peninsula and eastern shore of Georgian Bay, where their long-term viability is threatened by development. Protected habitat in these areas can be found in several national and provincial parks, but the impact of increasing visitor use of these parks on snake populations is unknown. Thus, whether human disturbance affects eastern massasauga rattlesnakes is a question of increasing significance to the conservation of this species in Ontario.

To assess the effects of human disturbance on eastern massasauga rattlesnakes, we used radio telemetry to determine the behavioral responses of snakes to disturbance, and mark-recapture data to compare body condition, growth rates, and female fecundity of snakes from disturbed and undisturbed areas. If eastern massasauga rattlesnakes are sensitive to human disturbance, we predicted that snakes would be less visible in disturbed than in undisturbed areas, because many animals increase their use of cover when predation risk is high (e.g., Werner et al. 1983; Yarmoloy et al. 1988). Snakes in disturbed areas should also be found closer to retreat sites, because many reptiles flee to protective refugia when threatened (Greene 1988). We also predicted that human disturbance would affect snake movement patterns. If snakes attempt to avoid human contact, then those in disturbed areas should move further, or more often, than undisturbed snakes. Alternatively, because movement is generally incompatible with cryptic behavior (Lima and Dill 1990), snakes in disturbed areas might move less than those in undisturbed areas. In either case, we predicted that snake movement patterns would differ between disturbed and undisturbed locations.

If, as predicted, eastern massasauga rattlesnakes respond behaviorally to human disturbance, we expected disturbed snakes to suffer fitness costs. For example, by causing snakes to move less and use refugia more, human disturbance could reduce foraging and interfere with behavioral thermoregulation, with the latter adversely affecting physiological processes such as digestion and growth (Lillywhite 1987). Thus, we predicted that snakes in disturbed areas would be in poorer condition and grow more slowly than individuals in undisturbed areas. In addition, because stress is thought to cause reductions in viable clutch size (Farr and Gregory 1991), we predicted that female eastern massasauga rattlesnakes in disturbed areas would produce fewer live young than undisturbed snakes.

Materials and methods

Study site

We conducted this study in Killbear Provincial Park (80°12′ W and 45°21 N), located on a peninsula on the eastern shore of Georgian Bay, Ontario. This 1,756 ha park attracts more than 200,000 visitors annually, but development is limited to eight campgrounds and three hiking trails. Human activity is concentrated in these areas and along the shoreline because most visitors engage in aquatic-based recreation. Other areas receive little use and are relatively undisturbed. We selected two study sites within the park that reflected this pattern of visitor use. Our goal in selecting these study sites was to ensure that we obtained data from snakes that were exposed to substantial human activity and others that were not. However, as we explain below, for most analyses we quantified human disturbance of the habitat used by individual snakes, so individual snakes and not study sites were our units of replication. Both study sites were approximately 150 ha in area and were 1 km apart, and both appeared to us to include similar habitats and topography, although we did not explicitly confirm this assumption. The disturbed site includes a number of campsites, a heavily-used hiking trail, several roads, and a parking lot, and is bordered by seasonal residences just outside the park's boundary. There is regular contact between people and snakes in this area. For example, nine eastern massasauga rattlesnakes were captured on campsites from 1990–1993 (C. Parent, unpublished data). In contrast, the undisturbed site has no development and is rarely visited by humans.

To confirm that visitor use differed between these two sites, we quantified human activity. At the disturbed site we counted visitors at the entrance to the hiking trail over randomly selected 1-h sampling periods from 0900 to 2100 hours between 26 May and 22 August 1995. We recorded the number of vehicles that passed and the number of people entering the trail. The disturbed site was so rarely used by park visitors that we considered formal sampling inefficient. Instead, we simply recorded any use of this area in the course of fieldwork, which provided a sampling intensity similar to that of the disturbed site.

Radio telemetry

Thirty adult eastern massasauga rattlesnakes captured opportunistically in the two study sites were surgically implanted with radio transmitters (Holohil Systems, model S1–2T) and tracked from May to October in 1995 and 1996. Transmitters weighed 7.8 g or 9.4 g and were functional for 12 or 24 months, respectively. To minimize the effects of transmitter implantation, snakes were chosen so that transmitter mass was less than 5% of their body mass. Snakes were also selected so that nearly-equal numbers of gravid females, non-gravid females, and males received transmitters. Transmitter implantation generally followed the procedures of Reinert and Cundall (1982), but snakes were anesthetized by halothane inhalation and sterile conditions were maintained. Snakes were given 24 h to recover from anesthesia and then released within 15 m of their capture location. Data collection did not begin until 3 days after release because implantation may affect snake behavior (Weatherhead and Anderka1984; Lutterschmidt and Rayburn 1993). We located snakes every second day (May-August) or twice weekly (September-October) using a Wildlife Materials (Model TRX-1000S) receiver with a hand-held 3-element yagi antenna.

It was critical to our study that our own activity locating snakes and quantifying habitat did not disturb the snakes and thereby confound our goals. Radio telemetry allowed us to locate snakes with minimal disturbance. We always approached snakes cautiously, and only close enough to determine their location. We flagged each location and then returned to quantify the habitat and get a GPS position of the exact location after the snake had moved. Most importantly, all snakes were treated the same way, so any effect of the ambient levels of human disturbance in their habitat was not attributable to our methods.

