The Effects of Human Disturbance on Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) in Killbear Provincial Park, Ontario

by

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ABSTRACT

I examined the response of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) to behavioural disturbance by humans in Killbear Provincial Park, Ontario. Thirty adult snakes were surgically implanted with radio transmitters and tracked from May-October in 1995 and 1996. Gravid females were less visible the greater their exposure to human disturbance. Analysis of 16 structural habitat variables revealed that rattlesnakes did not use habitat randomly, and that the habitat structure of snake-selected and randomly-chosen locations differed between the most and least disturbed areas of the park. Average distance moved per day declined in gravid females, non-gravid females and males with increasing exposure to human disturbance. However, analysis of mark-recapture data revealed no effects of human disturbance on snake condition or growth rates, or on the brood size, offspring size, or parturition date of gravid females.

"It is not enough to understand the natural world; the point is to defend and preserve it."

Edward Abbey

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I could not have completed this thesis without the assistance and cooperation of a great many people.

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Table of Contents

List of Tables

Table Page

List of Figures

INTRODUCTION

Biologists are increasingly concerned about the environmental impact of human activities. Recent attention has focused on the effects of agricultural development and deforestation, because such large-scale land cover changes are clearly responsible for the contemporary decline and extinction of many animal species (Diamond 1989, McNeely 1995). In contrast, outdoor recreation is often considered benign because it involves the non-consumptive use of wilderness areas (Flather and Cordell 1995). However, human intrusion into natural habitats may, in itself, negatively affect wildlife (Hammitt and Cole 1987). In this thesis I examine the effects of human disturbance on a population of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) in Killbear Provincial Park, Ontario, Canada.

Human disturbance is defined here as any anthropogenic stimulus that unintentionally (and perhaps unknowingly) causes wildlife to interrupt their activities or otherwise alter their behaviour. Such reactions may range from increased vigilance to flight, but are typically defensive in nature, because many animals, even those not traditionally hunted by humans, perceive people as threatening (Bouskila and Blumstein 1992). In fact, humans are often used as simulated predators in studies of flight initiation distance (Rand 1964, Bonenfant and Kramer 1996) and avian nest defense (Weatherhead 1979, Montgomerie and Weatherhead 1984).

The fact that wildlife generally view humans as potential predators is cause for concern because many animals will curtail foraging activities (Edwards 1983, Rochette and Himmelman 1986, Skutelsky 1996) or limit reproductive behaviour (Tuttle and Ryan 1982, Chivers et al. 1995) in response to increased predation risk.

Such predator avoidance tradeoffs can carry significant costs. For example, Bluegill Sunfish (*Lepomis microchirus*) in ponds stocked with piscivorous Largemouth Bass (*Micropterus salmoides*) avoided open water in favour of safer vegetated areas with poorer foraging returns, and as a result grew 27% less than fish in predator-free ponds (Werner et al. 1983). Similarly, stoneflies (*Paragnetina media*) vulnerable to predacious Rainbow Trout (*Oncorhynchus mykiss*) produced approximately 40% fewer eggs than individuals not exposed to the fish (Feltmate and Williams 1991). Such demonstrations of the fitness costs of predator avoidance behaviour have fuelled speculation that, at the population level, the indirect effects of predation may be greater than the direct (lethal) effects (Dill 1987).

Does human disturbance impose extraneous predator avoidance costs on wildlife? The potential certainly exists, since many investigators have already shown that animals exhibit spatial or temporal avoidance of areas subject to human intrusion. For example, McLellan and Shackleton

(1988) found that Grizzly Bears (*Ursus arctos*) usually avoided roads, but if they approached them, they did so only at night. Similarly, Mountain Lions (*Felis concolour*) selected home ranges with lower-than-average road densities and few or no human residences (Van Dyke et al. 1986). Pets may accentuate wildlife avoidance responses (Knight and Cole 1995). For example, Alpine Marmots (*Marmota marmota)* respond more strongly to hikers with leashed dogs that those without (Mainini et al. 1993).

The consequences for wildlife of human avoidance are rarely examined. Nevertheless, human disturbance has been shown to impose fitness costs in birds, including reductions in parental nest attendance (Keller 1989, Fernández and Azkona 1993), hatching success and chick survival (Safina and Burger 1983, Giese 1996), and feeding rates of young (Fernández and Azkona 1993, Mikola et al. 1994). Unfortunately, such effects are subtle and easily-overlooked, since few animals exhibit obvious behavioural responses to disturbance (Macarthur et al. 1982, Giese 1996).

That human disturbance may impose significant yet subtle costs on wildlife is particularly alarming given current trends in human leisure activities. Ecotourism has recently experienced rapid and sustained growth (Boo 1990, Filion et al. 1994) and participation in most forms of outdoor recreation continues to expand following dramatic increases in the 1960s and 1970s (Hammitt and Cole 1987). Given the growing popularity of parks and nature reserves, and the ready accessibility of many former wilderness areas, animals are likely to encounter humans with increasing frequency. This suggests that a better understanding of the potential effects of human disturbance would be prudent for conservation purposes, especially in relation to rare or endangered species (Garber and Burger 1995, Berger and Cunningham 1995).

In this thesis I examine a population of the threatened Eastern Massasauga Rattlesnake in a heavily-used provincial park in Ontario, Canada. I investigate whether human disturbance resulting from the park's recreational activities causes changes in snake behaviour, and attempt to determine the costs (if any) of such responses.

The Eastern Massasauga Rattlesnake is a shy and unaggressive venomous snake that grows to a total length of < 100 cm (Conant 1975). Historically the species was found in southern Ontario and northwestern Pennsylvania west to eastern Iowa and northeastern Missouri (Figure 1). However, due to human destruction of both individuals and habitat, the Eastern Massasauga Rattlesnake is now considered rare or endangered by most jurisdictions in which it is still found (Ernst and Barbour 1989). Four disjunct populations remain in Ontario. Of these, the largest occur on the Bruce Peninsula and the Eastern shore of Georgian Bay, where their long-term viability is threatened by industrial, residential and recreational

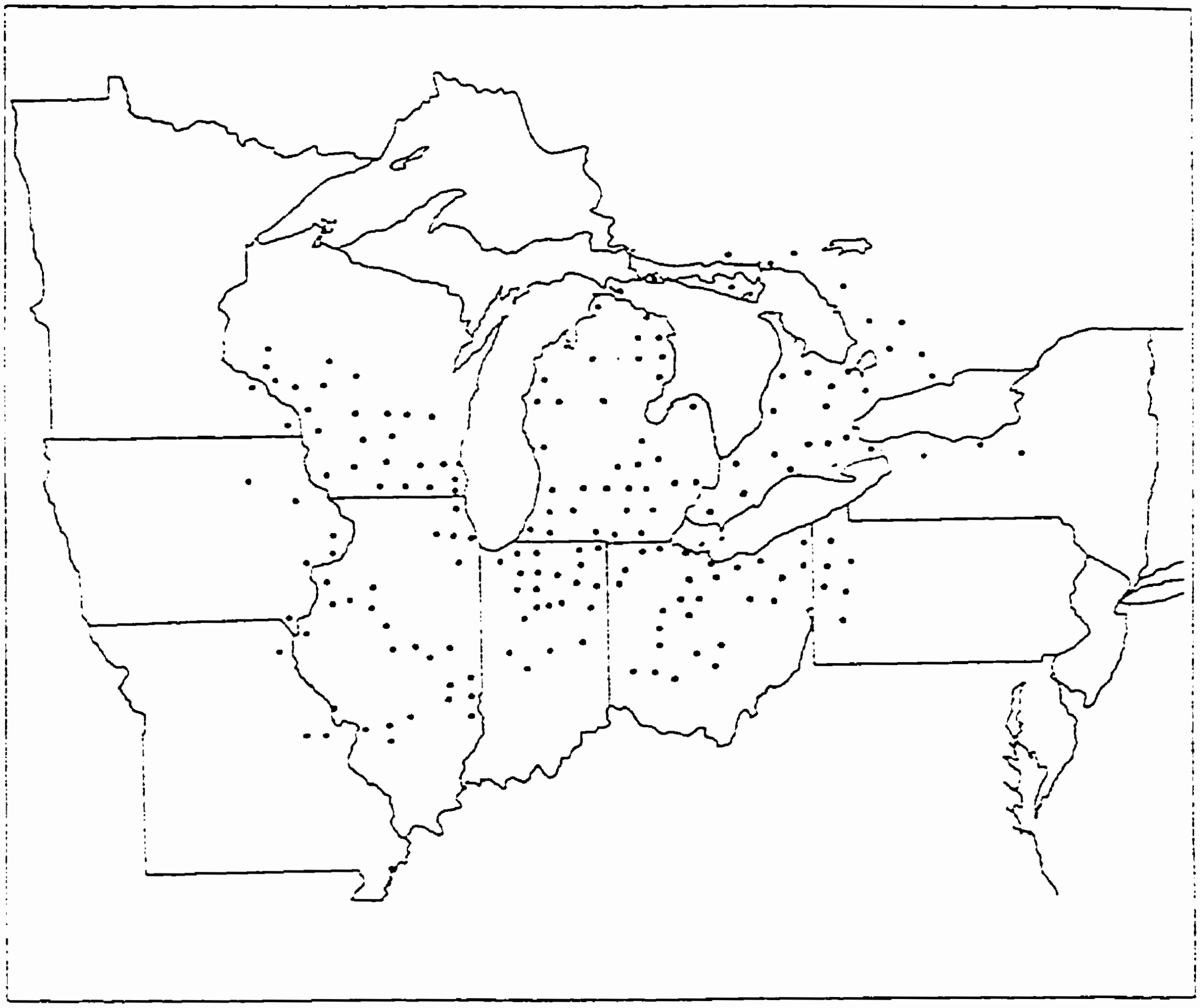

Figure 1: Historical range of *Sistrurus catenatus catenatus* in North America. Each dot represents the geographic centre of a county with confirmed occurrence. Adapted from Beltz (1993).

development (Prior and Weatherhead in review). Protected habitat in these areas can be found in a number of national and provincial parks, though the impact of the increasingly heavy use of these parks on snake populations is not known (Prior and Weatherhead in review). Thus, whether human disturbance affects Eastern Massasauga Rattlesnakes is a question of increasing significance to the conservation of this species in Ontario.

The effects of human disturbance on reptiles are rarely studied. For example, of the 166 articles on the effects of outdoor recreation on wildlife reviewed by Boyle and Samson (1985), only four per cent applied to herpetofauna. Yet reptiles might be especially vulnerable to the adverse effects of human disturbance, because, relative to birds and mammals, the mobility of many reptiles is limited, so they cannot avoid disturbance simply by moving to a less disturbed area. In addition, reptilian ectothermy is a physiological constraint to behavioural avoidance of disturbance because reptiles are often tied to specific activity periods, habitats or retreat sites (Heatwole 1977, Pough 1983, Huey et al. 1989).

Snakes are particularly difficult research subjects due to their cryptic nature, and human impacts on snakes are rarely reported. This may be due to the dislike people feel for snakes (Kellert 1985, Dodd 1993) and the subsequent lack of funds for snake conservation (Mittermeier et al. 1992).

However, many anthropogenic threats to snake populations have been recognized (Dodd 1987), including unregulated harvest or persecution (Galligan and Dunson 1979, Gannon and Secoy 1984, Reinert 1990), road mortality (Campbell 1956, Seigel 1986, Rosen and Gowe 1994), and loss of habitat (Shine and Fitzgerald 1989, Warwick 1990). Although a number of investigators have suggested that human disturbance may affect snakes (Greene 1988, Peterson 1990, Brown 1993), to the best of my knowledge this is the first study to address this issue systematically.

To assess the effects of human disturbance on Eastern Massasauga Rattlesnakes, I examined individuals from areas of Killbear Provincial Park that experience different levels of visitor use. I employed two separate approaches. First, I used radiotelemetry to determine the behavioural responses of snakes to disturbance, including changes in patterns of movement, use of cover and habitat utilization. Second, I examined snakes from disturbed and undisturbed areas for differences in life history features, including body condition, female fecundity, and individual growth rates.

If Eastern Massasauga Rattlesnakes in Killbear Provincial Park are sensitive to human disturbance, snakes in disturbed areas should behave differently from snakes in undisturbed areas. Specifically, I predicted that snakes in disturbed areas would exhibit lower, or more variable, body temperatures than undisturbed snakes, since predator avoidance behaviour, including crypsis and the use of refugia, may restrict movements between different thermal environments and thus impede behavioural thermoregulation. Secondly, because insects (Heads 1986), fish (Werner et al. 1983) and deer (Yarmoloy et al. 1988) attempt to avoid predator detection by increasing their use of cover in areas of high predation risk, I expected Eastern Massasauga Rattlesnakes to do the same. Thus, I predicted that snakes in disturbed areas would be less visible to human observers than snakes in undisturbed areas. Thirdly, I predicted that snakes in disturbed areas would be found closer to some form of retreat site, because many reptiles flee to protective refugia when threatened by predators (Greene 1988). Fourthly, as a consequence of my previous three predictions, I also predicted that Eastern Massasauga Rattlesnake habitat use would differ between disturbed and undisturbed areas. Finally, I predicted that the snakes' spatial or temporal patterns of movement would differ between disturbed and undisturbed areas. If encounters with humans cause Eastern Massasauga Rattlesnakes to abandon favoured habitat, as Timber Rattlesnakes (*Crotalus horridus*) are believed to do (Brown 1993), snakes in areas of Killbear Provincial Park prone to disturbance would probably move further, or more often, than undisturbed snakes. Alternatively, because movement is generally incompatible with cryptic behaviour (Lima and Dill 1990), snakes in disturbed areas might not move as far, or as frequently, as snakes in disturbed areas. In either case, I believed that snake movement patterns would differ between disturbed and undisturbed areas.

I expected Eastern Massasauga Rattlesnakes in heavily-used areas of Killbear Provincial Park to suffer a number of fitness costs as a result of their behavioural responses to human disturbance. First, I believed that human disturbance would affect energy intake and assimilation. For example, human disturbance could disrupt foraging, if, as predicted, snakes in disturbed areas alter their movement patterns and use of habitat. Human disturbance might also interfere with thermoregulatory behaviour (see above) which, in turn, would adversely affect physiological processes such as digestion (Lillywhite 1987). Therefore, I predicted that snakes in disturbed areas would be in poorer condition and have slower rates of growth than those individuals in undisturbed areas.

I also expected human disturbance to affect female reproduction. Eastern Massasauga Rattlesnakes are viviparous and gravid females remain at specific rookery sites until parturition (pers. obs). While males and non-gravid females could abandon disturbed areas, gravid females would likely remain in place and thus be continually exposed to human disturbance.

I predicted that female Eastern Massasauga Rattlesnakes in disturbed areas would produce fewer young than undisturbed snakes, because stress has been implicated as a possible cause of reductions in viable clutch size (Farr and Gregory 1991). For similar reasons, I predicted that human disturbance would negatively affect the length and mass of neonates, because King (1993) has demonstrated that captivity reduces offspring size in Brown Snakes (*Storeria dekayi*). Finally, I also expected human disturbance to affect parturition dates. Gravid snakes maintain higher (Graves and Duvall 1993, Tu and Hutchison 1994) or less variable (Charland and Gregory 1990) body temperatures than non-gravid conspecifics, and such behaviour is thought to promote embryonic development. Therefore, because human disturbance is expected to disrupt thermoregulation, I predicted that the average parturition date of disturbed females would be later than those of undisturbed females.

MATERIALS AND METHODS

Study Site

Killbear Provincial Park (80°12′ W and 45°21′ N) is located on a peninsula on the eastern shore of Georgian Bay, Ontario (Figure 2). The park is 1,756 ha in area and consists of mature second growth forest and scattered bedrock outcrops. The dominant forest community is Maple-Beech (*Acer saccharum-Fagus americanus*), but the park also contains a number of Hemlock (*Tsuga canadensis*) stands and a large Black Spruce (*Picea mariana*) bog. In the nearby town of Parry Sound, average daily temperatures are below freezing from December-March but range from 2.0-19.1 °C between April and November (Environment Canada 1982).

Killbear Provincial Park attracts more than 200,000 visitors annually (OMNR 1989, 1994), primarily during the months of July and August. Development is limited to eight campgrounds and three hiking trails (Figure 3). Human activity is concentrated in these areas and along the shoreline because visitors engage in mainly aquatic-based recreation. Other areas receive little use and are relatively undisturbed. Park visitors encounter rattlesnakes fairly frequently. For example, 21 were captured on campsites from 1990-1993 (C. Parent unpubl. data). The popularity of the park, and the frequency of human-snake interactions, make Killbear Provincial Park an ideal place to study the effects of human disturbance

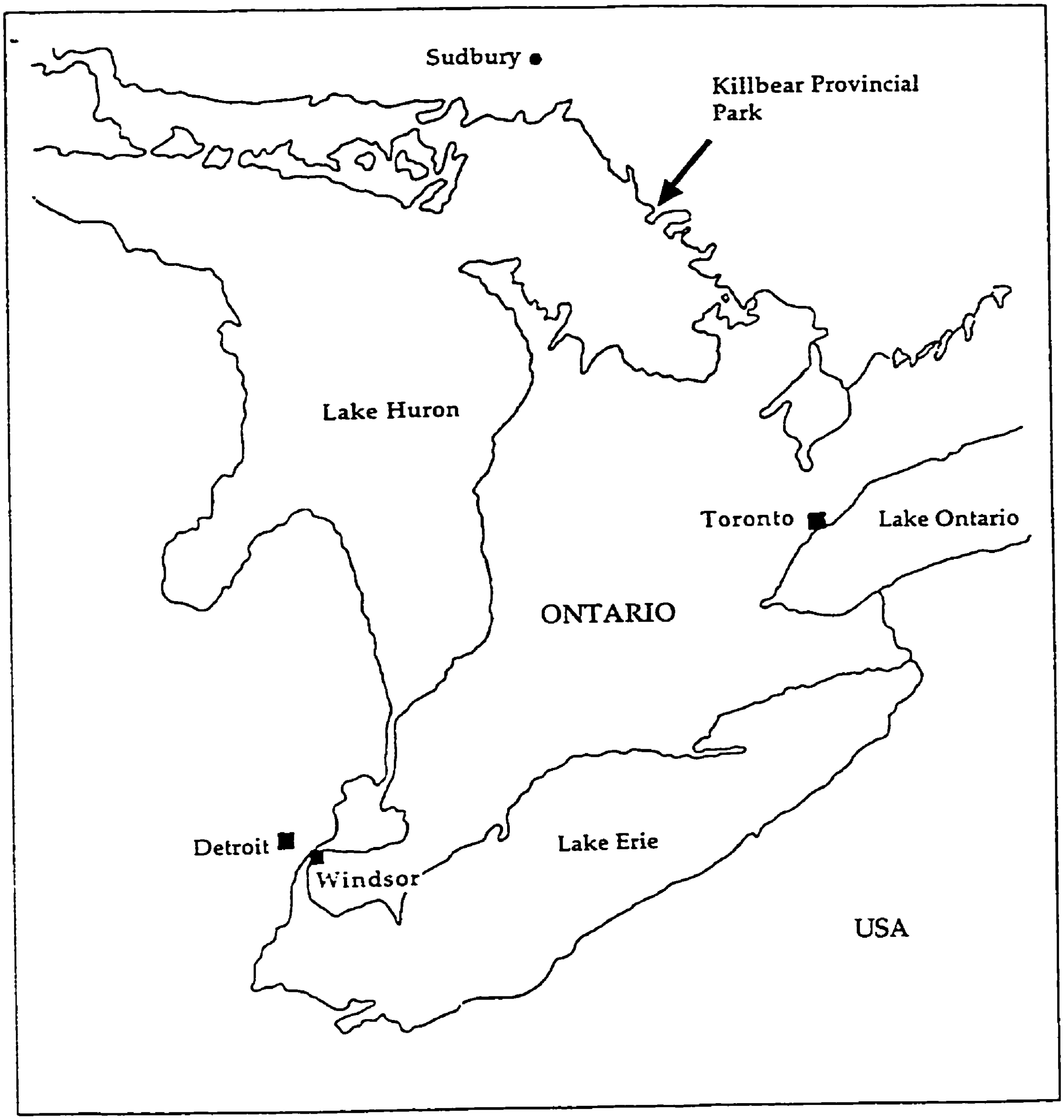

Figure 2: Location of Killbear Provincial Park.

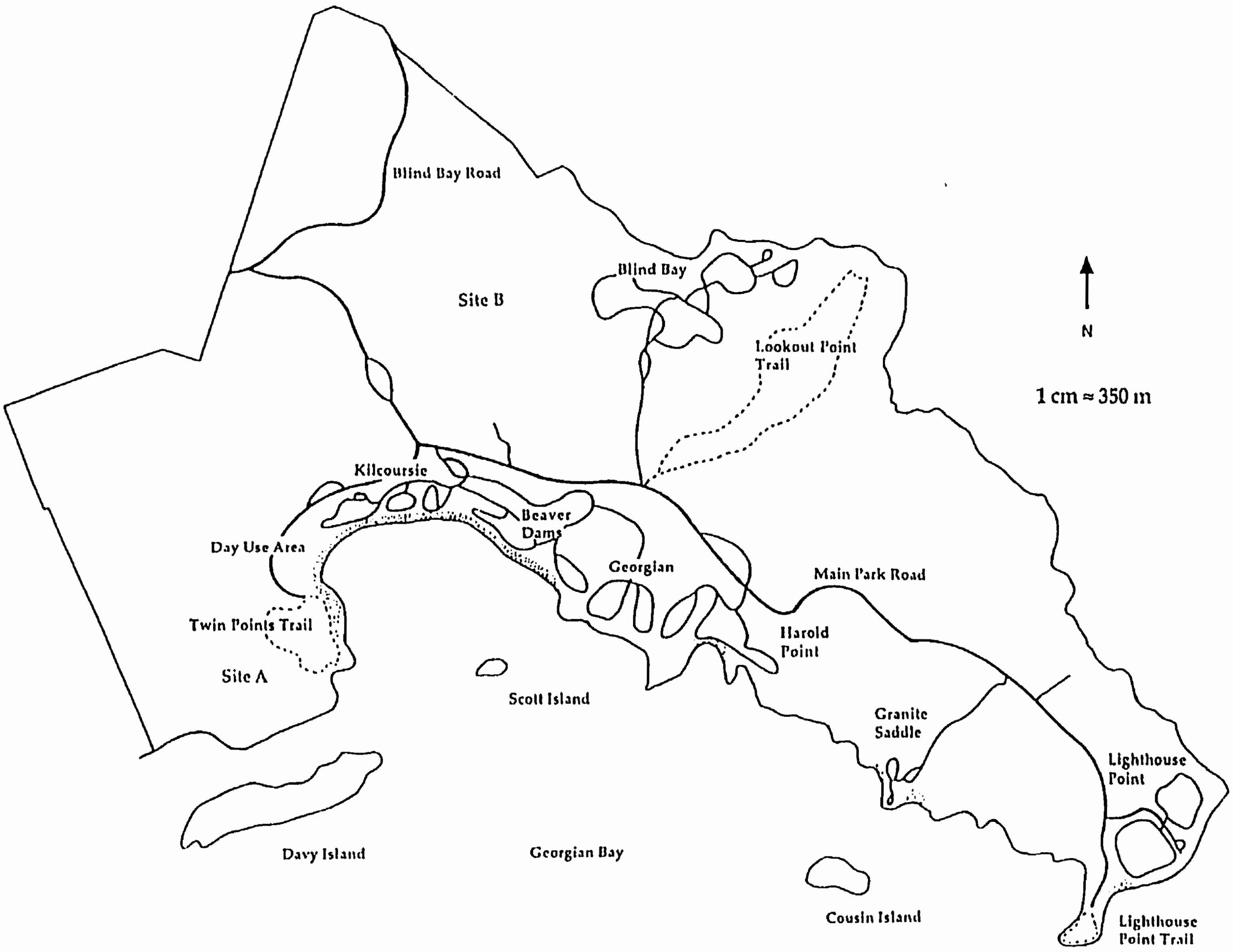

Figure 3: Killbear Provincial Park.

on Eastern Massasauga Rattlesnakes.

General Data Collection

A preliminary mark-recapture study of Eastern Massasauga Rattlesnakes in Killbear Provincial Park was conducted from 1992-1994. However, most data were collected from May-October in 1995 and 1996. Unless otherwise indicated, all data were collected with the aid of a single field assistant in 1994 and 1995 and four field assistants in 1996.

Radiotelemetry

Thirty adult Eastern Massasauga Rattlesnakes captured in Killbear Provincial Park were surgically implanted with temperature-sensitive 172 MHz radio transmitters (Holohil System Ltd, model S1-2T) weighing 7.8 g or 9.4 g, with battery lifespans of 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 procedures generally followed those 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 but were usually not held any longer in order to minimize the stress of captivity. All snakes were released within 15 m of their location of capture. Data collection did not begin until three days after release because implantation may affect snake behaviour (Weatherhead and Anderka 1984, Lutterschmidt and Rayburn 1993). When not in hibernation, implanted snakes were generally located every second day using either an AVM Instrument Company (Model LA12-DS) or a Wildlife Materials Incorporated (Model TRX-1000S) receiver with a hand-held 3-element yagi antenna.

To assess whether human disturbance interferes with normal behavioural thermoregulation, three temperatures were determined each time a transmitter-equipped snake was located. Transmitter pulse rate (pulses/minute) was recorded and later used to calculate snake body temperature (T_b) from previously-determined standard curves. Air temperature, in shade, 1 m above ground (T_a) and substrate temperature (T_s) were measured as close as possible to the snake in order to account for their influence on T_b. Both T_a and T_s were measured using a Cole Parmer (Model 8110-20) thermistor thermometer.

To determine whether Eastern Massasauga Rattlesnakes in disturbed areas increase their use of cover or remain closer to potential refugia, the visibility (0=not visible, 1=partly covered and 2=in open) and distance to nearest retreat site of transmitter-equipped snakes were recorded every time they were located. Retreat sites were subjectively defined as any location in which a snake could not be captured, such as a rodent burrow or a crevice under a large rock.

To examine patterns of snake habitat use, 16 structural variables (Table 1) were quantified from 100 sites chosen at random from each of two study sites (defined below) and from each (1995) or every second (1996) snake location determined by radiotelemetry. Habitat variables and sampling procedures largely follow those of Reinert (1984a,b) in order to facilitate comparison between studies (Reinert 1993).

To determine habitat structure, a 1-m^2 plot, divided into four quadrats, was centred on each location to be analyzed. Ground cover within the 1-m^2 plot was determined by placing an acetate grid over a photograph of the plot and calculating the percentage of grid squares occupied by rocks, leaf litter, vegetation or log cover, and the number of woody stems and the height of the tallest woody stem within the 1-m^2 plot were determined. Canopy cover was measured using an optical device that provided a cone-shaped view through a plexiglass grid. Canopy cover was calculated as the percentage of grid squares containing > 50% canopy cover from readings taken from the plot centre and from positions

Table 1. Structural habitat variables quantifed within a 1-m^2 quadrat centred on the location analyzed. See text for definition of variables and further explanation of sampling method.

Variable	Description
ROCK	Per cent rock cover
LEAF	Per cent leaf cover
VEG	Per cent vegetation cover
LOG	Per cent log cover
WSD	Number of woody stems
WSH	Height of tallest woody stem
DNOV	Distance to nearest overstory tree
DNUN	Distance to nearest understory tree
DNR	Mean distance to nearest rocks
MLR	Mean maximum length of nearest rocks
DNS	Mean distance to nearest shrubs
DNL	Mean distance to nearest logs
WNL	Mean diameter of nearest logs
DBHOV	Mean diameter at breast height of nearest overstory trees
DBHUN	Mean diameter at breast height of nearest understory trees
COVER	Per cent canopy cover

3 m north, south, east and west of the plot centre. Remaining variables (Table 1) within a sampling radius of 30 m from the centre of the 1-m^2 plot were quantified in each of four quadrats and the average value calculated. Only rocks ≥ 10 cm in length and logs with a maximum diameter ≥ 7.5 cm were quantified. Woody stems ≤ 2 m in height were defined as shrubs and those > 2 m as trees. Trees were characterized by diameter at breast height (dbh) as either overstory (dbh ≥ 7.5 cm) or understory (dbh <7.5 cm).

Snakes found moving were considered in transit and the habitat variables at these locations were not quantified. To minimize disturbance, each snake location was marked with flagging tape and distance to retreat site and habitat variables were measured after the snake had moved.

To assess the effects of disturbance on the movement patterns of Eastern Massasauga Rattlesnakes, the distances and bearings between each transmitter-equipped snake's subsequent locations were determined. Distances <100 m were measured in the field using a tape measure and compass. Positions of locations separated by >100 m were determined using a Trimble GeoExplorer GPS (Trimble Navigation Limited 1994a) and differentially corrected to within ± 2 m using Geo-PC 1.00 software (Trimble Navigation Limited 1994b). Corrected points were plotted using MapInfo 4.0 (MapInfo Corporation 1995) on a 1:10000 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.

Mark-Recapture

In order to assess the effects of human disturbance on the relative condition and growth rates of Eastern Massasauga Rattlesnakes, snakes were captured, measured, marked and released. Snakes were located by searching suitable habitat or were discovered and reported by park staff and visitors. Captured snakes were taken to a field laboratory for measurement. Snout-vent length (SVL) was measured 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 average 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

(Fitch 1987). Blood samples (Esra et al. 1975) were also taken from each snake as part of a larger investigation of population genetics.

Three methods were used to mark snakes for individual identification. Initially (1992-1994) a soldering iron was used to brand unique combinations of ventral scales (Weary 1969). Beginning in 1995, larger snakes were injected subcutaneously with sterilized PIT tags (Model Tx1400L1, Anitech Identification Systems). Neonate snakes were judged too fragile for either method and instead their dorsal patterns were photographed (Galligan and Dunson 1979, Sheldon and Bradley 1989). These markings are unique to the individual and do not change over time (C. Parent unpubl data). Snakes were generally released at their location of capture, but those found near roads or campsites were translocated approximately 15 m away to limit conflict with park users.

To assess the effects of human disturbance on the reproduction of Eastern Massasauga Rattlesnakes, I used ultrasonography to determine the reproductive condition (gravid vs. non-gravid) of captured females and to estimate the brood size of those found to be gravid. Examinations were initially conducted using a Hewlett-Packard 500 with a 5 MHz medium focus sector array transducer with liquid standoff. Later we used 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. Female snakes were held in captivity until once-weekly ultrasonography appointments and released at their location of capture following examination.

Females found to be gravid and not implanted with transmitters were opportunistically monitored following release. Dates of parturition were determined by monitoring gravid females on a daily basis near expected delivery date. Six snakes previously found to be gravid were recaptured shortly before parturition and kept in captivity until they gave birth. Neonates not born in captivity were captured shortly after birth to be measured and photographed.

Quantifying Snake Exposure to Human Disturbance

I used two methods to quantify the exposure of rattlesnakes to human disturbance in Killbear Provincial Park. First, I assigned the locations of transmitter-equipped snakes 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; $50 \text{ m} \geq d \geq 10$ 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. Thus, regardless of the park's occupancy rate, roads, trails and campgrounds receive the heaviest human use (pers. obs).

Life history data were collected from snakes not implanted with radio transmitters, so their exposure to human disturbance could not be quantified directly. Instead, each snake was assigned a disturbance status (disturbed or undisturbed) based on its location of capture. I defined two sites in Killbear Provincial Park in which rattlesnakes were found. Site A is a heavily-used area centred on the Twin Points Trail, and includes the Day Use road, parking lot, and surrounding areas. In contrast, Site B is rarely disturbed by humans, and consists of the area bordered by the Blind Bay Road to the west, the Blind Bay Campground to the east, and the main park road to the south (Figure 3). Snakes from Site A were assumed to have a higher exposure to human disturbance (disturbed) than those from Site B (undisturbed).

To confirm this perceived pattern of differential visitor use, human presence in both study sites was quantified. My assistants and I noted use (vehicles and people) of Site A by direct count at the entrance to the Twin

Points Trail over randomly selected 1 hour sampling periods from 09:00-21:00 between May 26 and August 22, 1995. In contrast, we simply recorded any use of Site B in the course of fieldwork, because previous experience indicated that the area was so rarely used by park visitors that formal sampling was considered an inefficient use of time.

General Data Analysis

Eastern Massasauga Rattlesnakes exhibit pronounced seasonal activity patterns associated with their migration to and from hibernation sites. Based on these movements, I divided each snake's locations into four functional activity periods. The emergence and return periods involve, respectively, the egress from, and the ingress to, hibernacula. These periods bound the primary active period, during which foraging and reproduction occur. Finally, the overwintering period consists of time spent in hibernation.

A snake's emergence period began on the first day it was found above ground in the spring and continued until it moved away from its hibernation site. If the snake's movements were short (usually < 10 m) and non-directional, I considered the snake's migration complete when it had travelled > 30 m from the hibernation site. If the snake moved directly from the hibernaculum, I considered the migration complete when the snake ceased consecutive, straight line (< 90° variance) long distance (often > 100 m) movements.

I defined the primary active period for gravid females as the time from the end of the migration away from the hibernation site until parturition. For males and non-gravid females, I defined the primary active period as the time between the end of the movements away from the hibernation site, and the beginning of the return migration. Thus, the return periods of gravid females began with parturition, while those of male and non-gravid females began with their first movements towards their eventual hibernation sites. Again, if the snake's movements were usually < 10 m and non-directional, I considered the migration to have begun when the snake was within 30 m of the hibernaculum. If the snake moved directly towards the hibernation site, I considered the return migration to have commenced when the snake began consecutive, straight line (< 90° variance from initial bearing) long distance movements. For both groups, the end of the return period was defined as the last autumn location in which the snake was observed above ground. Finally, I defined each snake's overwintering period as the time between the end of its return period and the beginning of its emergence period. During this time, snakes did not move and were not observed above ground.

To control for the potentially confounding effects of seasonal activity patterns, I excluded from analysis emergence, return and overwintering period data. Therefore, I focused on primary active period locations, which not only constitute the majority of radiotelemetry data but, perhaps more importantly, broadly overlap the period during which the park receives its heaviest human use (see results). Thus, I expected that any effect of human disturbance on Eastern Massasauga Rattlesnakes would be most pronounced (and thus most-easily detected) during this time.

Analysis of Radiotelemetry Data

My analyses of radiotelemetry data include only snakes tracked for a minimum of one month and for which I had observations from at least 12 locations. Thus, for most analyses, the value of the response variable represents, for each snake, an average of ≥ 12 separate measurements collected over ≥ 30 days time. If snakes were tracked over two summers, I pooled data between years.

Analysis of Snake Body Temperature Data

Snakes are ectothermic and as a result their body temperatures are strongly influenced by their surrounding environment (Lillywhite 1987). To examine this effect, I conducted a simple linear regression of snake body temperature (Tb) on air temperature (Ta) and a second simple linear regression of Tb on substrate temperature (Ts). In both regressions I used data from emergence, return, and primary activity periods in order to include a broad range of ambient temperatures.

To control for ambient temperature effects, I calculated the residuals of the regression of Tb on Ts. I used Ts as a control because Ta and Ts were correlated (r=0.79) and because Ts explained a greater proportion of the observed variance in Tb.

To examine the effects of human disturbance on snake body temperature, I analyzed active period observations using a 3x3 ANOVA with demographic group (gravid female, non-gravid female or male) and disturbance rating (1, 2 or 3) as treatments. I used the mean residual body temperature of individual snakes, calculated within disturbance rating levels, as the response variable.

I did not incorporate Ts as an ANCOVA covariate in order to avoid using data from individual locations as units of replication, thus limiting pseudoreplication (Aebischer et al. 1984) and the associated inflation of Type I error-rate. However, snakes found in areas with different disturbance ratings were included more than once in the analysis.

To determine whether the body temperatures of disturbed snakes were more variable than those of undisturbed snakes, I repeated the 3x3

ANOVA using the standard deviation of the residual body temperatures (variance of residuals about a predicted Tb for a given Ts) of individual snakes as the response variable. Again, snakes found in areas with different disturbance ratings were included more than once in the analysis.

Analysis of Visibility Data

Because snakes control their body temperatures by moving between different thermal environments (e.g. shade vs. direct exposure to sunlight) their use of cover is likely influenced by thermoregulatory considerations. Sex and reproductive condition may also strongly influence the use of cover by snakes. For example, male snakes may rarely use cover during their breeding season because their mate-seeking behaviour results in frequent and extensive movements (Gregory et al. 1987). In contrast, gravid females might use cover more often than non-gravid females because they rely on crypsis rather than locomotory escape or defensive displays to avoid potential predators (Graves 1989).

To control for thermoregulatory effects, I used the 25% and 75% quantile divisions of the distribution of substrate temperature (Ts) to classify each snake location as cool (<21 °C), warm (≥21 °C and ≤27 °C) or hot (>27 °C). By treating Ts as a categorical, rather than a continuous variable, I avoided using data from individual locations as units of replication, and thus limited pseudoreplication.

I used a two-factor ANOVA to assess the effects of disturbance on snake visibility, with substrate temperature class (cool, warm or hot) and disturbance rating (1, 2 or 3) as treatments, and the average visibility of individual snakes, calculated within treatment categories (e.g. cool, dr=1), as the response variable. Snakes found in areas with different disturbance ratings were included more than once in the analysis.