To determine whether human disturbance affected use of cover or proximity to refugia by snakes, we scored visibility (0= not visible, 1= partly covered and 2= in open) and distance to nearest retreat site each time we located a transmitter-equipped snake. We defined anything that reduced snake visibility as cover (e.g., tall grass), but classified only those locations in which a snake could avoid capture (e.g., a crevice under a large rock), as retreat sites. To control for potential effects of temperature on snake behavior, we measured substrate temperature (T_s) near the snake using a Cole Parmer (Model 8110–20) thermistor thermometer. We chose substrate as similar as possible to that occupied by the snake (e.g., in the shade under a shrub). We used the 25% and 75% quartile divisions of the distribution of all substrate temperatures measured to classify each snake location as cool (<21°C), warm (≥21°C and ≤27°C) or hot (>27°C).

To assess the effects of disturbance on rattlesnake movement, we recorded distances and bearings between consecutive locations of each transmitter-equipped snake. Distances <100 m were measured in the field using a tape measure. Positions separated by >100 m were determined using a Trimble GeoExplorer GPS (Trimble Navigation 1994a) and differentially corrected to within ±2 m using Geo-PC 1.00 software (Trimble Navigation 1994b). Corrected points were plotted using MapInfo 4.0 (MapInfo 1995) on a 1:10,000 digital Ontario Base Map overlaid on a aerial photograph of the park. Distances between points were measured using the program's ruler tool and bearings determined by protractor using a printed map of plotted points. To ensure accuracy of points, those that could not be reconciled with known landmarks or other points (n=13) were eliminated. Distance and bearing data were taken between points previous to and subsequent to any discarded locations.

To control for the potentially confounding effects of seasonal patterns of movement, we restricted analysis of radio telemetry data to the period following migration away from hibernation sites and before migration back to hibernation sites. We defined the end of this period for gravid females as coinciding with parturition. For most snakes, migration consisted of several consecutive, straight-line (<90° variance), long distance (often >100 m) movements, although the migratory paths of some snakes were less direct. For these individuals, we considered the emergence migration complete when the snake had traveled >30 m from its hibernation site, and the return migration to have begun when the snake was within 30 m of its eventual destination. We only used data from the 25 snakes that we tracked for a minimum of 1 month and for which we had at least 12 observations. For snakes tracked over two summers, we pooled data between years. We controlled for sex and reproductive condition in all analyses of radio telemetry data due to their potential influence on snake behavior (e.g., Gibbons and Semlwitch 1987).

Mark-recapture

To assess the effects of human disturbance on the condition and growth rates of eastern massasauga rattlesnakes, we captured, measured, and individually marked snakes in both study sites from 1992 to 1996. We located snakes by searching suitable habitat or by capturing snakes reported by park staff and visitors. Initially (1992–1994) we marked snakes by branding unique combinations of ventral scales using a soldering iron. Beginning in 1995, larger snakes were injected subcutaneously with sterilized PIT tags (Model Tx1400L1, Anitech Identification Systems). Newborn snakes appeared too fragile for either method, so we photographed their dorsal pigmentation patterns (Sheldon and Bradley 1989). These markings are unique to individuals and do not change over time (C. Parent, unpublished data). Snakes were generally released at their capture location, but those found near roads or campsites were released approximately 15 m away to limit conflict with park users.

We measured snout-vent length (SVL) to the nearest cm using a flexible measuring tape while the snake was held firmly behind the head (Fitch 1987) and its body rested on a flat surface. To reduce measurement error, SVL was recorded as the mean of two separate measurements and was always determined by the same investigator (Yezerinac et al. 1992). Mass was determined to the nearest gram using Pesola scales or an Ohaus balance, and snakes were sexed by probing. We used the residuals from a regression of body mass on SVL as an index of condition (Weatherhead and Brown 1996). Because snakes that are gravid weigh more than those that are not (e.g., Graves and Duvall 1993), we estimated condition for gravid females separately from non-gravid females and males. Two points should be noted regarding our analysis of condition. First, by estimating condition rather than including both mass and length as variables in an analysis assessing the effect of disturbance on condition, we were more likely to find a significant relationship because of the reduced degrees of freedom. Second, in estimating condition we used least-squares linear regression (LLR) rather than reduced major axis regression (RMA), despite there being error in both X and Y variables. LLR is more appropriate when the goal is to control for for the effect of one variable on another (as we did here), because with RMA, residuals will be correlated with the independent variable (Harvey and Pagel 1991). The same reasoning applies to our use of residuals in other analyses (below).

To calculate individual growth rates, we divided the difference in SVL between initial capture and recapture by the number of days between captures, excluding time in hibernation. Growth is negligible during hibernation (e.g., Waye and Gregory 1998), so this period is generally omitted from the calculation of capture intervals (e.g., Forsman 1993). Based on our observations of snakes implanted with radio transmitters, we set the no-growth period for eastern massasauga rattlesnakes in Killbear Provincial Park from 1 November to 30 April. In order to maintain statistical independence, growth rates of snakes recaptured more than once were determined using data from the first and last capture. Since growth rates typically decline with increasing SVL (Andrews 1982), we controlled for size by using the residuals (relative growth rate) from a regression of growth rate on SVL at initial capture. To control for annual effects resulting from climatic variation or fluctuating prey availability (e.g., Platt 1984; Forsman 1993), we identified the year that constituted the greatest proportion of each snake's capture interval. This period was assumed to have had the greatest effect on observed growth rate and was termed the main growth year. Snakes with more than 1 complete year between recaptures were excluded from the analysis because annual effects could not be controlled. Finally, because growth rates may decrease in gravid females (e.g., Macartney et al. 1990), we analyzed growth data from potentially reproductive females separately from that of males and known non-reproductive females. Female reproductive status (gravid vs non-gravid) was determined with each capture (see below), so we knew the reproductive history of female snakes captured annually. However, the interval between captures for some females extended 2 or more years, so their reproductive status in the intervening period was unknown. Therefore, based on the smallest gravid female captured during the course of this study, any females with SVL ≥50 cm was considered sexually mature.

To assess the effects of human disturbance on reproduction of eastern massasauga rattlesnakes, captured females were examined by ultrasonography to determine their reproductive condition (gravid or non-gravid) and to estimate their brood size if gravid. Initially we used a Hewlett-Packard 500 with a 5 MHz medium focus sector array transducer with liquid standoff. Later examinations were conducted with a General Electric Logic 500 with a 7 MHz variable focus linear array transducer. A Registered Diagnostic Medical Stenographer (RDMS) technician with more than 10 years experience conducted all ultrasonography examinations and interpreted the resulting images. To confirm the validity of litter-size estimates, as part of another study we recaptured 15 females for which we had ultrasound estimates of litter size and maintained them in captivity until parturition. Of the 15 litters, we had estimated 11 exactly, and the remaining four within 15% (C. Parent, unpublished data).

Quantifying exposure to human disturbance

We collected life history data from snakes not implanted with radio transmitters, so we could not quantify their exposure to human disturbance directly. Therefore, we simply classified each snake as being disturbed or undisturbed, based on the study site where it was captured. In the case of snakes used to analyze growth, both their capture and recapture locations were in the same study site. For snakes tracked by radio telemetry, finer resolution of their exposure to disturbance was possible. Transmitter-equipped snakes did not move between study sites, but because disturbance levels within each site were not uniform, we assigned each radio-telemetry location a disturbance rating (dr) based on the distance (d) to the nearest potential source (road, trail or campsite) of disturbance (d >50 m, dr=1; 50 m ≥ d ≥ 10 m, dr=2; d <10 m, dr=3). A non-zero value was purposely given to the lowest disturbance rating (dr=1) so as not to imply that any area of the park is entirely free of human use. Disturbance ratings are not an index of absolute levels of human use because park visitation varies seasonally. However, disturbance ratings accurately reflect relative levels of disturbance at any given time because visitors rarely stray from developed areas.

General statistical methods

Statistical analyses were performed on a Power Macintosh 6100/60 personal computer using JMP 3.1 (SAS 1994) software. We confirmed that F-test assumptions were met, and if violated, we modified the response variable using a suitable transformation (Zar 1984) and repeated the analysis. Where appropriate, we also tested for interaction effects, although we report only positive results. Unless otherwise indicated, we report mean values ±1 standard error and use an a-value of 0.05 to denote statistical significance.

Results

Human use of study sites

Over 54 sampling periods in May (n=3), June (n=17), July (n=21) and August (n=13) of 1995, we observed an average of 9.0±1.4 vehicles and 33.4±4.6 visitors each hour in the disturbed study area. However, during a single sampling period in August, over 40 vehicles and 125 people were recorded. Thus, dozens of vehicles and hundreds of people moved through the area on a daily basis. In contrast, during 2 years of fieldwork only three people were ever seen in the undisturbed site.

General radio telemetry results

We obtained a total of 1,217 radio telemetry locations from 30 different snakes, including 11 males, 10 gravid females and 8 non-gravid females. Another female, gravid in 1995 but non-gravid in 1996, was treated as two separate individuals for analytical purposes. We could not confirm the reproductive condition of one female by ultrasonography, but considered her to be non-gravid because she was never seen in association with neonates.

Snakes were tracked for variable lengths of time, and often for periods far less than allowed by transmitter battery lifespan. For example, two snakes were killed by predators, two were run over by cars, three died in hibernation, and three died of unknown causes. In addition, transmitters were removed from three snakes following complications, and three transmitters failed prematurely. Locations incorporated in our analyses (i.e., excluding those associated with hibernation, or movement to and from hibernacula) comprised 67% of radio telemetry data.