I analyzed data from gravid females, non-gravid females, and males separately in order to control for the effects of sex and reproductive condition. I did not incorporate demographic group as a third treatment in a 3x3x3 ANOVA because I lacked sufficient data for gravid females from areas with a disturbance rating of 3 to conduct a full factorial analysis. Thus, I conducted a 3x2 ANOVA for gravid females, and separate 3x3 ANOVAs for non-gravid females and males.

Analysis of Retreat Site Data

Sex and reproductive condition likely affect the defensive behaviour of snakes. For example, male snakes may stray further from retreat sites during the breeding season due to their frequent and extensive movements while seeking potential mates (Gregory et al. 1987). In contrast, gravid females might remain closer to protective refugia than non-gravid conspecifics because the burdening effects of gravidity may impede locomotor escape (Shine 1980, Seigel et al. 1987).

To control for the potential effects of sex and reproductive condition, I used a two-factor ANOVA to determine whether human disturbance affected the distance at which snakes were found from retreat sites, with group (gravid female, non-gravid female or male) and disturbance rating (1, 2 or 3) as treatments. I used the average distance of individual snakes from retreat sites, calculated within disturbance rating levels, as the response variable. Snakes found in areas with different disturbance ratings were included more than once in the analysis.

Analysis of Habitat Data

To determine whether Eastern Massasauga Rattlesnakes use habitat randomly, and to assess intra-specific variation in habitat use, I compared data from gravid female, non-gravid female, and male snakes with data from locations chosen at random from both study sites. I also compared radiotelemetry locations with disturbance ratings of 1, 2 or 3 to examine the effect of human disturbance on snake habitat use. This analysis excluded data from gravid females because their use of habitat differed significantly from that of males and non-gravid females (see results). In addition, I compared habitat data from randomly-chosen locations with disturbance ratings of 1, 2 or 3, because any differences in snake habitat use between areas exposed to different levels of human use could reflect the nature of the available habitat, rather than habitat selection by snakes. Finally, since any observed differences in snake life history characteristics between study sites might be attributed to differences in habitat, I compared habitat data from randomly-chosen locations in both Sites A and B.

I used multivariate analysis of variance (MANOVA) and *post hoc* pairwise comparisons of Mahalanobis distances to determine whether habitat structure differed between groups. I used discriminant function analysis to characterize differences in habitat structure between groups found to be significantly different. Each discriminant function analysis produced linear combinations of the original habitat variables, termed discriminant functions, such that differences between group centroids (multivariate means) on each function were maximized. Each DFA produced one discriminant function less than the number of groups involved in the analysis. I used an F-approximation (Rao 1973) to test the discriminating power of each of the resulting discriminant functions and interpreted only those found to be significant. I used the correlations between individual response variables and the discriminant functions (the total structure coefficients) to interpret significant discriminant functions (Klecka 1980).

MANOVA and DFA share three main assumptions (Pimental 1979). First, within each group, the observations follow a multivariate normal distribution on the response variables. Since normality of each of the variables separately is a necessary condition for multivariate normality (Stevens 1992) I used the Shapiro-Wilk test to assess the distribution of each variable. A second assumption is that the covariance matrices of each group are equal. I tested this assumption using Box's test (Box 1949). Finally, observations are assumed to be independent. Although randomly-chosen locations are, by definition, independent, snake locations are not, because they include repeated observations on a limited number of individuals. Therefore, for each snake, I calculated the average value of habitat variables across all its primary activity period locations, and used these means in MANOVA and DFA.

MANOVA and DFA can only be performed when all subjects have been measured for all response variables (Scheiner 1993). Snake locations were averaged within activity periods, so single locations with missing values were not problematic. However, individual random locations with missing values (n=9) could not be incorporated into multivariate analyses and were eliminated.

When comparing randomly-chosen and snake-selected locations, I divided random locations into groups, calculated the average value of habitat variables within each group, and used these means in MANOVA and DFA. This was necessary to equalize group sample sizes, because I had far more independent observations from randomly-chosen locations than averaged values for individual snakes, and MANOVA results are not robust if group sample sizes are sharply unequal (Stevens 1992).

The total structure coefficients of discriminant functions may be unstable if sample size does not exceed the number of discriminating variables by at least a factor of three (Williams and Titus 1988). This condition was not met in either analysis of snake habitat structure, so to examine the effects of small sample size, I repeated the comparison of snake-selected and randomly-chosen habitats using individual locations as the unit of replication. In this analysis, I replaced missing values with mean values calculated across locations, averaging within individuals for snakes, and within study sites for random locations. I used only a random sub-sample of locations so that group sample sizes were equal.

I repeated all analysis three times, using raw, log-transformed, and a mixture of arcsine, square root and log-transformed data, and report the results from the analyses that best met statistical assumptions.

Analysis of Snake Movement Patterns

I used ANCOVA to examine the effects of human disturbance on snake movement patterns. To control for sex and reproductive condition, I incorporated group (gravid female, non-gravid female or male) as the model's main effect. I used the average disturbance rating of individual snakes, calculated across primary active period locations, as the covariate. Though 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.

I used the average distance moved per day as the ANCOVA response variable. I calculated each snake's average daily movement by summing the distances moved between subsequent locations and dividing by the number of days between the first and last location.

To assess the effects of human disturbance on the frequency of snake movements, I repeated the ANCOVA using each snake's average time between moves of > 10 m, termed persistence, as the response variable.

Analysis of Condition Data

The residuals of a regression of body mass on snout-vent length were used as a simple index of condition (Weatherhead and Brown 1996). Snakes that weighed more for their length than predicted by the regression line had positive residuals and were considered to be in good condition; conversely, those with negative residuals were judged to be in poor condition. To control for the effects of gravidity, one regression was used to determine the condition of gravid females and a separate regression used for males and non-gravid females. Gravidity could confound condition analysis because, for a given length, snakes that are gravid weigh more than those that are not (Graves and Duvall 1993). This effect would be particularly pronounced in the Killbear Provincial Park population of Eastern Massasauga Rattlesnakes, where clutch mass, calculated as the difference between pre-and post-parturition mass, averages 49.9 ± 1.6% of pre-parturition mass (C. Parent unpubl. data).

For both groups (gravid females, non-gravid females and males) the condition of snakes from the disturbed study site and the undisturbed study site was compared by a two-factor ANOVA with year of capture (1994, 1995 or 1996) and disturbance status (disturbed or undisturbed) as treatments. I controlled for year of capture because condition can vary annually due to climatic variation (Brown and Parker 1984) or fluctuating prey availability (Andrén and Nilson 1983).

Theoretically, condition analysis of gravid females could be confounded by sampling date if snakes increase in mass while gravid (e.g. Brown and Parker 1984). However, limited data (n=6) suggested that gravid females only gain an average of 3.4 ± 2.9% of their initial mass while gravid. This amount was considered negligible and consequently the effect of mass gain during gravidity was ignored.

Analysis of Growth Rates

To calculate individual growth rates, the difference in snout-vent length between initial capture and recapture was divided by the number of days between captures, excluding time spent in hibernation. Growth is negligible during hibernation so this period is generally omitted from calculations of capture interval (e.g. Macartney et al. 1990, Forsman 1993). For this study, the no-growth period of Eastern Massasauga Rattlesnakes in Killbear Provincial Park was set at November 1-April 30.

In order to maintain the statistical independence of samples, only a single growth rate was calculated for each snake. Growth rates of snakes recaptured more than once were determined using data from the first and last capture.

Analysis of snake growth rates must control for a number of potentially confounding effects. Growth rates may decrease in gravid females (Macartney et al. 1990, Houston and Shine 1994) and typically decline with increasing snout-vent length (Andrews 1982). Growth rates may also vary between years due to climatic variation (Forsman 1993) or fluctuating prey availability (Platt 1984, Lindell and Forsman 1996).

To control for the effects of gravidity, growth data from potentially reproductive females were analyzed separately from growth data for males and known non-reproductive females. Female reproductive status (gravid vs. non-gravid) was determined with each capture and as a result the reproductive history of female snakes captured annually was known. However, for some females, the interval between captures extended two or more years and consequently the incidence of their reproduction could not be determined. Therefore, based on the smallest gravid female captured, any female with SVL ≥ 50 cm was considered potentially reproductive.

To remove the effects of size, I calculated the residuals of a simple linear regression of growth rate on snout-vent length at initial capture, termed the relative growth rate, for both potentially reproductive females and for non-reproductive females and males.

To control for annual effects, I 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. For example, the main growth year of a snake captured on September 1, 1994 and recaptured on October 1, 1995 would be 1995. Similarly, the main growth year of a snake captured on July 15, 1993 and recaptured on May 30, 1995 would be 1994. Snakes with more than one complete year between recaptures were excluded from the analysis because year effects could not be controlled.

Finally, to examine the effects of disturbance on snake growth rates, I used a two-factor ANOVA with main growth year (1994, 1995 or 1996) and disturbance status (disturbed or undisturbed) as treatments and the relative growth rate (see above) as the response variable. Again, I conducted separate analyses for reproductive females and for non-reproductive females and males.

Analysis of Reproductive Data

I examined the effects of year (1995 or 1996), radio transmitter implantation (implanted or not implanted) and exposure to disturbance (disturbed or undisturbed) on brood size and average offspring size. However, I could not conduct full factorial (2x2x2 ANOVA) analyses because I did not have data for all treatment combinations. For example, I lacked data on broods of undisturbed females implanted with radio transmitters and gravid in 1995. Instead, wherever possible, I used ANOVA to test the effect of one treatment while keeping the levels of the other two treatments constant. For example, I tested the effect of year of gravidity (1995 vs. 1996) by comparing the broods of undisturbed females not implanted with transmitters, and the broods of disturbed females implanted with transmitters, from each of the two years.

Monitored gravid females were assigned a disturbance status (undisturbed or disturbed) based on the study site in which they were captured. Site A receives significantly more visitor use than Site B, so snakes from Site A are considered to have a higher exposure to human disturbance than those from Site B. However, levels of human disturbance within study sites are variable, so I also assigned each female's rookery location a disturbance rating (1, 2 or 3). Therefore, several females from Site A (disturbed) received low disturbance ratings, and one snake in a campground bordering Site B (undisturbed) received a high disturbance rating.

Initial analyses of the effects of human disturbance on female reproduction categorized snake exposure based on female disturbance status (undisturbed or disturbed). These analyses were repeated with female exposure to human disturbance classified by disturbance rating (1, 2 or 3). However, the results of these tests are not reported because they did not differ from those of the initial analyses.

Analysis of Brood Size Data

Snakes commonly exhibit intra-specific variation in brood size. The number of offspring in a brood is often positively correlated with female snout-vent length (Seigel and Ford 1987) and may also vary annually due to climatic variation (Seigel and Fitch 1985) or fluctuating prey availability (Andrén and Nilson 1983, Seigel and Ford 1987). In addition, radio transmitter implantation is known to cause reabsorption of developing follicles (Graves and Duvall 1993).

I examined the effects of the year of gravidity (1995 or 1996), radio transmitter implantation (implanted or not implanted) and disturbance status (disturbed or undisturbed) on brood size. I used ANOVA to test the effect of one treatment while keeping the levels of the other two treatments constant. To control for the effects of female body size, I performed a simple linear regression of female snout-vent length on brood size, and used the residuals as the response variable.

Analysis of Offspring Size Data

Maternal size can affect offspring size (Seigel and Ford 1987). To test for this effect, I conducted a multiple regression analysis with female mass, female snout-vent length and the interaction term as predictor variables and the mean within-brood offspring snout-vent length as the response variable. An identical analysis was performed to assess the effects of female size on mean within-brood offspring mass.

I examined the effects of the year of gravidity (1995 or 1996), radio transmitter implantation (implanted or not implanted) and disturbance status (disturbed or undisturbed) on mean within-brood offspring snout-vent length and mass. In both cases I used ANOVA to test the effect of one treatment while keeping the levels of the other two treatments constant. I did not control for female size because neither multiple regression revealed significant maternal effects on average offspring size (see results).

Parturition Date

In viviparous snake species, gravid females often maintain elevated body temperatures, presumably to accelerate the development of their young (Lillywhite 1987, Tu and Hutchinson 1994). However, the ability to thermoregulate is weather-dependent, so parturition dates may vary annually as a result of fluctuating climatic conditions (Saint Girons 1985). The size of a snake might also affects its ability to thermoregulate because the ratio of body surface area to body volume governs rates of heating and cooling. Consequently, parturition dates may also vary within a given year if gravid females within a population differ in size.

To examine the effects of disturbance on parturition date, I first removed the effects of year and female snout-vent length. To control for the effects of year, I expressed parturition dates in terms of number of days before (-) or after (+) the average date of birth for a given year. Thus, if on average, females gave birth in a given year on August 20, the parturition dates of snakes that gave birth on August 18 and August 25 would be -2 and 5, respectively. To remove the effects of female size, I performed a simple linear regression of parturition date on female snout-vent length, and used the residuals from this analysis in a 2x2 ANOVA to examine the effects of disturbance status (disturbed or undisturbed) and transmitter presence (implanted or not implanted) on parturition date.

General Statistical Methods

Most statistical analyses were performed on a Power Macintosh 6100/60 personal computer using JMP 3.1 (SAS Institute, Inc. 1994) software. I confirmed that F-test assumptions were met, and if violated, I modified the response variable using the appropriate transformation and repeated the analysis. Discriminant function analysis was performed using SAS 6.11 (SAS Institute, Inc. 1990). Unless otherwise indicated, I report mean values ± 1 standard error and use an α–value of 0.05 to denote statistical significance.

RESULTS

Human Use of Study Sites

Fifty-four hour-long sampling periods in May (n=3), June (n=17), July (n=21) and August (n=13) of 1995 were used to quantify human use of Site A. Since only three sampling periods occurred in May, observations from this month were combined with those from June in order to facilitate data analysis.

Overall, an average of 9.0 ± 1.4 vehicles and 33.4 ± 4.6 visitors were observed each hour in Site A. 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. However, neither the occurrence of vehicles ($F_{2,51}=22.25$, $p<0.0001$) nor visitors ($F_{2,51}=23.98$, $p<0.0001$) was uniform throughout the summer. Tukey-Kramer HSD tests revealed that vehicle numbers did not differ significantly between July and August, but were significantly higher than in June. The pattern of visitor use was similar (Figure 4). Thus, Site A received its heaviest human use during the period of greatest snake activity (see below).

In contrast to heavily-used Site A, during two years of fieldwork only three people were ever seen in Site B. Thus, my impression of

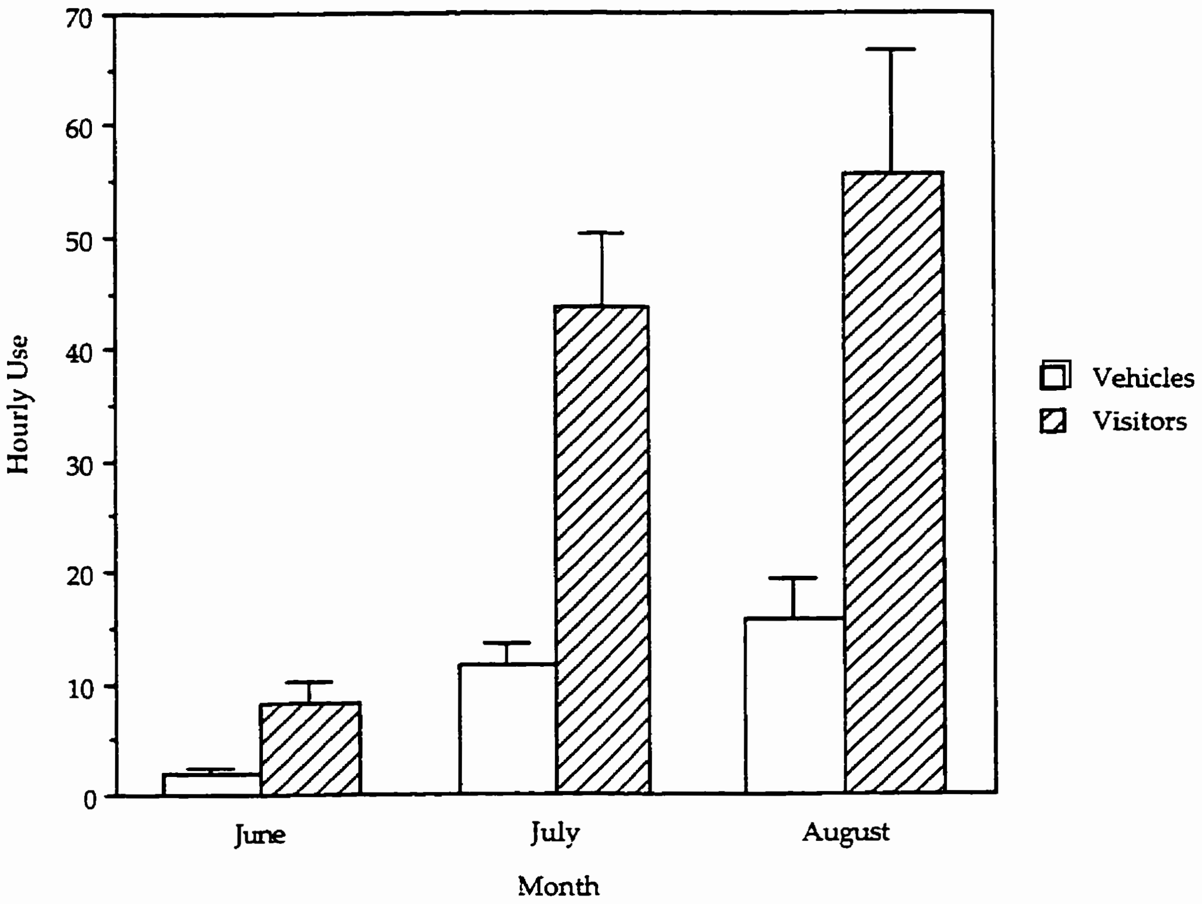

Figure 4: Mean (± standard error) visitor use of Site A in Killbear Provincial Park in 1995.

differential use of Sites A and B is supported by direct assessment of visitor activity.

General Radiotelemetry Results

I obtained a total of 1,217 radiotelemetry locations from 30 different snakes, including 11 males, 10 gravid females and 7 non-gravid females. The reproductive condition of one transmitter-equipped female could not be confirmed by ultrasonography. This snake was considered non-gravid because she was never seen in association with neonates. For analytical purposes, I treated another female as two separate individuals because she was gravid in 1995 but non-gravid in 1996.

Snakes were tracked for variable lengths of time, and often not simultaneously (Table 2). A snake's tracking period depended on the date of its transmitter implantation (a function of the snake's date of capture) and also on its ultimate fate. Many snakes were monitored for periods far less than allowed by transmitter battery lifespan. For example, ten snakes were killed during the course of the study. 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 snakes could not be relocated due to transmitter failure.