Visibility

We used a two-factor ANOVA to assess the effects of human disturbance on snake visibility, with substrate temperature class (cool, warm or hot) and disturbance rating (1, 2 or 3) as treatments, and the mean visibility of individual snakes, calculated within treatment categories (e.g., cool, dr=1) from a minimum of three observations (range 3–29, mean ± SD +8.5±5.6) as the response variable. Snakes found in areas with different disturbance

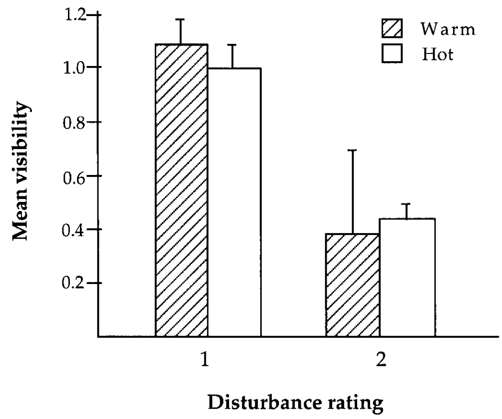

Fig. 1 Mean visibility (+1 SE) of gravid female eastern massasauga rattlesnakes relative to substrate temperature and disturbance rating. There were too few observations of gravid females at cool temperatures and with disturbance ratings of 3 to be included in the analysis

ratings were included more than once in the analysis (range 2–9, mean ± SD=3.4±2.2). The ANOVA model for males was not significant ($F_{8,30}$=0.84, P >0.57). The ANOVA model for non-gravid females was similar to the model for males but did not include one substrate temperature class (hot) because of insufficient data. This model also was not significant ($F_{5,23}$=2.17, P >0.09). Thus, neither substrate temperature nor human disturbance affected the visibility of male and non-gravid female eastern massasauga rattlesnakes. The model for gravid females did not include one substrate temperature class (cool) and one disturbance rating class (3) because of insufficient data. However, this model was significant ($F_{3,14}$=6.74, P <0.005). The mean visibility of gravid females did not vary significantly with substrate temperature (P >0.78), but did vary significantly with disturbance rating (P <0.0007). Gravid females were less visible when they were in more disturbed locations (Fig. 1).

Distance to retreat sites

We used a two-factor ANOVA to determine whether human disturbance affected the distance at which male and non-gravid female snakes were found from retreat sites, with group (male or non-gravid female) and disturbance rating (1, 2 or 3) as treatments. We lacked sufficient data for gravid females from locations with a disturbance rating of 3, so we conducted a separate ANOVA for this group with disturbance rating (1 or 2) as the treatment. For both analyses we used the mean distance of individual snakes from retreat sites, calculated within disturbance rating levels (from a minimum of three observations: range 3–55, mean ± SD=19±12), as the response variable. Snakes found in areas with different disturbance ratings were included more than once (range 1–3, mean ± SD=1.7±0.8) in the analyses. Both initial ANOVAs violated F-test assumptions, so the response variable was ln-

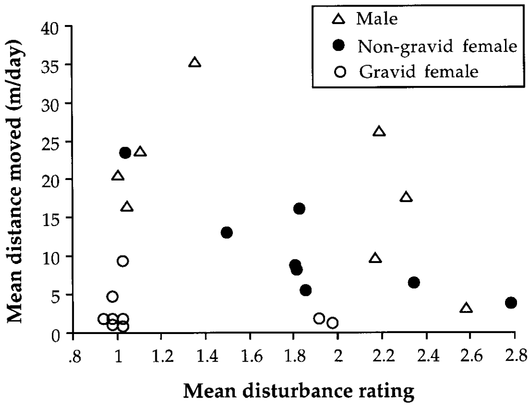

Fig. 2 Mean distance moved (m/day) by male, non-gravid female and gravid female eastern massasauga rattlesnakes relative to the mean level of human disturbance to which they were exposed

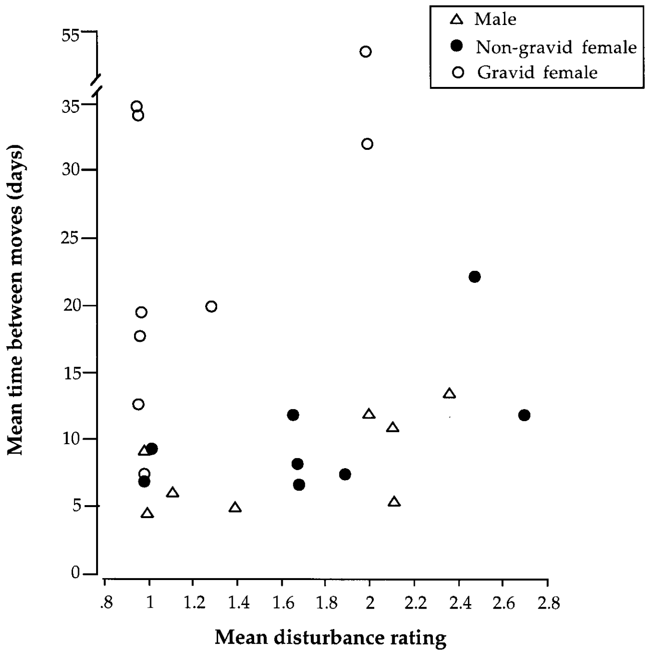

Fig. 3 Mean number of days between movements by male, non-gravid female and gravid female eastern massasauga rattlesnakes relative to the mean level of human disturbance to which they were exposed

transformed and the ANOVAs repeated. The resulting models for males and non-gravid females (F3,30=0.70, P>0.55) and for gravid females (F1,7=1.30, P>0.29) were not significant. Thus, neither sex or level of human disturbance affected the distance at which eastern massasauga rattlesnakes were found from retreat sites.

Movement patterns

To analyze the effects of human disturbance on snake movement, we used an ANCOVA with group (gravid female, non-gravid female or male) as the model's main effect and the mean disturbance rating of individual snakes as the covariate. Although defined categorically, disturbance ratings represent the relative exposure of snakes to human disturbance and thus have ordinal value. Therefore, disturbance ratings are also ranks, and calculating their mean value for individual snakes provides a true continuous variable. We used mean distance moved per day (total distance moved/number of days between the first and last location) as the response variable. The initial ANCOVA did not meet F-test assumptions, so we ln-transformed the response variable and repeated the analysis. The new ANCOVA model was significant ($F_{3,21}$=20.44, P<0.0001), as were the effects of group (P<0.0001) and mean disturbance rating (P<0.02). Gravid females moved the shortest distances and males moved the farthest, and all snakes moved less with increasing exposure to human disturbance (Fig. 2). When we repeated the ANCOVA excluding gravid females, the model remained significant ($F_{2,13}$=7.98, P<0.006), as did the effect of disturbance rating (P<0.005). However, the effect of group was not significant (P>0.15), indicating that mean distances moved by males and non-gravid females did not differ.

To assess the effects of human disturbance on the frequency of snake movements, we repeated the ANCOVA using each snake's mean time between moves of >10 m as the response variable. The initial model did not meet F-test assumptions so we ln-transformed the response variable. The model using transformed data was significant ($F_{3,21}$=13.75, P<0.0001). The effects of both group (P<0.0001) and disturbance (P<0.004) were significant. As exposure to human disturbance increased, the snakes spent more time between moves >10 m. To examine the effect of group on time between moves, we repeated the analysis excluding gravid females from the model. This ANOVA was significant (F3,12=3.52, P<0.05). However, although the effect of disturbance remained significant (P<0.009), the effect of group did not (P>0.30). Thus, the significant effect of group in the full analysis was attributable to gravid females moving less frequently than either males or non-gravid females (Fig. 3).

Condition

For males and non-gravid females, the initial regression of mass on SVL violated F-test assumptions, so we repeated the analysis using ln-transformed values for mass. The resulting model was significant (r^2=0.96, n=81, P<0.0001). We used a two-factor ANOVA to examine the effects of human disturbance on condition (i.e., residuals from the regression of mass on SVL) with year of capture and exposure to disturbance (i.e., whether the snake was captured in the disturbed or undisturbed study site) as treatments. The model was not significant ($F_{3,77}$=1.28, P>0.28). Thus, neither year nor human disturbance affected the condition of male and non-gravid female snakes.

Table 1 ANOVA results assessing effects of reproductive year, transmitter implantation, and study site (disturbed or undisturbed) on litter size corrected for maternal SVL. In each model two variables were held constant to assess the effect of the third variable on litter size (see text)

Effect	Treatment 1	Treatment 2	F	P
	Held constant	Held constant		
Year	Undisturbed	No transmitter	F1,6=0.35	0.57
Year	Disturbed	Transmitter	F1,3=0.57	0.50
Transmitter	1995	Undisturbed	F1,5=0.84	0.40
Transmitter	1996	Disturbed	F1,4=0.02	0.89
Site (disturbance)	1996	No transmitter	F1,7=0.01	0.93

The regression of mass on SVL for gravid female snakes was significant (r^2=0.61, n=25, P<0.0001). As above, the residuals of this regression were used as the response variable in a two-factor ANOVA with year of capture and exposure to disturbance (captured in the disturbed or undisturbed study site) as treatments. This model was also significant ($F_{2,22}$=5.08, P<0.02). Although year had a significant effect on condition (P<0.005; gravid females were heavier relative to their length in 1995 than in 1996), exposure to human disturbance did not have a significant effect (P>0.34).

Growth

To examine the effects of human disturbance on growth, we used a two-factor ANOVA with main growth year and exposure to disturbance (i.e., captured in the disturbed or undisturbed study site) as treatments, and relative growth rate (residuals from the regression of growth rate on SVL) as the response variable. Simple linear regression of growth rate on initial SVL was significant for males and non-reproductive females (r^2=0.12, n=35, P<0.04) and for reproductive females (r^2=0.46, n=16, P<0.005). However, the ANOVAs assessing the effects on relative growth rates were not significant either for males and non-reproductive females ($F_{2,32}$=0.64, P>0.53) or for reproductive females ($F_{2,13}$=2.52, P>0.11). Therefore, the growth rates of eastern massasauga rattlesnakes did not differ between years, and were not affected by exposure to human disturbance.

Litter size

Litter sizes ranged from 9 to 19 with a mean (± SD) of 13.33 (±2.74). We examined the effects of year of gravidity (1995 or 1996), transmitter implantation (implanted or not implanted) and exposure to disturbance (disturbed or undisturbed) on litter size. We could not conduct a full factorial (i.e., 2×2×2 ANOVA) analysis because we did not have data for all treatment combinations. For example, we had no gravid females from the undisturbed site in 1995 that were implanted with transmitters. Instead, wherever possible we used ANOVA to test the effect of one treatment while holding the levels of the other two treatments constant. For example, we tested the effect of year of gravidity (1995 vs 1996) by comparing the brood sizes of disturbed and undisturbed females with transmitters in the 2 years.