Table 2: Eastern Massasauga Rattlesnakes implanted with radio transmitters in Killbear Provincial Park.

Snake Number	Sex	Condition	Dates Monitored	Number of Locations
22237b4300	M	-	July 30, 1995 - October 25, 1996	93
2224164c3d	M	-	July 30, 1995 - October 26, 1996	86
22237c0528	M	-	July 30, 1995 - October 26, 1996	84
22240f0203	M	-	August 15, 1995 - October 6, 1996	80
222416730b	M	-	September 4, 1995 - October 26, 1996	72
222373203a	M	-	July 18, 1995 - October 23, 1995	33
22235a7d16	M	-	August 5, 1996 - October 25, 1996	26
2224151e7d	M	-	August 4, 1995 - October 27, 1996	22
22240e751e	M	-	August 21, 1995 - October 16, 1995	18
22240b3e2e	M	-	August 27, 1995 - October 21, 1995	16
222373787b	M	-	June 25, 1995 - July 18, 1995	11
2224187519	F	not gravid	July 31, 1995 - October 27, 1996	80
22236c4709	F	not gravid	July 25, 1995 - July 16, 1996	61
22237e0f3d	F	not gravid	May 21, 1996 - October 26,1996	56
2223703037	F	not gravid	April 19,1996 - August 25, 1996	50
22240e2d5f	F	not gravid	August 13, 1996 - October 25, 1996	23
22236e5e75	F	not gravid	August 13, 1995 - October 7, 1995	20
2224020c24	F	not gravid	August 13, 1996 - October 27, 1996	18
2224176e1e	F	not gravid	July 5, 1995 - July 19, 1995	9

Table 2 (continued): Eastern Massasauga Rattlesnakes implanted with radio transmitters in Killbear Provincial Park.

Snake Number	Sex	Condition	Dates Monitored	Number of Locations
2223703037	F	gravid	June 25, 1995 - October 20, 1995	45
1f6c607520	F	gravid	June 25, 1995 - October 23, 1995	43
22237c571b	F	gravid	July 24, 1996 - October 25, 1996	31
222417731f	F	gravid	July 29, 1995 - October 23, 1995	30
2224193663	F	gravid	July 28, 1996 - October 25, 1996	30
2224194e21	F	gravid	June 25, 1995 - August 20, 1995	30
2224033c4d	F	gravid	July 29, 1995 - October 23, 1995	29
22236e3902	F	gravid	June 25, 1995 - August 22, 1995	27
222404625d	F	gravid	August 5, 1996 - October 25, 1996	26
22237a3c5b	F	gravid	July 17, 1995 - August 23, 1995	20
2224110067	F	gravid	September 3, 1995 - October 23, 1995	12
22240e543e	F	unknown	July 16, 1996 - October 14, 1996	36

Primary active period locations comprised 72% of radiotelemetry data. The remaining locations were classified as return period (18%), emergence period (5%) or overwintering period (5%) data. Average beginning and end dates of functional activity periods are summarized in Table 3.

Effects of Human Disturbance on Snake Body Temperature

A simple linear regression of snake body temperature (Tb) on air temperature (Ta) was highly significant ($r^2=0.45$, n=1139, $p<0.0001$) and confirmed that Tb was positively correlated with Ta. Similarly, a simple linear regression of Tb on substrate temperature (Ts) was also highly significant ($r^2=0.62$, n=1139, $p<0.0001$) and demonstrated that Tb was positively correlated with Ts.

I used a 3x3 ANOVA to assess the effects of human disturbance on Tb, with demographic group (gravid female, non-gravid female or male) and disturbance rating (1, 2 or 3) as treatments, and the average residual body temperature of individual snakes as the response variable. The interaction term was not significant ($p> 0.22$) so it was removed from the initial model and the analysis repeated. The resulting model was not significant ($F_{4,43}=1.75$, $p>0.15$). Thus, I found no evidence that sex,

Table 3: Mean (± standard error) beginning and end dates of functional activity periods of Eastern Massasauga Rattlesnakes in Killbear Provincial Park. See text for definitions and further explanation.

Period	Group	Earliest Day	Latest Day
Emergence	Males	May 5 ± 0 days	June 2 ± 4 days
	Non-Gravid Females	May 6 ± 7 days	May 31 ± 6 days
	Gravid Females	-	-
Primary Active	Males	June 4 ± 4 days	September 15± 3 days
	Non-Gravid Females	June 3 ± 5 days	September 13 ± 5 days
	Gravid Females	-	August 27 ± 2 days
Return	Males	September 19 ± 3 days	October 12 ± 3 days
	Non-Gravid Females	September 18 ± 5 days	October 2 ± 3 days
	Gravid Females	August 30 ± 2 days	October 22 ± 1 day
Overwintering	Males	October 12 ± 3 days	May 3 ± 1 day
	Non-Gravid Females	October 8 ± 5 days	May 5 ± 1 day
	Gravid Females	October 25	-

reproductive condition, or level of human disturbance affected Eastern Massasauga Rattlesnake body temperatures.

To determine whether the body temperatures of disturbed snakes were more variable than undisturbed snakes, I repeated the ANOVA analysis using the standard deviation of the residual body temperatures (variance of residuals about a predicted Tb for a given Ts) of individual snakes as the response variable. In the initial model, the interaction term was not significant ($p>0.43$), so it was removed and the analysis repeated. The resulting model was not significant ($F_{4,43}=1.20$, $p>0.32$). Therefore, sex, reproductive condition, and exposure to human disturbance did not affect the variability of snake body temperatures.

Visibility

To assess the effects of human disturbance on snake visibility, I used a two-factor ANOVA with temperature class (cool, warm, or hot) and disturbance rating (1, 2 or 3) as treatments and the average visibility of snakes within each treatment category (e.g. cool, dr=1) as the response variable. To control for the effects of sex and reproductive condition, I analyzed data from gravid females, non-gravid females, and males separately.

The interaction terms were not significant in initial models for males ($p>0.35$), non-gravid females ($p>0.87$) or gravid females ($p>0.23$) so they were removed. Subsequent models for males ($F_{4,52}=1.50$, $p>0.21$) and non-gravid females ($F_{4,46}=1.28$, $p>0.29$) were not significant. Thus, neither substrate temperature or human disturbance affected the visibility of male and non-gravid female Eastern Massasauga Rattlesnakes. However, the model for gravid females was significant ($F_{3,23}=8.29$, $p<0.001$). The average visibility of gravid females varied significantly with substrate temperature ($p<0.001$) and disturbance rating ($p<0.05$). Gravid females were significantly less visible in more disturbed areas (Figure 5).

I used ANOVA to assess the effect of substrate temperature on the visibility of gravid females. To control for the effects of disturbance, each of the two analyses was limited to locations with the same disturbance rating. For locations with a disturbance rating of 1, the effect of substrate temperature was significant ($F_{2,17}=12.57$, $p<0.001$). Tukey-Kramer HSD tests revealed that the average visibility of gravid females was significantly lower when substrate temperatures were cool. Average visibility did not differ significantly between warm and hot substrate temperatures. The effect of substrate temperature was not significant

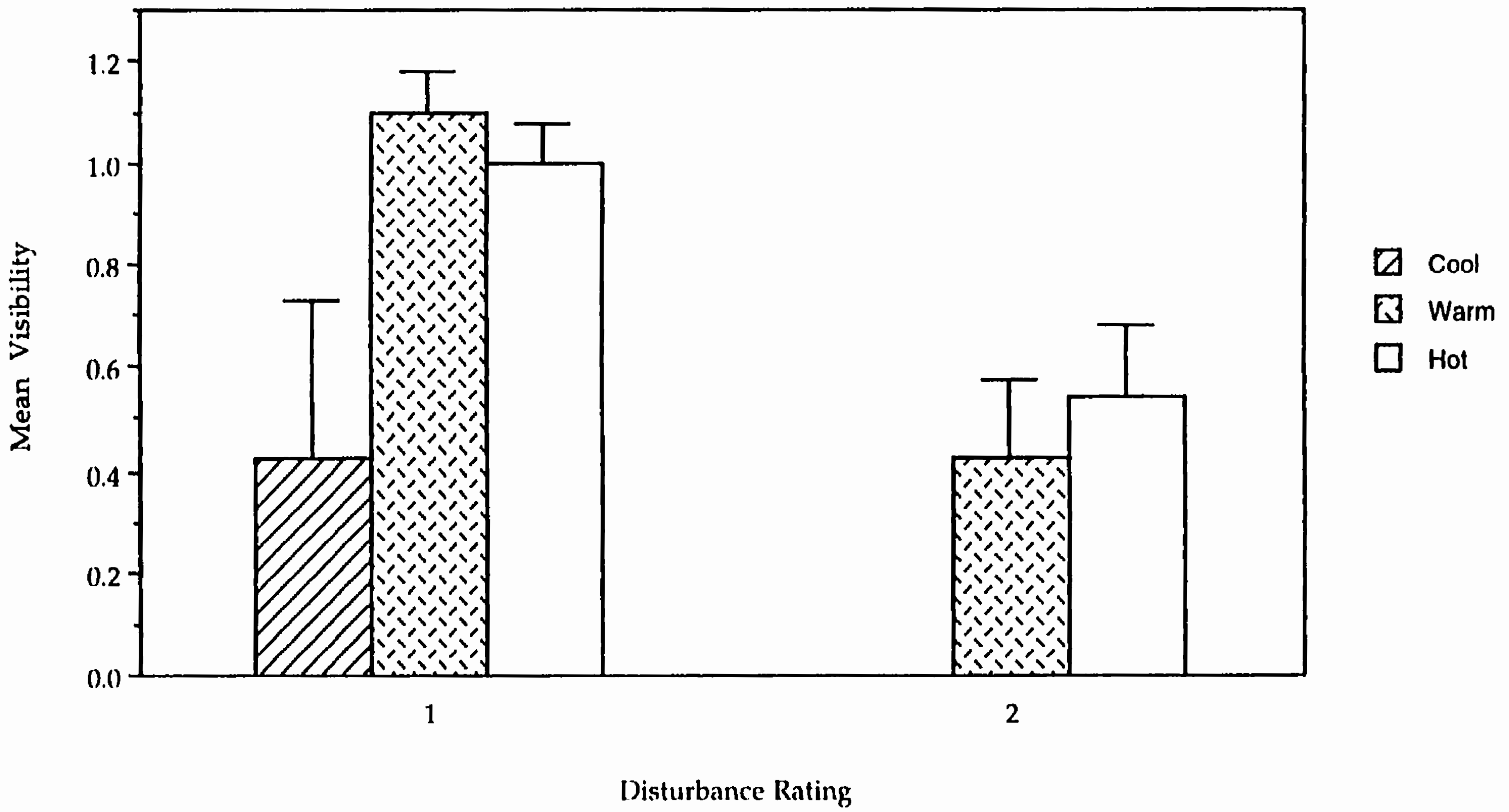

Figure 5: Mean visibility (± standard error) of gravid female Eastern Massasauga Rattlesnakes by substrate temperature and disturbance rating.

($F_{1,4}=1.10$, $p>0.35$) for locations with a disturbance rating of 2 (Figure 5).

Distance to Retreat Sites

I used ANOVA to determine whether human disturbance affected the distance at which snakes were found from retreat sites, with group (gravid female, non-gravid female or male) and disturbance rating (1,2 or 3) as treatments and the average distance from retreat site as the response variable.

The initial analysis violated F-test assumptions, so the response variable was ln-transformed and the ANOVA repeated. In the following analysis, the interaction term was not significant ($p>0.17$) so it eliminated. The resulting model was also not significant ($F_{4,43}=1.92$, $p>0.12$). Thus, neither sex, reproductive condition, nor level of human disturbance affected the distance at which Eastern Massasauga Rattlesnakes were found from retreat sites.

Habitat Structure

The habitat structure of snake-selected and randomly-chosen locations differed significantly (Wilk's $\lambda=0.0058$, $F_{48,60}=5.84$, $p<0.0001$). Males ($F_{16,20}=6.83$, $p<0.001$), non-gravid females ($F_{16,20}=5.95$, $p<0.001$)

and gravid females ($F_{16,20}$=25.33, p<0.001) all used habitat that differed significantly from that of random sites. Male ($F_{16,20}$=11.95, p<0.001) and non-gravid female ($F_{16,20}$=13.54,p<0.001) habitat use differed significantly from that of gravid females, but not from each other ($F_{16,20}$=0.68, p>0.78). Average values of habitat variables for gravid females, non-gravid females, males and random locations are summarized in Table 4.

Discriminant function analysis of snake-selected and random locations produced two significant ($F_{30,42}$=2.51, p<0.004) discriminant functions that together explained > 98% of group differences. A third discriminant function was not significant ($F_{14,22}$=0.72, p>0.73). DFA results are illustrated in Figure 6.

Total structure coefficients for both significant discriminant functions are listed in Table 5. The largest three coefficients of the first discriminant function include DNR (0.683), COVER (0.677) and LEAF (0.655). I interpreted this function to represent a gradient from rocky locations with open canopy and little leaf cover to those locations with fewer rocks, denser canopy cover, and more fallen leaves. Similarly, the largest three coefficients of the second discriminant function include VEG (-0.718), DNOV (-0.631) and LEAF (0.591). I interpreted this function to

Table 4: Mean values (± standard deviation) of habitat variables for snake-selected and randomly-chosen locations. See Table 1 and text for definition of habitat variables.

Variable	Gravid Females	Non-Gravid Females	Males	Random
ROCK (%)	24.2 ± 12.9	6.4 ± 6.1	5.6 ± 5.4	4.0 ± 3.6
LEAF (%)	10.3 ± 5.7	19.0 ± 14.5	11.9 ± 6.9	50.3 ± 7.0
VEG (%)	64.5 ± 17.8	72.0 ± 15.1	80.0 ± 8.8	43.2 ± 4.9
LOG (%)	0.6 ± 1.6	1.8 ± 1.5	0.9 ± 1.4	1.1 ± 0.9
WSD (#)	28.5 ± 20.1	11.6 ± 11.1	14.4 ± 8.7	11.2 ± 3.0
WSH (m)	0.6 ± 0.5	1.5 ± 0.8	1.8 ± 1.0	1.1 ± 0.4
DNUN (m)	5.3 ± 2.5	3.1 ± 1.8	4.0 ± 4.6	2.0 ± 0.4
DNOV (m)	4.2 ± 1.6	6.5 ± 3.8	6.1 ± 3.7	2.4 ± 0.4
DNR (m)	1.8 ± 1.3	4.8 ± 3.6	6.0 ± 4.3	6.7 ± 1.0
MLR (m)	1.2 ± 0.9	0.6 ± 0.3	0.6 ± 0.2	0.5 ± 0.1
DNS (m)	1.9 ± 0.7	1.4 ± 1.3	1.6 ± 1.8	1.3 ± 0.3
DNL (m)	10.5 ± 4.5	7.2 ± 3.0	6.7 ± 3.3	4.9 ± 0.7
WNL (cm)	19.4 ± 4.7	14.3 ± 2.1	15.1 ± 3.2	15.0 ± 0.9
DBHOV (cm)	21.1 ± 2.9	18.7 ± 6.1	18.2 ± 6.4	20.8 ± 1.6
DBHUN (cm)	2.8 ± 0.6	2.7 ± 0.5	2.4 ± 0.7	3.0 ± 0.0
COVER (%)	23.5 ± 16.5	39.0 ± 20.4	36.0 ± 22.3	88.5 ± 3.2

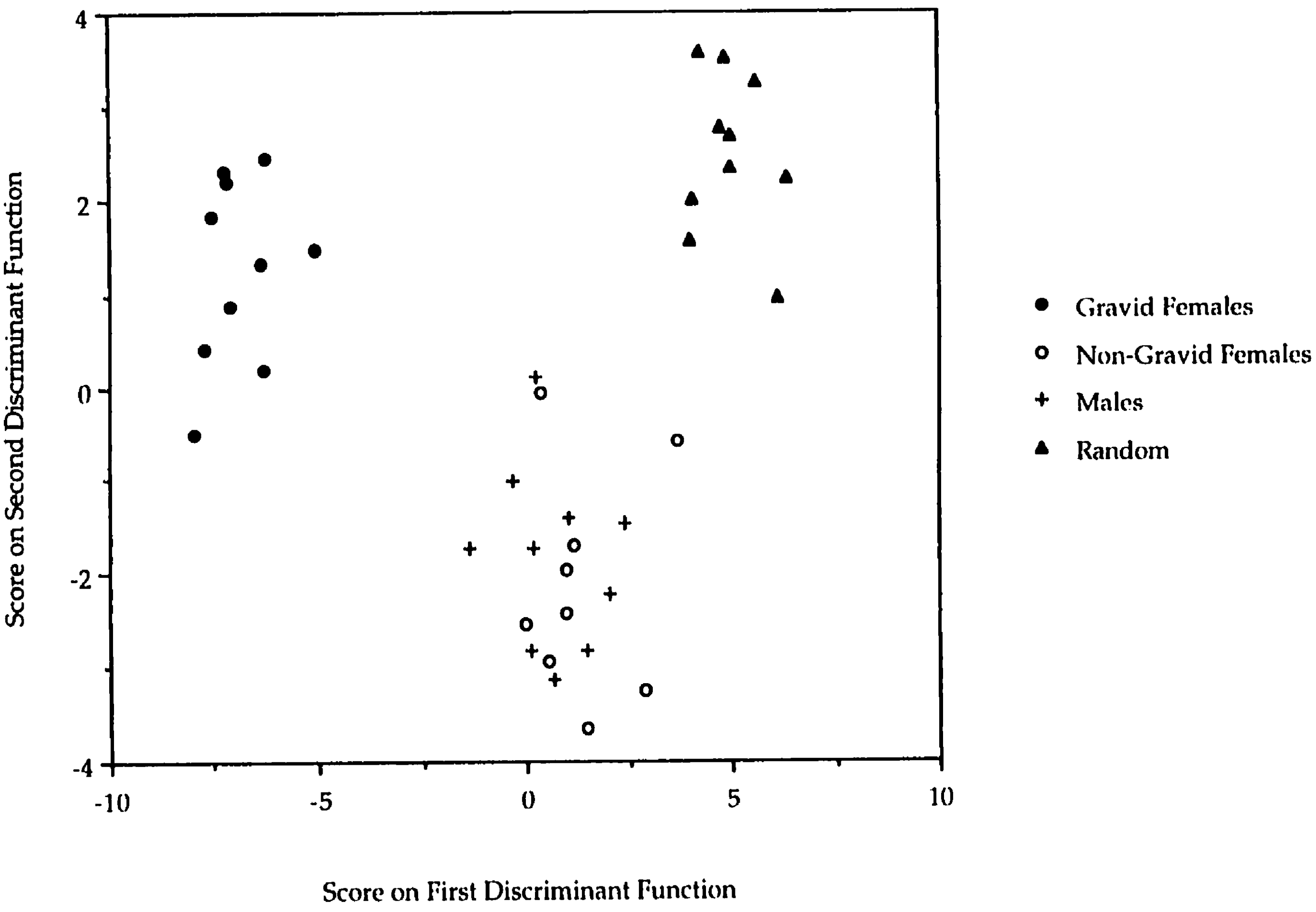

Figure 6: Discriminant function scores of randomly-chosen locations and gravid female, non-gravid female, and male Eastern Massasauga Rattlesnakes.