Brood size was positively correlated with female SVL ($F_{1,19}$>8.70, r^2=0.31, P<0.009), so we used residuals from this regression as our response variable. None of the ANOVAs was significant (Table 1), indicating that relative litter sizes were unaffected by human disturbance, year, or transmitter implantation.

Discussion

Habitat loss caused by human activity is a major contributor to contemporary faunal extinction (Diamond 1994). Thus, areas that preserve natural habitat may be central to the long-term viability of species in serious decline, such as the eastern massasauga rattlesnake. However, most parks serve not only to protect wildlife habitat, but also to provide outdoor recreational opportunities for the public. There is growing recognition that even apparently benign use of wilderness areas can have a deleterious effect on wildlife because the very presence of people can affect animal behavior (e.g., Boyle and Samson 1985). Although several authors have suggested that human disturbance can affect snakes (Greene 1988; Peterson 1990; Brown 1993), we are unaware of any previous research that has quantified how such effects are manifested, either behaviorally, or in the longer term, through negative effects on life history traits. In this study we found that eastern massasauga rattlesnakes responded to human disturbance, although not all snakes reacted in a similar manner.

Gravid females were significantly less visible to human observers in more disturbed locations. The females of several snake and lizard species are known to behave more cryptically when gravid (Graves 1989; Schwarzkopf and Shine 1992) because gravidity impairs locomotor ability, and thus the ability to escape predators (Shine 1980; Seigel et al. 1987). Experimental evidence indicates that eastern massasauga rattlesnakes rely primarily on passive defense to avoid confrontation with potential predators, but will flee if approached (Prior and Weatherhead 1994). Our results suggest that gravid females modify microhabitat use when they perceive predation risk to be high, thereby reducing the likelihood of direct confrontation with predators, and thus the need to rely on flight for protection.

If gravid females view people as potential predators, so too should non-gravid females and males. Thus, it is interesting that these snakes did not modify their visibility in response to human disturbance. For these individuals, the benefit of increased crypsis may not have warranted the cost of reduced activity (Lima and Dill 1990).

Gravid females are sedentary, rarely feed during gestation (e.g., Graves and Duvall 1993), and may be able to thermoregulate effectively through subtle postural changes rather than overt shuttling movements (e.g, Shine and Fitzgerald 1996). Thus, greater use of cover may not represent a substantial cost to them. In contrast, males and non-gravid females must forage to acquire sufficient resources for growth and future reproduction, and male mate-seeking typically involves frequent and extensive movement (Gregory et al. 1987). Behaving more cryptically seems likely to conflict with these needs.

Snakes in disturbed areas of Killbear Provincial Park were not found any closer to retreat sites than individuals in less disturbed areas. This is consistent with the snakes' apparent heavy reliance on crypsis (see discussion above), and their potential for active defense (rattling and striking) if discovered. Alternatively, this may simply reflect our inability to recognize potential refugia.

Human disturbance did affect snake movement. Gravid females, non-gravid females and males all moved shorter distances and moved less frequently in disturbed sites. Given that eastern massasauga rattlesnakes typically respond to disturbance by remaining motionless (Prior and Weatherhead 1994), it is not surprising that snakes in areas of extensive human activity move shorter distances and less frequently. Nevertheless, these findings do not support the suggestion that human disturbance causes snakes to abandon preferred habitat (Brown 1993). Were this the case, snakes in disturbed areas might be expected to move further, or more frequently, than those in undisturbed areas.

One explanation for this discrepancy is that eastern massasauga rattlesnakes reduce movement in disturbed areas, but if human activity is sufficiently pronounced or persistent, they move away from its source. Eastern massasauga rattlesnakes in Killbear Provincial Park were only rarely observed by park visitors (who often passed within 5 m of them), and thus the snakes were rarely molested. In contrast, the timber rattlesnakes (Crotalus horridus) observed by Brown (1993) abandoned "snake rocks" after they were captured, or the rocks themselves were disrupted. Thus, the different responses may simply reflect differences in perceived risk. This interpretation is supported by the finding that non-gravid female and male eastern massasauga rattlesnakes in Pennsylvania moved an average of 9.1±1.6 m/day (Reinert and Kodrich 1982), and males in New York moved an average of 20.5±2.3 m/day (Johnson 1995). In contrast, non-gravid females and males that were subject to experimental human approaches several times weekly in Ontario (Prior and Weatherhead 1994) moved an average of 56.2±12.4 m/day (Weatherhead and Prior 1992). Whatever the explanation, it is clear that human activity does affect the snakes' behavior.

While it may be interesting that eastern massasauga rattlesnakes respond to human activity, this change in behavior is only relevant to their conservation if it negatively affects their well-being. We found no evidence of such effects. Snakes captured in the disturbed study site were not in poorer condition, nor did they grow more slowly, than snakes caught in the undisturbed study site. Furthermore, relative litter sizes of females from the disturbed and undisturbed study sites were not significantly different. These results may indicate that the behavioral changes we documented are too minor to have produced any long-lasting effect. Alternatively, human disturbance may negatively affect the snakes' condition, growth, or reproduction, but our methods did not allow us to detect these effects. One reason to give this latter possibility serious consideration concerns our method for determining a snake's exposure to human disturbance. Life history data were collected from snakes that were not implanted with radio transmitters. Thus, unlike the snakes used for the behavioral study for which disturbance was measured directly, we were forced to assume that a snake captured and recaptured in a given study site (i.e., disturbed or undisturbed) spent most of its time in that area. It is quite possible that at least some individuals spent much of their time between captures in areas quite different, in terms of disturbance, from their capture locations. Assessment of this possibility would require a radio telemetry study of much greater scope than that which we undertook here.

Finally, it is important to note that we have examined a situation with a relatively moderate level of disturbance, and have only investigated a subset of the ways in which human disturbance could negatively affect the snakes. For example, decreased movement by snakes in areas subjected to heavy human disturbance could change patterns of mating and gene flow by disrupting long distance mate searching by males. Sufficient human disturbance could isolate populations and thus contribute to inbreeding (e.g., Madsen et al. 1995). Similarly, human disturbance could affect the survival and dispersal of neonates, which in turn could affect population age and genetic structure and viability. Thus, it is interesting in this regard that the massasauga rattlesnake population in Killbear Provincial Park shows significant genetic structure over distances <2 km, indicating very restricted gene flow (Gibbs et al. 1997). Whether human disturbance has contributed to this phenomenon is unknown, but the fact that the snakes respond to disturbance by restricting their movement makes this a possibility worth investigating.

To summarize, eastern massasauga rattlesnakes in Killbear Provincial Park appear to respond to people as potential predators. Presumably to reduce their risk of detection, gravid females became less visible, and all snakes moved less with increasing exposure to human disturbance. However, mark-recapture results revealed no effects of human disturbance on snake condition or growth rates, or on the brood size of gravid females. Thus, minor behavioral changes in response to human disturbance may not result in pronounced detrimental, long-term effects. However, given that disturbance affected the snakes' behavior, and given potential shortcomings in the mark-recapture data, more detailed research is required before this conclusion can be accepted. Furthermore, other potential negative effects of human disturbance not addressed in his study remain to be investigated.

Acknowledgements We thank the management and staff of Killbear Provincial Park for logistical support and assistance with fieldwork, and park visitors and local cottagers for their cooperation, Leslie Caldwell, Amy Jakubowski, Jeremy Rouse, and Rob Willson for fieldwork, Rob Kelly for ultrasonography, René Blier for GPS assistance, Dr. Dale Smith for providing instruction on the implantation of radio transmitters in snakes, and Dr. Hillary Turnbull, Dr. Sue West and Tammy Perks of the Georgian Animal Hospital for performing the surgeries. Financial support for this project was provided by an Ontario Graduate Scholarship awarded to Chris Parent, a Natural Sciences and Engineering Research Council operating grant to Patrick Weatherhead, and funding from Ontario Parks, and the Endangered Species Recovery Fund, sponsored by World Wildlife Fund Canada and the Canadian Wildlife Service.

References

Andrews RM (1982) Patterns of growth in reptiles. In: Gans C, Pough FH (eds) Biology of the reptilia, vol 13. Academic Press, Toronto, pp 273–320

Boo E (1990) Ecotourism: the potentials and pitfalls. World Wildlife Fund. Washington, DC

Boyle SA, Samson FB (1985) Effects of nonconsumptive recreation on wildlife: a review. Wildl Soc Bull 13:110–116

Brown WS (1993) Biology, status and management of the timber rattlesnake (Crotalus horridus): a guide for conservation. Soc Study Amphib Rept Herpetol Circ 22:1–78

Diamond JM (1989) The present, past and future of human-caused extinctions. Philos Trans R Soc Lond B 325:469–477

Farr DR, Gregory PT (1991) Sources of variation in estimating litter characteristics of the garter snake, Thamnophis elegans. J Herpetol 25:261–268

Fitch HS (1987) Collecting and life-history techniques. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Collier Macmillan Canada, Toronto, pp 143–164

Forsman A (1993) Growth rate in different colour morphs of the adder, Vipera berus, in relation to yearly weather variation. Oikos 66:279–285

Gander H, Ingold P (1997) Reactions of male alpine chamois Rupicapra r. rupicapra to hikers, joggers, and mountainbikers. Biol Conserv 79:107–109

Gibbons JW, Semlitsch RD (1987) Activity patterns. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Collier Macmillan Canada, Toronto, pp 396–421

Gibbs HL, Prior KP, Weatherhead PJ, Johnson G (1997) Genetic structure of populations of the threatened eastern massasauga rattlesnake, Sistrurus c. catenatus: evidence from microsatellite DNA markers. Mol Ecol 6:1123–1132

Giese M (1996) Effects of human activity on adelie penguin Pygoscelis adeliae breeding success. Biol Conserv 75:157–164

Graves BM (1989) Defensive behavior of female prairie rattlesnakes (Crotalus viridis) changes after parturition. Copeia 1989:791–794

Graves BM, Duvall D (1993) Reproduction, rookery use, and thermoregulation in free-ranging, pregnant Crotalus v. viridis. J Herpetol 27:33–41