Table 5: Correlations (r) between the original variables and the discriminant functions separating habitat structure of snake-selected and randomly-chosen locations. Variables are defined in Table 1.

Variable	Correlation With Discriminant Function	
	Function 1	Function 2
ROCK	-0.637	0.212
LEAF	0.655	0.591
VEG	-0.254	-0.718
LOG	0.342	-0.105
WSD	-0.480	0.192
WSH	0.410	-0.487
DNUN	-0.523	-0.021
DNOV	-0.194	-0.631
DNR	0.683	-0.031
MLR	-0.557	0.154
DNS	-0.254	0.123
DNL	-0.552	-0.052
WNL	-0.499	0.312
DBHOV	-0.086	0.363
DBHUN	-0.059	0.562
COVER	0.677	0.511

represent a gradient from heavily vegetated locations with few overstory trees and little leaf cover to less vegetated locations with more overstory trees and increased leaf cover.

The first discriminant function separated three groups. Gravid females were found close to rocks, in open areas with little leaf cover. Non-gravid females and males occupied areas further from rocks, with denser canopy cover and more fallen leaves, while random locations were furthest from rocks, and had the densest canopy cover and the most leaves (Table 4). The second discriminant function separated random locations from those selected by non-gravid females and males. Areas used by these snakes were more heavily vegetated, further from overstory trees and had less leaf cover than random locations (Table 4).

The habitat use of male and non-gravid female snakes differed significantly between locations with disturbance ratings (dr) of 1, 2 or 3 (Wilk's $\lambda=0.0406$, $F_{32,18}=5.84$, $p<0.04$). Habitat use in locations with a dr of 3 differed significantly from habitat use in locations with a dr of 1 ($F_{16,9}=3.67, p<0.03$) but not two ($F_{16,9}=2.21, p>0.11$). Habitat use in locations with a dr of 1 did not differ significantly from habitat use in locations with a dr of 2 ($F_{16,9}=1.47, p>0.28$). Average values of habitat variables for male and non-gravid female locations with disturbance ratings of 1, 2 or 3 are summarized in Table 6.

DFA of snake-selected locations with disturbance ratings of 1, 2 or 3 produced two discriminant functions but only the first was significant ($F_{32,18}$=2.23, p<0.04). This function explained 74% of group differences. Total structure coefficients for this function are listed in Table 7. The three largest coefficients include DNL (-0.522), DNUN (0.513) and DBHOV (0.510). I interpreted this function as a gradient from early successional forest with few logs, many understory trees, and small overstory trees to mature forest with more logs, fewer understory trees and larger overstory trees. In disturbed areas, the structure of snake habitat reflected that of early successional forest. The less disturbed the area, the more the structure of snake habitat reflected that of mature forest (Figure 7).

Significant differences (Wilk's λ=0.367, $F_{32,102}$=2.08, p<0.004) in habitat structure were also found between randomly-chosen locations with disturbance ratings of 1, 2 or 3. The habitat structure of locations with a dr of 3 differed significantly from that of locations with a dr of 1 ($F_{16,51}$=3.67,p<0.001) and 2 ($F_{16,51}$=1.94,p<0.04). Habitat structure in locations with a dr of 1 did not differ significantly from that of locations with a dr of 2 ($F_{16,51}$=1.21,p>0.29). Average values of habitat variables for

Table 6: Mean values (± standard deviation) of habitat variables for snake-selected locations with disturbance ratings (dr) of 1, 2, or 3. See Table 1 and text for definition of habitat variables.

Variable	dr=1	dr=2	dr=3
ROCK (%)	5.3 ± 5.3	7.4 ± 11.3	8.9 ± 9.6
LEAF(%)	14.4 ± 12.6	20.1 ± 8.2	6.0 ± 5.4
VEG (%)	77.5 ± 15.9	69.0 ± 15.0	83.1 ± 13.8
LOG (%)	1.7 ± 2.0	0.3 ± 0.5	1.1 ± 1.6
WSD (#)	21.2 ± 21.8	12.3 ± 6.9	10.7 ± 8.9
WSH (m)	1.6 ± 0.9	3.8 ± 3.4	1.4 ± 0.4
DNUN (m)	4.1 ± 4.0	2.3 ± 1.4	1.5 ± 0.5
DNOV (m)	5.5 ± 3.8	3.5 ± 1.1	6.2 ± 3.1
DNR (m)	5.6 ± 4.0	3.4 ± 2.0	3.0 ± 2.0
MLR (m)	0.7 ± 0.2	0.7 ± 0.4	0.5 ± 0.4
DNS (m)	1.5 ± 1.6	0.9 ± 0.2	0.8 ± 0.3
DNL (m)	6.0 ± 2.7	7.3 ± 0.7	10.0 ± 4.2
WNL (m)	14.5 ± 2.0	14.9 ± 3.0	15.4 ± 5.1
DBHOV (cm)	20.2 ± 5.6	18.4 ± 4.1	14.7 ± 6.7
DBHUN (cm)	2.6 ± 0.9	3.1 ± 0.9	2.7 ± 0.5
COVER (%)	39.9 ± 21.0	61.3 ± 15.9	36.9 ± 17.3

Table 7: Correlations (r) between the original variables and the discriminant function separating snake-selected locations with disturbance ratings of 1, 2 or 3. Variables are defined in Table 1.

Variable	Correlation With Discriminant Function
ROCK	-0.148
LEAF	0.386
VEG	-0.209
LOG	0.136
WSD	0.265
WSH	0.047
DNUN	0.513
DNOV	-0.156
DNR	0.307
MLR	0.225
DNS	0.276
DNL	-0.522
WNL	-0.031
DBHOV	0.510
DBHUN	0.077
COVER	0.066

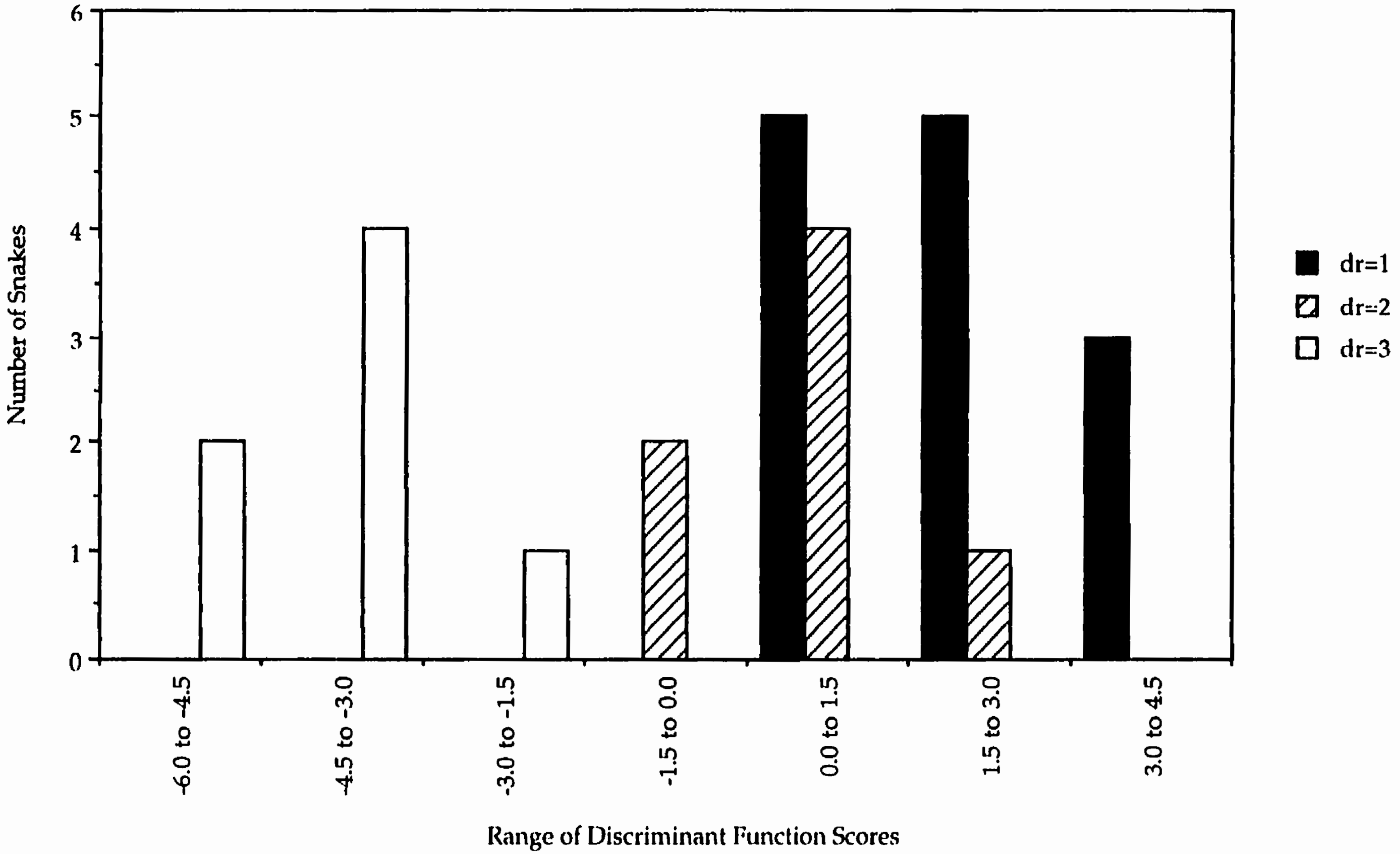

Figure 7: Distribution of scores of the discriminant function separating the habitat structure of locations used by non-gravid female and male Eastern Massasauga Rattlesnakes with disturbance ratings (dr) of 1, 2 or 3.

randomly-chosen locations with different disturbance ratings are summarized in Table 8.

DFA of random locations with disturbance ratings of 1, 2 or 3 produced two discriminant functions, but only the first was significant ($F_{32,102}=2.08$, $p<0.004$). This function explained approximately 82% of group differences. Total structure coefficients for this function are listed in Table 9. The three largest coefficients include DNL (-0.783), DNS (-0.612) and WSD (0.536). I interpreted this function as a gradient of general cover, from locations with few logs, shrubs and other woody stems to locations with more logs, shrubs and woody stems. Areas that receive heavy human disturbance (dr=3) have fewer logs, shrubs and other woody stems than areas exposed to intermediate (dr=2) or low (dr=1) levels of disturbance (Figure 8).

Finally, the habitat structure of Sites A and B differed significantly (Wilk's $\lambda=0.820$, $F_{16,174}=2.08$, $p<0.004$). Average values of habitat variables for both sites are summarized in Table 10. The total structure coefficients of the sole discriminant function are listed in Table 11. The three largest coefficients include DNUN (-0.463), DNR (-0.441) and DNS (-0.422). Thus, locations in Site A are rockier and have more understory trees and shrubs than those in Site B (Figure 9).

Table 8: Mean values (± standard deviation) of habitat variables for randomly-chosen locations with disturbance ratings (dr) of 1, 2, or 3. See Table 1 and text for definition of habitat variables.

Variable	dr=1	dr=2	dr=3
ROCK (%)	2.7 ± 9.6	10.6 ± 27.2	8.3 ± 22.8
LEAF(%)	54.2 ± 26.0	44.8 ± 33.7	37.1 ± 39.5
VEG (%)	40.6 ± 27.8	41.8 ± 29.9	29.6 ± 37.1
LOG (%)	2.6 ± 6.2	0.9 ± 3.2	0.7 ± 3.1
WSD (#)	13.9 ± 14.5	7.3 ± 6.2	5.3 ± 9.4
WSH (m)	0.8 ± 0.5	1.0 ± 1.3	1.7 ± 5.3
DNUN (m)	2.5 ± 2.9	2.1 ± 1.7	3.1 ± 2.1
DNOV (m)	2.1 ± 1.1	2.8 ± 2.4	3.9 ± 2.9
DNR (m)	7.8 ± 6.5	5.2 ± 3.4	6.1 ± 3.6
MLR (m)	0.5 ± 0.2	0.5 ± 0.2	0.4 ± 0.2
DNS (m)	1.1 ± 1.2	1.4 ± 1.7	3.2 ± 2.5
DNL (m)	3.3 ± 2.3	6.8 ± 4.7	11.1 ± 5.6
WNL (m)	15.2 ± 6.8	14.3 ± 4.7	15.7 ± 5.6
DBHOV (cm)	22.5 ± 8.2	19.8 ± 9.0	20.4 ± 7.6
DBHUN (cm)	3.1 ± 1.3	2.8 ± 1.1	2.9 ± 1.1
COVER (%)	91.1 ± 17.2	78.6 ± 35.9	76.4 ± 32.9

Table 9: Correlations (r) between the original variables and the discriminant function separating randomly-chosen locations with disturbance ratings of 1, 2 or 3. Variables are defined in Table 1.

Variable	Correlation With Discriminant Function
ROCK	-0.134
LEAF	0.291
VEG	0.298
LOG	0.278
WSD	0.536
WSH	0.180
DNUN	-0.263
DNOV	-0.403
DNR	0.029
MLR	0.307
DNS	-0.612
DNL	-0.783
WNL	-0.117
DBHOV	0.121
DBHUN	0.068
COVER	0.310

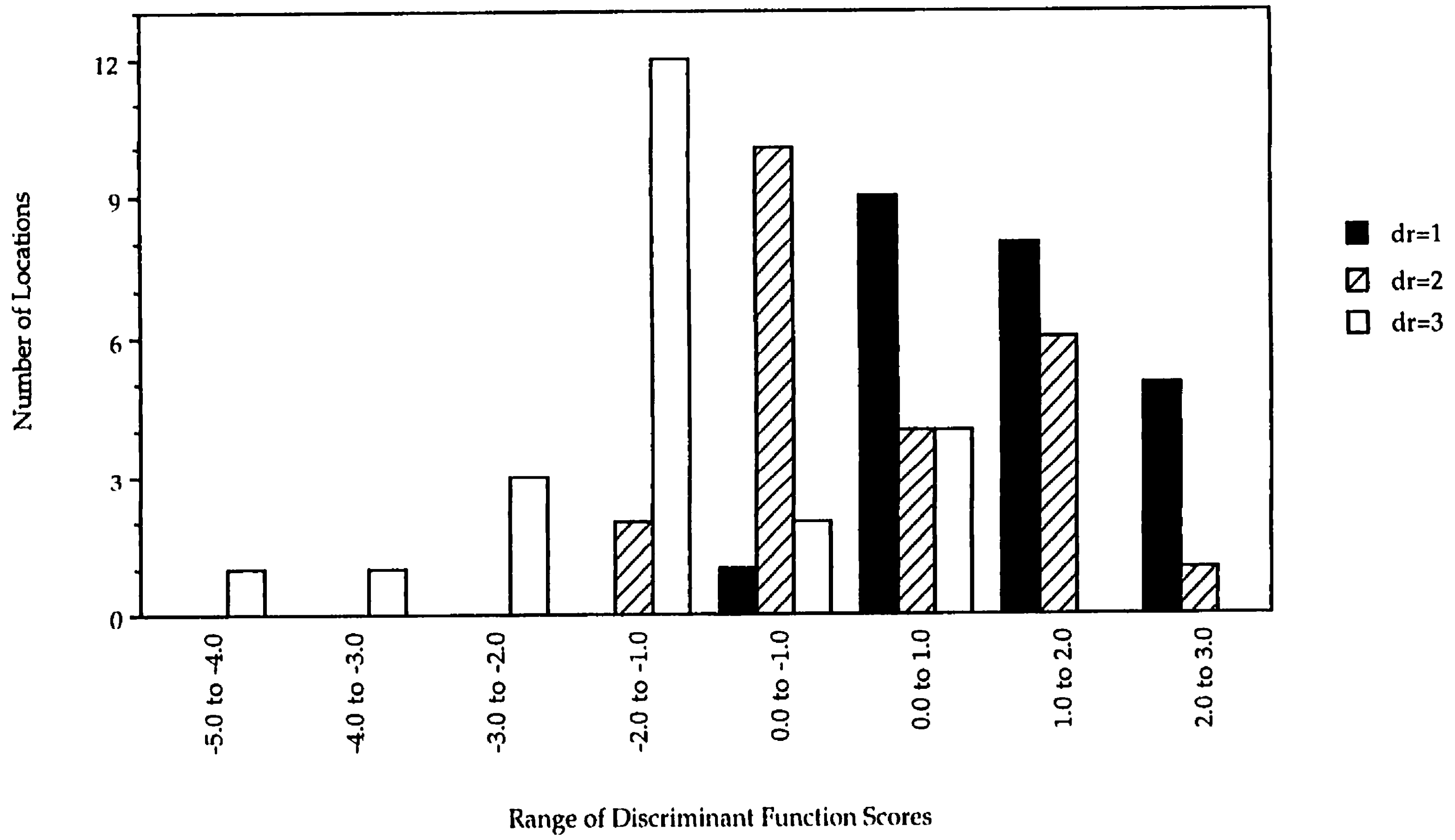

Figure 8: Distribution of scores of the discriminant function separating the habitat structure of random locations with disturbance ratings (dr) of 1, 2 or 3.

Table 10: Mean values (± standard deviation) of habitat variables for Sites A and B in Killbear Provincial Park. See Table 1 and text for definition of habitat variables.

Variable	Site A	Site B
ROCK (%)	4.5 ± 16.7	3.1 ± 12.7
LEAF (%)	51.9 ± 28.9	48.5 ± 30.5
VEG (%)	41.6 ± 27.9	44.7 ± 28.4
LOG (%)	1.1 ± 3.8	1.1 ± 3.9
WSD (#)	10.8 ± 9.3	11.3 ± 11.9
WSH (m)	1.0 ± 1.6	1.2 ± 2.2
DNUN(m)	1.6 ± 1.2	2.4 ± 2.1
DNOV (m)	2.4 ± 2.2	2.4 ± 1.7
DNR (m)	7.4 ± 5.0	5.9 ± 4.5
MLR (m)	0.5 ± 0.3	0.5 ± 0.3
DNS (m)	1.0 ± 1.1	1.5 ± 1.6
DNL (m)	4.6 ± 3.3	5.2 ± 4.0
WNL (cm)	15.8 ± 6.8	14.5 ± 4.1
DBHOV(cm)	21.3 ± 7.5	20.7 ± 6.9
DBHUN (cm)	3.1 ± 1.2	3.1 ± 1.4
COVER (%)	90.0 ± 25.8	87.3 ± 25.9

Table 11: Correlations (r) between the original variables and the discriminant function separating randomly-chosen locations from Sites A and B. Variables are defined in Table 1.