Greene HW (1988) Antipredator mechanisms in reptiles. In: Gans C, Huey RB (eds) Biology of the reptilia, vol 16. Liss, New York, pp 1–152

Gregory PT, Macartney JM, Larsen KW (1987) Spatial patterns and movements. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Collier Macmillan Canada, Toronto, pp 366–395

Hammitt WE, Cole DN (1987) Wildland recreation. Wiley, Toronto

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford

Heatwole H (1977) Habitat selection in reptiles. In: Gans C, Tinkle DW (eds) Biology of the reptilia, vol 7. Academic Press, New York, pp 137–155

Johnson G (1995) Spatial ecology, habitat preference, and habitat management of the eastern massasauga, Sistrurus c. catenatus in a New York weakly-minerotrophic peatland. Ph.D. thesis, State University of New York, New York

Lillywhite HB (1987) Temperature, energetics and physiological ecology. In: Seigel RA, Collins JT, Novak SS (eds) Snakes: ecology and evolutionary biology. Collier Macmillan Canada, Toronto, pp 422–477

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68: 619–640

Lutterschmidt WI, Rayburn LA (1993) Observations of feeding behavior in Thamnophis marcianus after surgical procedures. J Herpetol 27:95–96

Macartney JM, Gregory PT, Charland MB (1990) Growth and sexual maturity of the western rattlesnake, Crotalus viridis, in British Columbia. Copeia 1990:528–542

Madsen T, Stille B, Shine R (1995) Inbreeding depression in an isolated population of adders Vipera berus. Biol Conserv 75: 113–118

MapInfo Corporation (1995) MapInfo professional user's guide. MapInfo, Troy, NY

McLellan BN, Shackleton DM (1988) Grizzly bears and resource extraction industries: effects of roads on behaviour, habitat use and demography. J Appl Ecol 25:451–460

Peterson A (1990) Ecology and management of a timber rattlesnake (Crotalus horridus L.) population in south-central New York state. NY St Mus Bull 471:255–261

Platt DR (1984) Growth of Bullsnakes (Pituophis melanoleucus sayi) on a sand prairie in south central Kansas. In: Seigel RA, Hunt LE, Knight JL, Malaret L, Zuschlag NL (eds) Vertebrate ecology and systematics: a tribute to Henry S. Fitch. Univ Kans Mus Nat Hist Spec Publ 10:41–55

Pough FH (1983) Amphibians and reptiles as low-energy systems. In: Aspey WP, Lustick SI (eds) Behavioral energetics: the cost of survival in vertebrates. Ohio State University Press, Columbus, Ohio, pp 141–188

Prior KA, Weatherhead PJ (1994) Response of free-ranging eastern massasauga rattlesnakes to human disturbance. J Herpetol 28:255–257

Reinert HK, Cundall D (1982) An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705

Reinert HK, Kodrich WR (1982) Movements and habitat utilization by the massasauga, Sistrurus catenatus catenatus. J Herpetol 16:162–171

SAS(1994) JMP statistics and graphics guide. SAS Institute, Cary, NC

Safina C, Burger J (1983) Effects of a human disturbance on reproductive success in the black skimmer. Condor 85:164–171

Schwarzkopf L, Shine R (1992) Costs of reproduction in lizards: escape tactics and susceptibility to predation. Behav Ecol Sociobiol 31:17–25

Seigel RA, Huggins MM, Ford NB (1987) Reduction in locomotor ability as a cost of reproduction in gravid snakes. Oecologia 73:481–485

Sheldon S, Bradley C (1989) Identification of individual adders (Vipera berus) by their head markings. Herpetol J 1:392–396

Shine R (1980) "Costs" of reproduction in reptiles. Oecologia 46:92–100

Shine R, Fitzgerald M (1996) Large snakes in a mosaic rural landscape: the ecology of carpet pythons Morelia spilota (Serpentes: Pythonidae) in coastal eastern Australia. Biol Conserv 76:113–122

Szymanski J (1988) Status assessment for the eastern massasauga (Sistrurus c. catenatus). US Fish Wildl Serv

Trimble Navigation (1994a) GeoExplorer operation manual. Trimble Navigation, Sunnyvale, Calif

Trimble Navigation (1994b) Geo-PC software user guide. Trimble Navigation, Sunnyvale, Calif

Waye HL, Gregory PT (1998) Determining the age of garter snakes (Thamnophis spp.) by means of skeletochronology. Can J Zool 76:288–294

Weatherhead PJ, Anderka FW (1984) An improved radio transmitter and implantation technique for snakes. J Herpetol 18: 264–269

Weatherhead PJ, Brown GP (1996) Measurement versus estimation of condition in snakes. Can J Zool 74:1617–1621

Weatherhead PJ, Prior KA (1992) Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (Sistrurus c. catenatus). J Herpetol 26:447–452

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548

Yarmoloy C, Bayer M, Geist V (1988) Behavior responses and reproduction of mule deer, Odocoileus hemionus, does following experimental harassment with an all-terrain vehicle. Can Field-Nat 102:425–429

Yezerinac SM, Lougheed SC, Handford P (1992) Measurement error and morphometric studies: statistical power and observer experience. Syst Biol 41:471–482

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall, Englewood Cliffs, NJ