Variable	Correlation With Discriminant Function
ROCK	0.067
LEAF	0.158
VEG	-0.130
LOG	0.000
WSD	0.025
WSH	0.002
DNUN	-0.463
DNOV	-0.047
DNR	0.441
MLR	0.269
DNS	-0.422
DNL	-0.119
WNL	0.162
DBHOV	0.108
DBHUN	-0.004
COVER	0.161

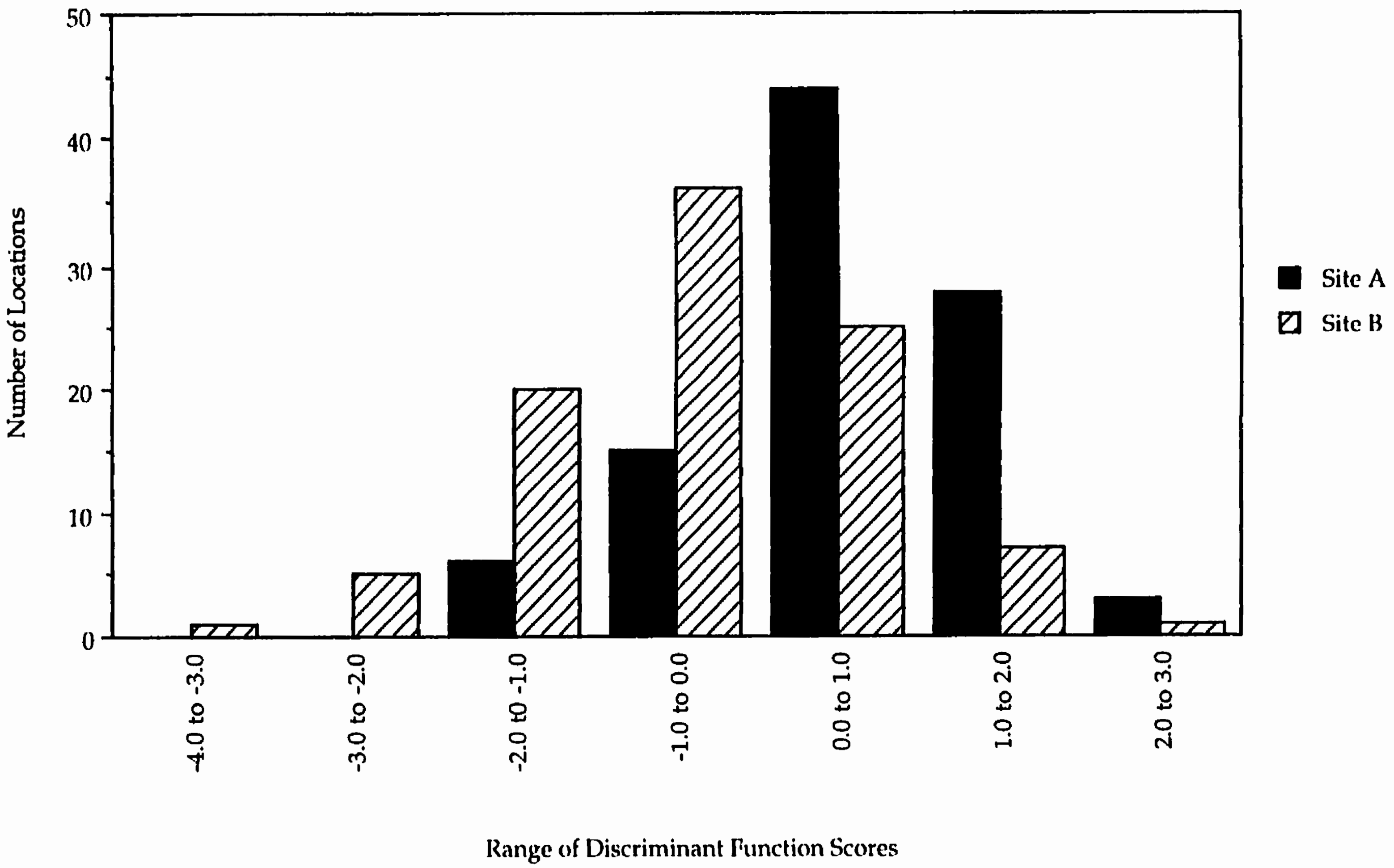

Figure 9: Distribution of scores of the discriminant function separating the habitat structure of random locations from Sites A and B.

MANOVA and DFA results were similar when snake-selected and randomly-chosen habitats were compared using individual locations as the unit of replication. Once again, habitat structure differed significantly (Wilk's λ=0.1632, $F_{48,658}$=11.51, $p<0.001$). The habitat used by males ($F_{16,221}$=13.66, $p<0.001$), non-gravid females ($F_{16,221}$=12.75, $p<0.001$) and gravid females ($F_{16,221}$=26.41, $p<0.001$) differed significantly from that of random locations. Male ($F_{16,221}$=11.29, $p<0.001$) and non-gravid female ($F_{16,221}$=14.79,$p<0.001$) habitat use differed significantly from that of gravid females, and from each other ($F_{16,221}$=1.82, $p<0.04$).

When individual locations were used to compare the habitat of snake-selected and randomly-chosen locations, DFA produced three significant ($F_{14,223}$=1.78, $p<0.05$) discriminant functions. Total structure coefficients for these discriminant functions are listed in Table 12. While not identical, these coefficients define similar gradients as the DFA using average values of habitat variables (cf. Table 5). For example, the largest five coefficients from the first discriminant function in both analyses are associated with the same five habitat variables. Therefore, reduced sample size as a consequence of using averaged values did not greatly affect the stability of DFA total structure coefficients.

Table 12: Correlations (r) between the original variables and the discriminant functions separating habitat structure of snake-selected and randomly-chosen locations. Variables are defined in Table 1.

Variable	Correlation With Discriminant Function		
	Function 1	Function 2	Function 3
ROCK	0.547	0.282	0.147
LEAF	-0.555	0.336	0.193
VEG	0.380	-0.561	-0.296
LOG	0.024	-0.089	0.462
WSD	0.333	0.208	-0.230
WSH	-0.163	-0.574	-0.055
DNUN	0.431	0.192	0.444
DNOV	0.230	-0.429	0.237
DNR	-0.462	-0.040	-0.333
MLR	0.470	0.216	0.185
DNS	0.077	0.177	0.228
DNL	0.338	0.156	-0.024
WNL	0.382	0.355	0.079
DBHOV	0.031	0.272	0.045
DBHUN	0.023	0.363	0.342
COVER	-0.742	0.388	0.017

No analysis of habitat structure met the assumptions of MANOVA and DFA. Analyses incorporating a mixture of arcsine, square root and log-transformed data most closely met the assumption of normality, but at best, only 11 of the 16 habitat variables were normally distributed. The assumption of equal covariance matrices was also violated. When individual locations were used as the unit of replication, the covariance matrices of snake-selected and randomly-chosen habitats differed significantly ($M=1345.56, F_{408,118343}=2.90, p<0.01$). The covariance matrices of random locations with disturbance ratings of 1, 2 or 3 were also significantly different ($M=634.97, F_{272,11428}=1.50, p<0.01$), as were those of Sites A and B ($M=239.97, F_{136,110285}=1.61, p<0.01$). I could not conduct Box's test for remaining analyses due to covariance matrix singularities.

Spatial Movement Patterns

I used ANCOVA to assess the effects of disturbance on snake movements with group (gravid female, non-gravid female or male) as the main effect, average disturbance rating as the covariate, and average distance moved per day as the response variable. The interaction effect was removed from the initial model because it was not significant

($p>0.44$). The subsequent model was significant ($F_{3,19}=12.74$, $p<0.002$) as were the effects of group ($p<0.0001$) and average disturbance rating ($p<0.008$). Therefore, the average distance moved per day differed significantly between gravid females, non-gravid females, and males, but all snakes moved less with increasing exposure to human disturbance (Figures 10 and 11).

To determine whether the significant group effect was due to the influence of gravid females, I repeated the ANCOVA using only data from males and non-gravid females. The interaction effect was not significant ($p>0.74$) so it was removed from the initial model. The subsequent model was significant ($F_{2,12}=6.03$, $p<0.02$), as was the effect of average disturbance rating ($p<0.02$). However, in contrast to the model that included gravid females, the effect of group was not significant ($p>0.12$). Thus, gravid females moved significantly less per day than did males and non-gravid females (Figure 12).

Persistence

I used ANCOVA to examine the effects of human disturbance on persistence, with group (gravid female, non-gravid female or male) as the main effect, average disturbance rating as the covariate, and the average

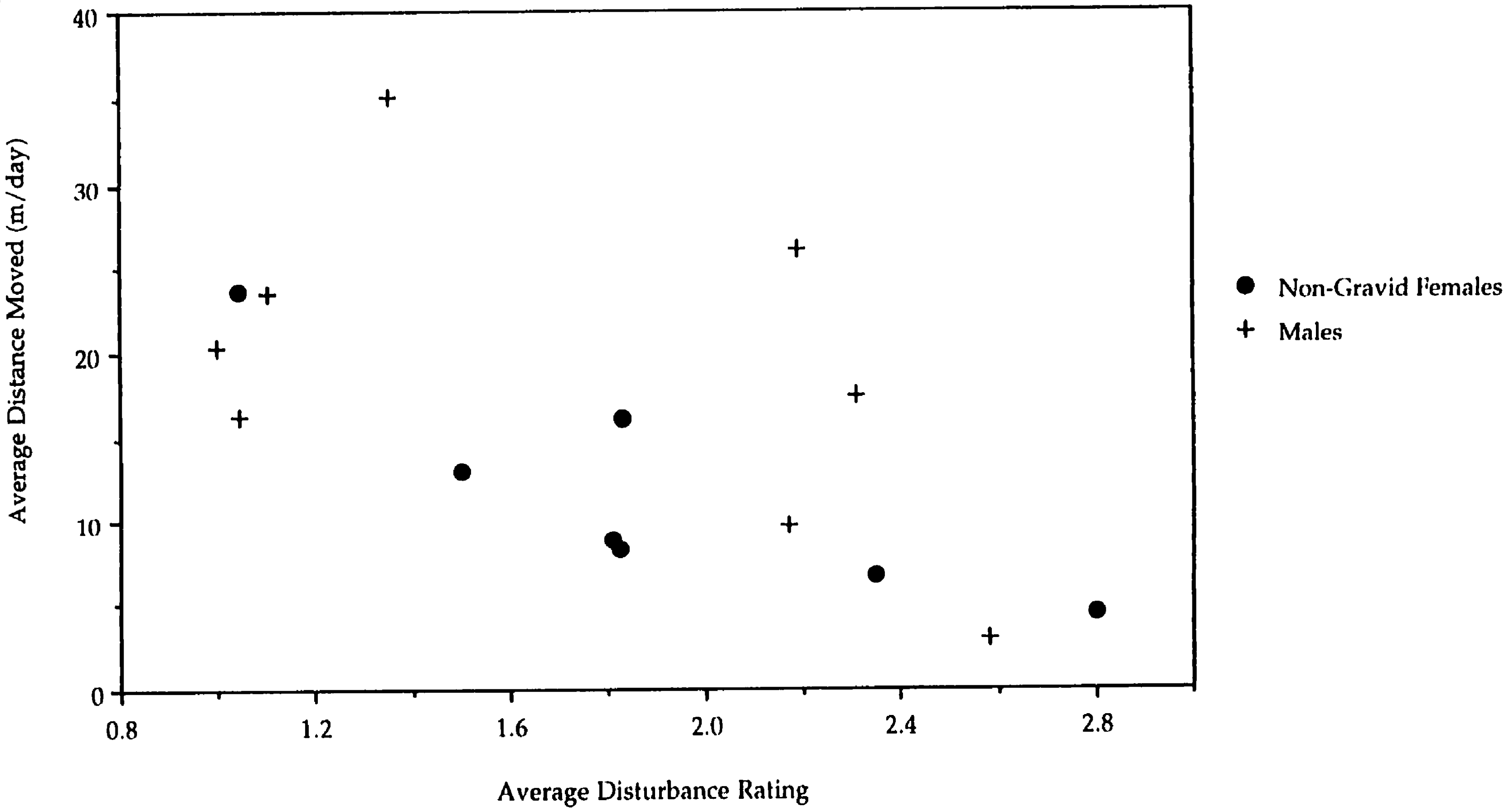

Figure 10: Mean distance moved (m/day) by male and non-gravid female Eastern Massasauga Rattlesnakes exposed to varying levels of human disturbance.

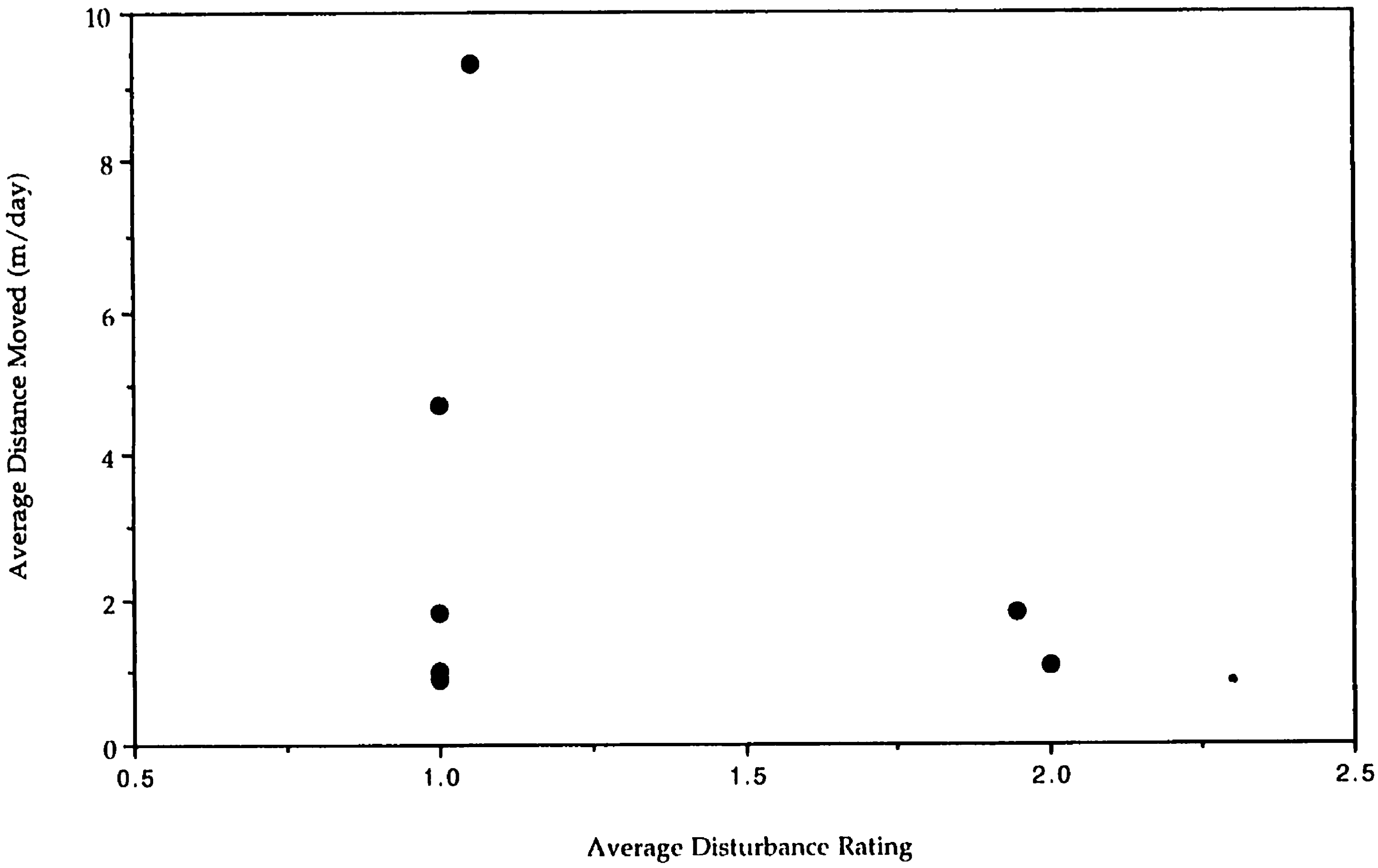

Figure 11: Mean distance moved (m/day) by gravid female Eastern Massasauga Rattlesnakes exposed to varying levels of human disturbance.

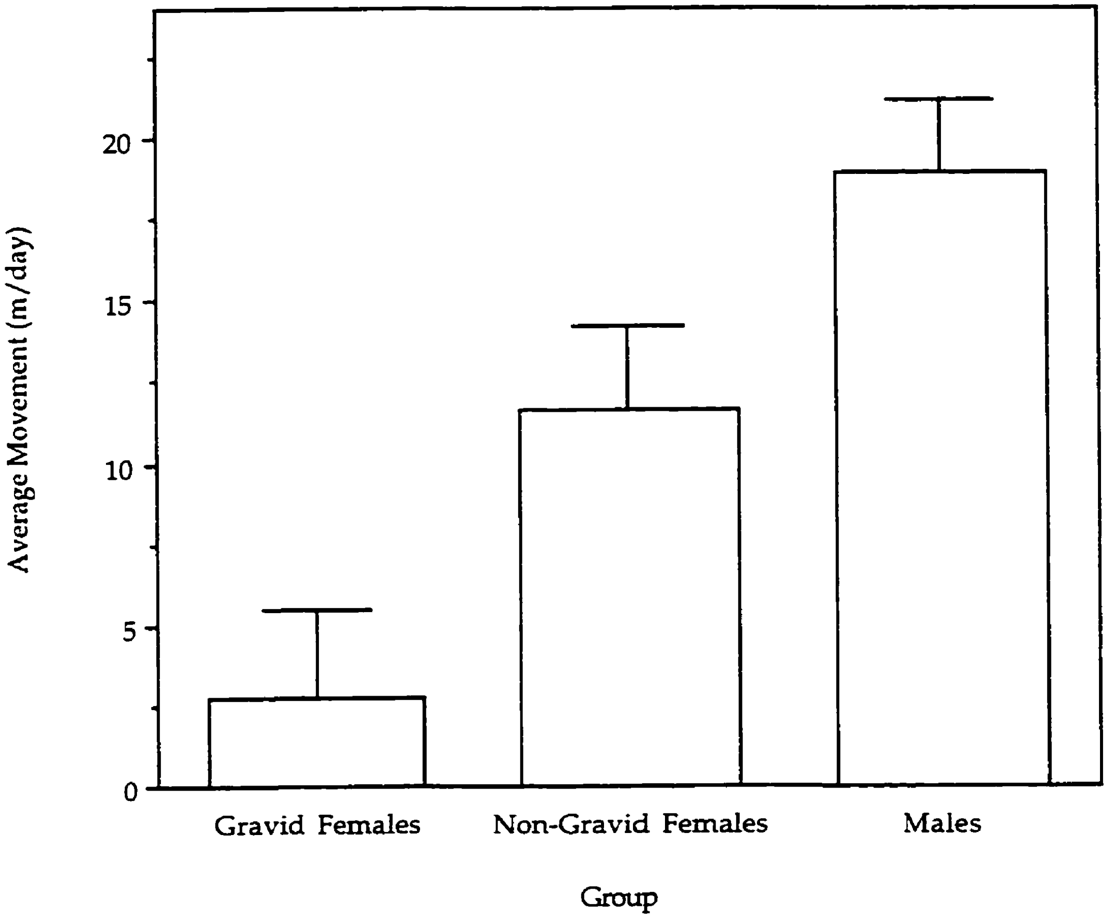

Figure 12: Mean daily movements (± standard error) of Eastern Massasauga Rattlesnakes in Killbear Provincial Park.

time between moves of > 10 m as the response variable. Initial models did not meet F-test assumptions so I transformed the response variable by taking the square root of its values. In the first model using transformed data, the interaction term was eliminated because it was not significant ($p>0.63$). The subsequent model was significant ($F_{3,25}=6.35$, $p<0.003$). However, although the effect of group was significant ($p<0.001$), the average disturbance rating effect was not ($p>0.51$). Therefore, the average period between movements of > 10 m differed significantly between gravid females, non-gravid females, and males, but did not vary with levels of human disturbance.

To examine the effect of group on average persistence I repeated the analysis without the effect of average disturbance rating in the model. This ANOVA was significant ($F_{2,26}=9.51$, $p<0.001$). A Tukey-Kramer HSD test revealed that the average persistence of males and non-gravid females did not differ significantly, but that gravid females moved significantly less frequently than snakes in either of the other groups (Figure 13).

Condition

For males and non-gravid females, the initial regression of mass on snout-vent length violated F-test assumptions, so the response variable

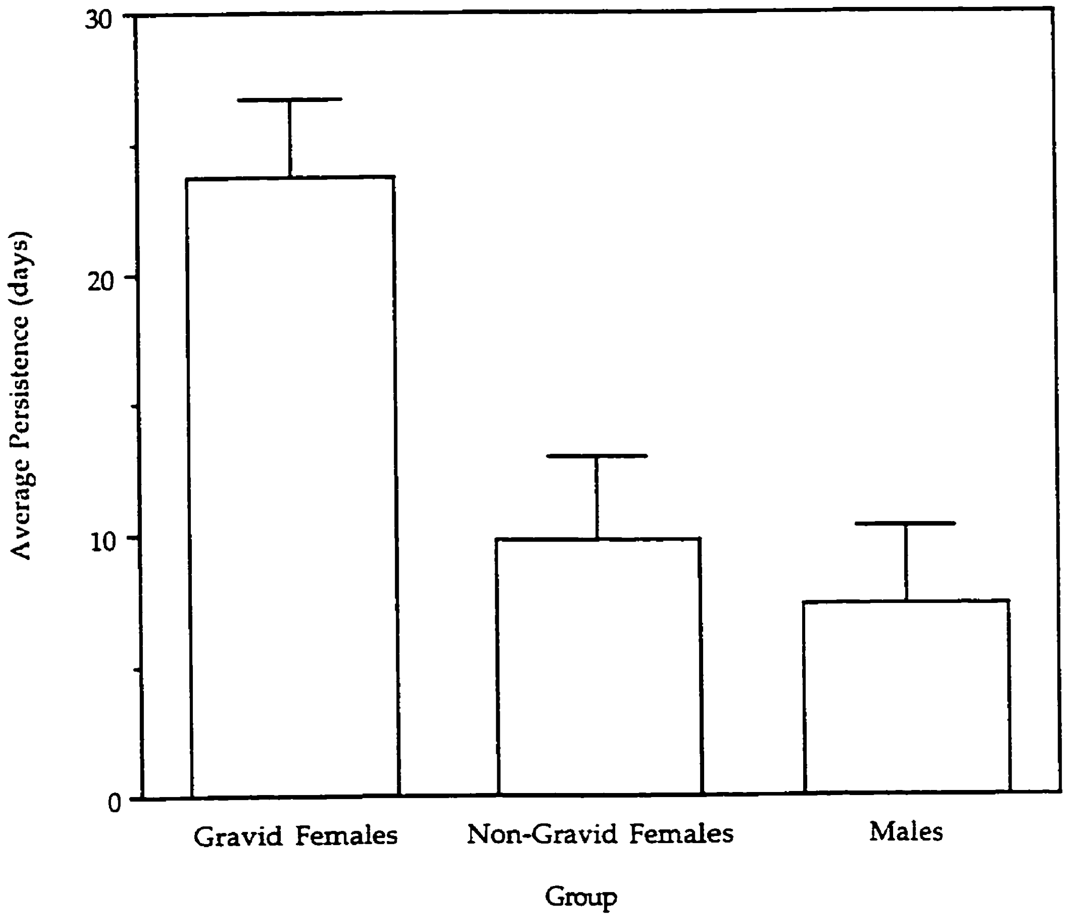

Figure 13: Mean persistence (± standard error) of Eastern Massasauga Rattlesnakes in Killbear Provincial Park.

was ln-transformed and the analysis repeated. The resulting model was significant (r^2=0.96, n=81, p<0.0001). The residuals of this regression (condition) were used as the response variable in a two-factor ANOVA with disturbance status (disturbed or undisturbed) and year of capture (1994, 1995 or 1996) as treatments. The interaction term was not significant (p>0.79) so it was dropped from the model and the analysis repeated. The resulting model was not significant ($F_{3,77}$=1.28, p>0.28). Thus, neither year nor exposure to human disturbance affected the condition of male and non-gravid female snakes.

Similarly, a regression of mass on snout-vent length using only gravid female snakes was highly significant (r^2=0.61, n=25, p<0.0001). The residuals of this regression were also used as the response variable in a two-factor ANOVA with disturbance status (disturbed or undisturbed) and year of capture (1995 or 1996) as treatments. The interaction term was not significant (p>0.82) so it was eliminated and the analysis repeated. The resulting model was significant ($F_{2,22}$=5.08, p<0.02). The effect of disturbance status was not significant (p>0.34) but the year effect was (p<0.005). Controlling for snout-vent length, gravid females weighed more in 1995 than in 1996 (Figure 14).

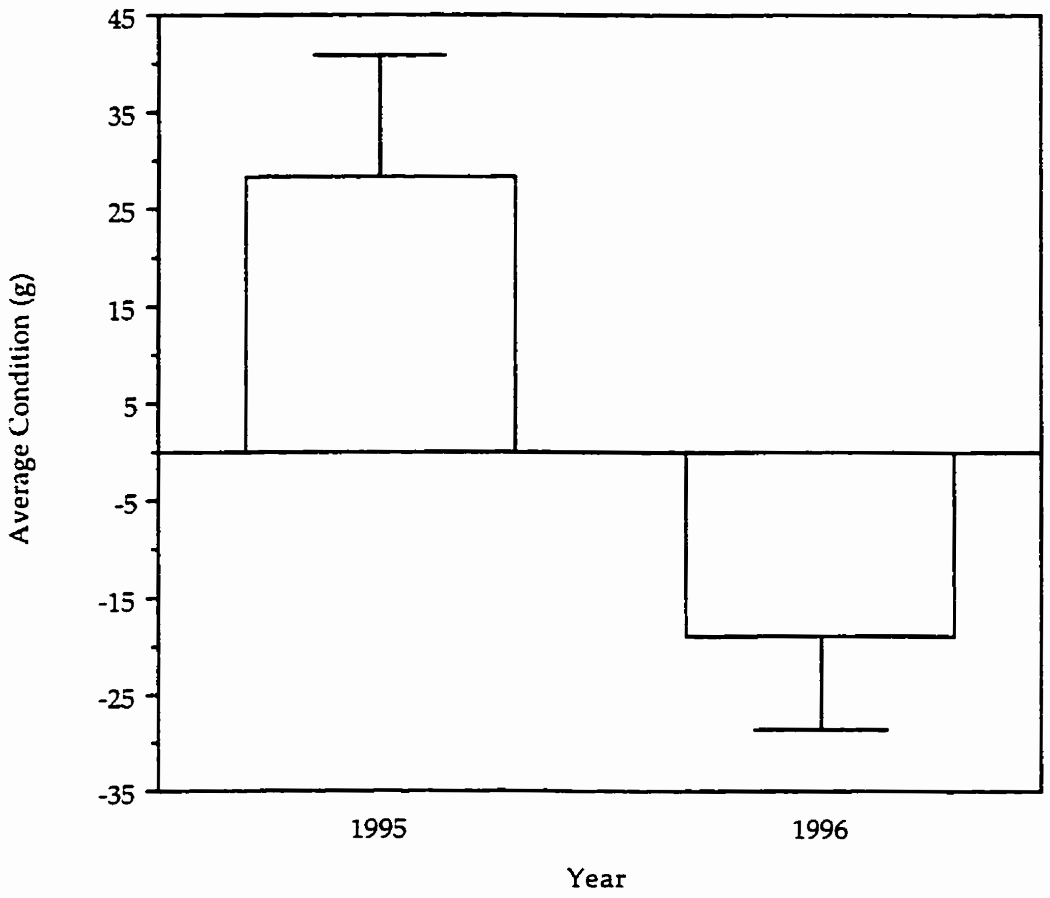

Figure 14: Mean condition (± standard error) of gravid Eastern Massasauga Rattlesnakes in Killbear Provincial Park in 1995 and 1996.

Growth Rates

For male and non-reproductive female snakes, a simple linear regression of growth rate on initial snout-vent length was significant (r^2=0.12, n=35, $p<0.04$). The residuals of this regression were used in a two-factor ANOVA with disturbance status (disturbed or undisturbed) and main growth year (1995 or 1996) as treatments. In the initial model the interaction term was not significant ($p>0.85$) so it was eliminated. The resulting model was not significant ($F_{2,32}=0.64$, $p>0.53$). Similarly, for gravid female snakes, a simple linear regression of growth rate on snout-vent length at initial capture was significant (r^2=0.46, n=16, $p<0.005$). The residuals of this regression were used in a two-factor ANOVA with disturbance status (disturbed or undisturbed) and main growth year (1994 or 1995) as treatments. The interaction term was not significant ($p>0.72$) so it was removed from the initial model. Again, the subsequent model was not significant ($F_{2,13}=2.52$, $p>0.11$). Therefore, the growth rates of Eastern Massasauga Rattlesnakes did not differ between years, and were not affected by exposure to human disturbance.

Brood Size

Brood size was positively correlated with female snout-vent length ($F_{1,19}>8.70$, $r^2=0.31$, $p<0.009$). Mean brood sizes are given in Table 13. After removing the effects of female snout-vent length, no effects of disturbance status, year, or transmitter implantation were found on residual brood size. Results of individual ANOVAs are shown in Table 14.

Offspring Snout-Vent Length

Mean within-brood offspring snout-vent lengths are given in Table 15. A multiple linear regression of female snout-vent length, mass and an interaction effect on mean within-brood offspring snout-vent length was not significant ($F_{3,19}=0.60$, $p>0.62$). The effect of human disturbance was also not significant. However, offspring born to females found in the undisturbed study site were significantly larger in 1995 than those born in 1996 (Figure 15). Transmitter implantation also affected mean within-brood offspring snout-vent length. Of females found in the undisturbed study site in 1995, individuals implanted with transmitters produced significantly larger young than those not implanted (Figure 16). Results of individual ANOVAs are shown in Table 16.

Table 13: Mean brood sizes of female Eastern Massasauga Rattlesnakes in Killbear Provincial Park in 1995 and 1996.

Year	Transmitter	Disturbance Status	Mean Brood Size	Standard Deviation	Sample Size
1995	no	undisturbed	13.7	2.1	3
1995	no	disturbed	-	-	0
1995	yes	undisturbed	14.0	3.4	4
1995	yes	disturbed	15.0	3.6	3
1996	no	undisturbed	13.8	2.9	5
1996	no	disturbed	11.5	2.4	4
1996	yes	undisturbed	-	-	0
1996	yes	disturbed	11.5	0.7	2

Table 14: Tests of effects of year (1995 vs. 1996), transmitter implantation (implanted vs. not implanted) and exposure to human disturbance (disturbed vs. undisturbed) on mean brood size of Eastern Massasauga Rattlesnakes. I examined the effect of one treatment while keeping the levels of the other two treatments constant.

Effect Tested	Value of Treatment 1 Held Constant	Value of Treatment 2 Held Constant	F-Statistic	p
Year	Undisturbed	Not Implanted	$F_{1,6}=0.348$	$p>0.57$
Year	Disturbed	Implanted	$F_{1,3}=0.573$	$p>0.50$
Transmitter Implantation	1995	Undisturbed	$F_{1,5}=0.842$	$p>0.40$
Transmitter Implantation	1996	Disturbed	$F_{1,4}=0.021$	$p>0.89$
Disturbance Status	1996	Not Implanted	$F_{1,7}=0.007$	$p>0.93$

Table 15: Mean within-brood offspring snout-vent length of Eastern Massasauga Rattlesnakes born in Killbear Provincial Park in 1995 and 1996.

Year	Transmitter	Disturbance Status	Average Within-Brood SVL	Standard Deviation	Sample Size
1995	no	undisturbed	20.4	0.67	3
1995	no	disturbed	-	-	0
1995	yes	undisturbed	17.6	1.30	3
1995	yes	disturbed	19.8	0.85	3
1996	no	undisturbed	19.3	0.63	7
1996	no	disturbed	19.0	0.40	5
1996	yes	undisturbed	20.1	-	1
1996	yes	disturbed	-	-	0

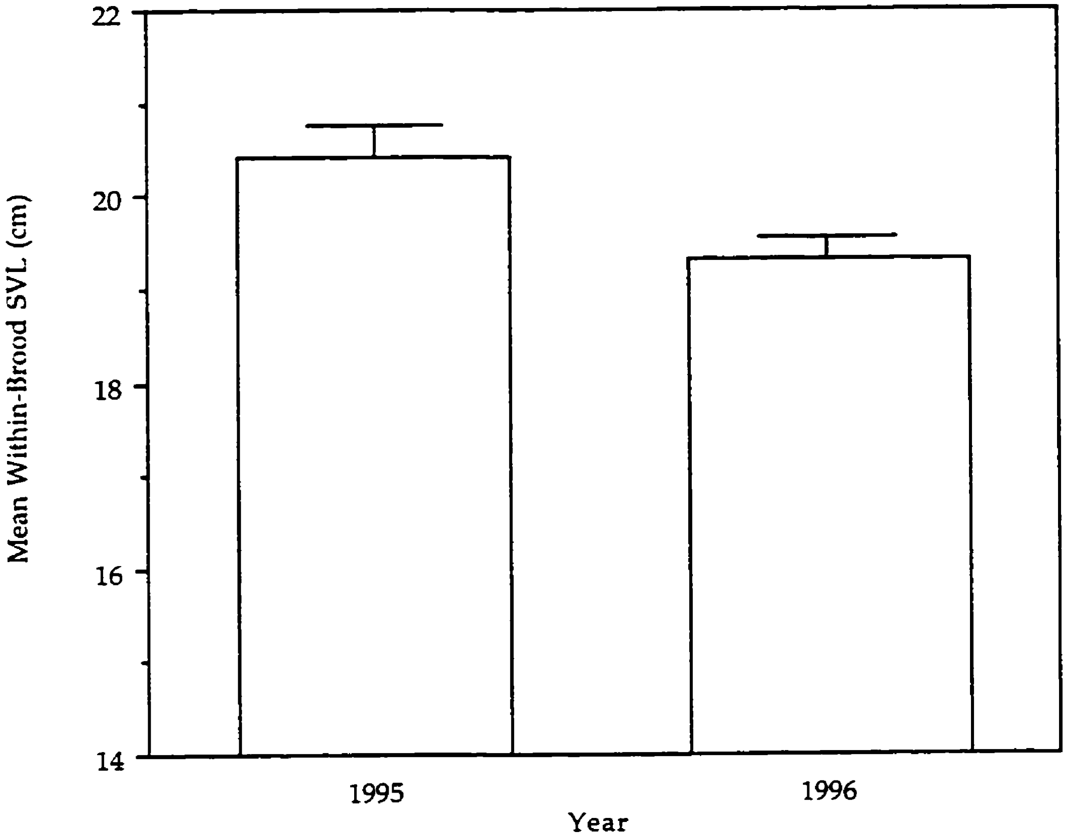

Figure 15: Mean (± standard error) within-brood offspring snout-vent length (SVL) of Eastern Massasauga Rattlesnakes not implanted with transmitters, from Site B, in 1995 and 1996.

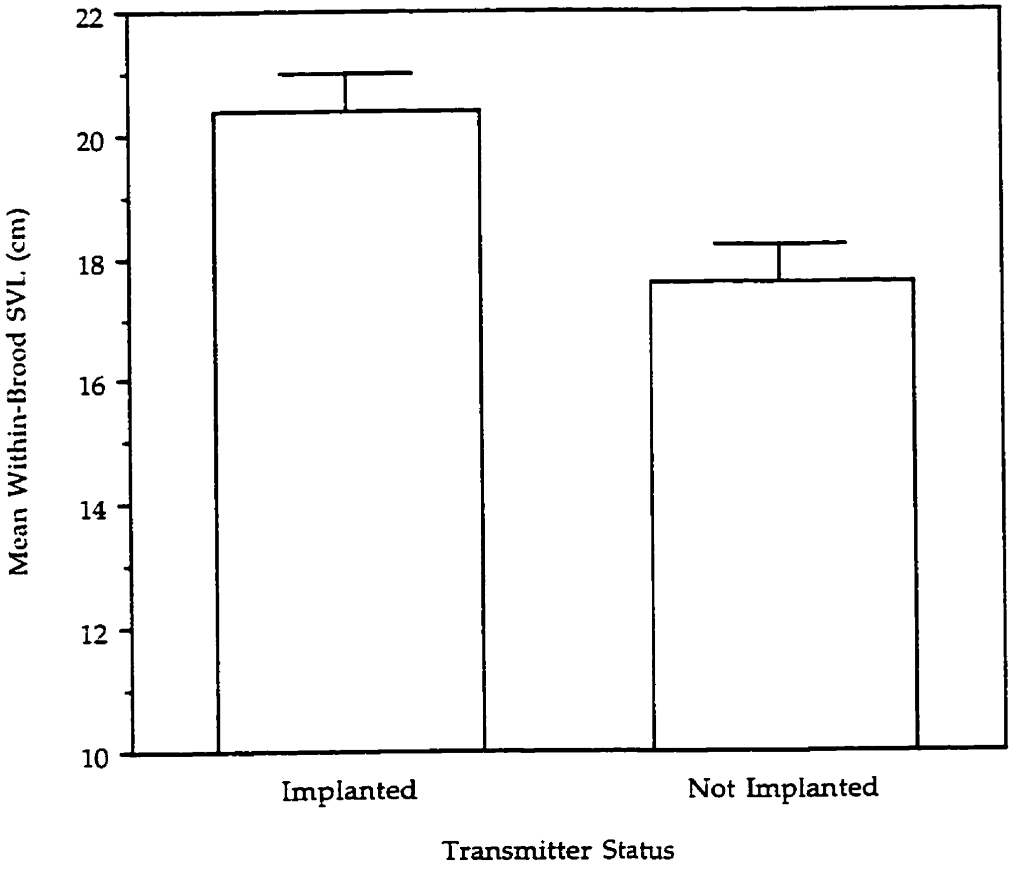

Figure 16: Mean (± standard error) within-brood offspring snout-vent length of Eastern Massasauga Rattlesnakes from Site B and gravid in 1995.

Table 16: Tests of effects of year (1995 vs. 1996), transmitter implantation (implanted vs. not implanted) and exposure to human disturbance (disturbed vs. undisturbed) on mean within-brood offspring snout-vent length of Eastern Massasauga Rattlesnakes. I examined the effect of one treatment while keeping the levels of the other two treatments constant.

Effect Tested	Value of Treatment 1 Held Constant	Value of Treatment 2 Held Constant	F-Statistic	p
Year	Undisturbed	Not Implanted	$F_{1,8}=6.33$	$p<0.04$
Transmitter Implantation	1995	Undisturbed	$F_{1,4}=11.29$	$p<0.03$
Disturbance Status	1995	Implanted	$F_{1,4}=6.20$	$p>0.06$
Disturbance Status	1996	Not Implanted	$F_{1,10}=1.33$	$p>0.27$

Offspring Mass

Mean within-brood offspring masses are given in Table 17. Again, a multiple linear regression of mean within-brood offspring mass on female snout-vent length, mass and an interaction effect was not significant ($F_{3,21}=0.58$, $p>0.63$). No significant effects of year, transmitter implantation or exposure to human disturbance were found. Results of individual ANOVAs are shown in Table 18.

Parturition Date

The regression of parturition date on female snout-vent length was significant ($r^2=0.26$, $n=18$, $p<0.03$). Parturition date was negatively correlated with snout-vent length. Thus, the larger the female, the sooner she gave birth.

I used the regression residuals in a 2x2 ANOVA to examine the effects of disturbance status (disturbed or undisturbed) and transmitter presence (implanted or not implanted) on parturition date. I eliminated the interaction term from the initial model because it was not significant ($p>0.79$). The subsequent model was not significant ($F_{2,15}=2.39$, $p>0.12$). Thus, neither transmitter implantation nor exposure to human disturbance affected parturition dates of gravid females.

Table 17: Mean within-brood offspring mass of Eastern Massasauga Rattlesnakes born in Killbear Provincial Park in 1995 and 1996.

Year	Transmitter	Disturbance Status	Average Within-Brood Mass	Standard Deviation	Sample Size
1995	no	undisturbed	11.5	1.51	3
1995	no	disturbed	-	-	0
1995	yes	undisturbed	9.80	0.57	3
1995	yes	disturbed	10.50	1.48	3
1996	no	undisturbed	10.6	0.71	7
1996	no	disturbed	10.2	0.72	5
1996	yes	undisturbed	9.20	-	1
1996	yes	disturbed	-	-	0

Table 18: Tests of effects of year (1995 vs. 1996), transmitter implantation (implanted vs. not implanted) and exposure to human disturbance (disturbed vs. undisturbed) on mean within-brood offspring mass of Eastern Massasauga Rattlesnakes. I examined the effect of one treatment while keeping the levels of the other two treatments constant.

Effect Tested	Value of Treatment 1 Held Constant	Value of Treatment 2 Held Constant	F-Statistic	p
Year	Undisturbed	Not Implanted	$F_{1,8}=1.96$	$p>0.19$
Transmitter Implantation	1995	Undisturbed	$F_{1,3}=2.12$	$p>0.24$
Disturbance Status	1995	Implanted	$F_{1,3}=0.38$	$p>0.58$
Disturbance Status	1996	Not Implanted	$F_{1,10}=0.65$	$p>0.43$

DISCUSSION

Human use of parks, nature reserves and wilderness areas has increased dramatically as a result of the growing popularity of outdoor recreation and ecotourism (Hammitt and Cole 1987, Boo 1990). The ecological impacts of these activities, though subtle, can be significant (Hammitt and Cole 1987). In particular, biologists are increasingly concerned that human intrusion into natural habitats may impose extraneous predator avoidance costs on wildlife.

To date, research into the effects of human disturbance has focused largely on mammals and birds, whereas reptiles have received relatively little attention (Boyle and Sampson 1985, Flather and Cordell 1992). Yet reptiles may be especially vulnerable to the adverse effects of human disturbance. Not only does reptilian ectothermy constrain behavioural avoidance of humans, but the limited mobility of most species effectively precludes emigration from disturbed areas.

The few field studies to examine the effects of human disturbance on reptiles have dealt almost exclusively with the impact of beach use on nesting sea turtles (e.g. Arianoutsou 1986, Johnson et al. 1996). Although several authors have suggested that human disturbance can affect snakes (Greene 1988, Peterson 1990, Brown 1993) information to date has been largely anecdotal (but see Prior and Weatherhead 1994) and to the best of my knowledge, this is the first study to provide quantitative evidence.

Snake Body Temperature

The discovery that Eastern Massasauga Rattlesnake body temperatures are positively correlated with both air and substrate temperatures was not entirely unexpected, given that a number of previous studies have reported similar results for several other snake species (Gibson and Falls 1979, Gregory 1984, Gannon and Secoy 1985). However, I was somewhat surprised that gravid females did not maintain significantly higher, or less variable, body temperatures than non-gravid conspecifics, because reproductive condition significantly affects snake thermoregulation (Peterson et al. 1993). Since snake body temperatures are determined by numerous interacting factors (Peterson et al. 1993), I suspect this result simply reflects this study's coarse sampling protocol (each snake's temperature was only measured once every second day) and the cursory attempt to control for environmental effects.

There is very little information about the effects of predators on snake thermoregulation (Peterson et al. 1993). Nevertheless, I predicted that predator avoidance behaviour would impede movements between different thermal environments and thus negatively affect the ability of snakes to thermoregulate. However, exposure to human disturbance did not affect average body temperatures, nor did it affect the variance of body temperatures. Again, this result might reflect shortcomings in sampling methodology. Alternatively, this could suggest that human disturbance does not affect behaviour in such a way as to influence thermoregulation. Crypsis permits lizards to bask in exposed locations without increased predation risk (Schwarzkopf and Shine 1992) and snakes are often able to thermoregulate effectively through subtle postural changes rather than overt shuttling movements (e.g. Shine and Fitzgerald 1996). Snakes can also thermoregulate while remaining under cover (Huey et al. 1989).

Visibility

The visibility of male and non-gravid female Eastern Massasauga Rattlesnakes was not affected by ambient temperatures. This finding was not entirely unexpected, because snake activity patterns are generally not based on thermoregulatory considerations alone. For example, snakes may accept lower or more variable body temperatures as a consequence of the conflicting demands of other important activities, such as foraging (Peterson et al. 1993).

The visibility of males and non-gravid females did not vary with increasing exposure to human disturbance. This finding was somewhat unexpected, given that many other animals use cover to avoid detection by potential predators (Werner et al. 1983, Heads 1986, Yarmoloy et al. 1988). However, this apparent lack of response may actually reflect a perception of constant predation risk (Lima and Dill 1990). Snakes are notoriously cryptic and many investigators, including Fitch and Shirer (1971), Tiebout and Cary (1987), Weatherhead and Prior (1992) and Shine and Fitzgerald (1996) have noted their avoidance of open areas. Thus, snakes may try to remain inconspicuous regardless of the actual risks of predation.

The visibility of gravid females varied with substrate temperature. Since T_b is highly correlated with T_s, this suggests that thermoregulatory considerations affect their use of cover. This interpretation is consistent with the finding that gravid females used more open habitat than males and non-gravid females.

The visibility of gravid females was also affected by disturbance. Snakes in disturbed areas were significantly less visible than those in undisturbed areas, suggesting that gravid females increase their use of cover when they are more vulnerable to predation. Such behaviour is apparently common among viviparous reptiles. The females of several snake and lizard species are known to become more cryptic when gravid (Bauwens and Thoen 1981, Graves 1989, Schwarzkopf and Shine 1992) perhaps because gravidity impairs locomotor ability and thus reduces the probability of escape (Shine 1980, Seigel et al. 1987, Cooper et al. 1990).

Distance to Retreat Sites

Many animals rely on flight to protective refugia as their primary means of predator avoidance. Since an individual's probability of escape is inversely proportional to the distance it must flee if attacked, a number of animals remain closer to potential retreat sites as the risk of predation increases (Lima and Dill 1990). However, snakes in disturbed areas of Killbear Provincial Park were not found any closer to retreat sites than individuals in less disturbed areas. While this could imply that snakes do not view humans as threatening, there is considerable evidence to suggest otherwise (e.g. Duvall et al. 1985, Klauber 1997). Instead, I believe that the antipredator behaviour of Eastern Massasauga Rattlesnakes simply does not emphasize flight. This interpretation is consistent with the snakes' apparently heavy reliance on crypsis (see discussion above), and their potential for active defense (rattling and striking) if discovered. Alternatively, given that snakes are known for their ability to escape into seemingly non-existent holes and crevices, this finding may also simply reflect the observers' inability to recognize potential refugia.

Habitat Structure

A number of investigators have described the habitat use of Eastern Massasauga Rattlesnakes, at least in terms of vegetational communities

(Wright 1941, Reinert and Kodrich 1982, Weatherhead and Prior 1992). However, there is growing recognition that snake habitat preferences are influenced by the physical arrangement of environmental components (Reinert 1993). This study provides the first structural description of Eastern Massasauga Rattlesnake habitat in Ontario.

The habitat use of Eastern Massasauga Rattlesnakes in Killbear Provincial Park was not random. This finding was not unexpected, given that a number of researchers have demonstrated non-random habitat use in this species (Weatherhead and Prior 1992, Johnson 1995) and in others (e.g. Madsen 1984, Reinert 1984b, Tiebout and Carey 1987).

Snake-selected locations had, among other features, fewer overstory trees, less canopy cover and fewer fallen leaves than random locations, suggesting that Eastern Massasauga Rattlesnakes in Killbear Provincial Park avoided forested areas. Although Reinert and Kodrich (1982) also found that this species avoided forested habitat, Seigel (1986) reported that the snakes used "deciduous woods," while Weatherhead and Prior (1992) found that the snakes preferred coniferous forests but avoided mixed forest. Such discrepancies emphasize the importance of habitat descriptions based on structural features (Reinert 1993).

Gravid female Eastern Massasauga Rattlesnakes in Killbear Provincial Park were found closer to rocks, and in more open areas with less leaf cover, than males and non-gravid females. This intraspecific variation in habitat use was somewhat expected, because gravid female Eastern Massasauga Rattlesnakes from populations in Pennsylvania (Reinert and Kodrich 1982) and New York (Johnson 1985) are known to prefer such open habitat.

Interestingly, similar structural habitat preferences have been reported for gravid females of other rattlesnake species. For example, gravid female Timber Rattlesnakes select rockier, more open areas than non-gravid females and males (Reinert 1984b), while gravid female Prairie Rattlesnakes (*Crotalus viridis*) are generally found close to large rocks (Duvall et al. 1985, Graves and Duvall 1993). This similarity of habitat structure supports these authors' suggestion that rookery sites are of functional significance to female reproduction.

Habitat use by male and non-gravid female Eastern Massasauga Rattlesnakes did not differ. This finding was also somewhat expected because both Weatherhead and Prior (1992) and Johnson (1995) reported similar results.

Random locations that received the heaviest human use (dr=3) had fewer logs, shrubs and other woody stems than the least disturbed (dr=1) areas. This result was not surprising, given that park visitors were often seen to collect logs and fallen branches for firewood, trample vegetation, and cut small trees to form roasting sticks, and that comparable impacts have been reported elsewhere (Hammitt and Cole 1987).

Similar differences were not found in the habitat use of non-gravid females and males. Rather, snake-selected locations that received heavy human use (dr=3) had fewer logs, more understory trees and smaller overstory trees than locations subject to minimal human disturbance (dr=1). Although these differences may represent modified snake habitat selection in response to human disturbance, it is difficult to interpret their ecological significance. Instead, these results probably reflect the early successional stages of human disturbed areas, because roads, trails, and campgrounds are essentially clearings in the surrounding forest.

Randomly-chosen locations in Site A were rockier and had more understory trees and shrubs than those in Site B. Since the biological implications of these differences to Eastern Massasauga Rattlesnakes cannot be readily assessed, any comparison of snake ecology between Sites A and B cannot dismiss the potential effects of habitat.

The habitat structure of snake-selected and randomly-chosen locations were compared twice, and the results of these analyses were similar. However, when individual locations were used as the unit of replication, additional significant differences were found. For example, the habitat use of males and non-gravid females differed significantly, and DFA produced three, rather than two, significant discriminant functions. These differences are probably due to increased sample size and the inflated degrees of freedom. In contrast, discrepancies in total structure coefficients are likely due to the need to equalize sample sizes, and thus result from using a random sub-sample of locations. Therefore, reduced sample size as a consequence of using mean values of habitat variables did not greatly affect the stability of DFA total structure coefficients. This finding was not unexpected, given that Reinert (1984a) performed a similar comparison and achieved similar results.

None of the habitat analyses met the assumptions of MANOVA and DFA. In most cases, habitat variables were not normally distributed, and group covariance matrices differed significantly. However, I believe my results are generally valid, because both MANOVA and DFA are relatively insensitive to moderate departures from normality (Pimental 1979). In addition, except under extreme heteroscedasticity, unequal covariance matrices affect the Type I error rate of MANOVA only if group sample sizes are markedly different (Stevens 1992). Since group sample sizes were equal, or very nearly so, in all five analyses, any effect of unequal covariance matrices should have been minimal. In fact, the conclusion of heteroscedasticity may itself have been flawed, because Box's test is sensitive to non-normality (Stevens 1992).

Thus, despite the fact that habitat variables were not normally distributed, and that covariance matrices were unequal, I believe the results of the five habitat analyses are generally valid. Nevertheless, the marginally significant ($p<0.04$) difference in habitat use of male and non-gravid female snakes in locations with disturbance ratings of 1, 2 or 3 should be interpreted with caution.

Movement Patterns

The discovery that gravid female Eastern Massasauga Rattlesnakes in Killbear Provincial Park did not move as far, or as often, as non-gravid female and male conspecifics was not entirely unexpected. Many other investigators have commented on the sedentary nature of gravid snakes (Gannon and Secoy 1985, Gregory et al. 1987, Graves and Duvall 1993), and similar results were reported for Eastern Massasauga Rattlesnakes in New York by Johnson (1995). Likewise, the lack of significant differences between males and non-gravid females in average distance moved/day and persistence was not surprising. Again, similar results were reported for Eastern Massasauga Rattlesnakes by Reinert and Kodrich (1982), Prior and Weatherhead (1992) and Johnson (1995).

Many authors have suggested that predators affect snake activity patterns (e.g. Gibbons and Semlitsch 1987, Gregory et al. 1987). However, few investigators have explicitly examined the influence of predation risk on snake movement, and to the best of my knowledge, none has assessed the effects of human disturbance.

A number of researchers have claimed that human disturbance can cause snakes to abandon preferred habitat (Brown 1993). If so, snakes in disturbed areas might be expected to move further, or more frequently, than those in undisturbed areas. Such responses were not observed among transmitter-equipped Eastern Massasauga Rattlesnakes in Killbear Provincial Park. However, despite frequenting hiking trails and campgrounds, the snakes were only rarely observed by park visitors (who often passed within 5 m of them), and thus rarely molested. In contrast, the Timber Rattlesnakes 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 possibility is supported by studies on Eastern Massasauga Rattlesnakes. Non-gravid females and males 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 (Prior and Weatherhead 1994) moved an average of 56.2 ± 12.4 m/day (Weatherhead and Prior 1992).

Our images of snake antipredator behaviour are heavily influenced by observed responses to human collectors (Greene 1988). As a result, the more passive defensive mechanisms used by snakes to avoid detection by potential predators have largely gone unnoticed. For example, Prior and Weatherhead (1994) suggested that Eastern Massasauga Rattlesnakes are frequently overlooked because they often do not rattle when approached.

There is growing evidence (Dill 1987, Lima and Dill 1990) that many animals become less active with increasing predation risk. Such evidence is generally lacking for snakes, though Shine and Lambeck (1985) suggested that avian predators were responsible for the short diurnal movements (<20 m/day) of Filesnakes (*Acrochordus arafurae).* However, many researchers, including Sweet (1985), Sazima (1993), Ford and Burghardt (1993) and Klauber (1997) have noted that snakes freeze or remain motionless when approached by humans. In areas subject to heavy human disturbance, this response could disrupt normal snake movement patterns, and I suggest that such behaviour explains the significant negative correlation between average distance moved/day and exposure to human disturbance by Eastern Massasauga Rattlesnakes in Killbear Provincial Park. Similar results were reported by Durner and Gates (1993), who found that the minimum distances travelled/move by

Black Rat Snakes (*Elaphe obsoleta*) in Maryland were significantly greater in undisturbed habitats that in human residential areas. They attributed these movement patterns to the differential availability of prey species, though they offered no evidence to support this hypothesis.

Condition and Growth Rates

A number of investigators have shown that the condition and growth rates of snakes may vary annually as a result of climatic variation (e.g. Brown and Parker 1984, Forsman 1993) or fluctuating prey availability (e.g. Andrén and Nilson 1983, Platt 1984). In this study, gravid female Eastern Massasauga Rattlesnakes were found to be in significantly better condition in 1995 than in 1996. However, I cannot readily explain this difference. Presumably, year-to-year variation in weather conditions would have to be fairly dramatic (e.g. Plummer 1983) to have perceptible impacts on snakes, yet I recognized no obvious differences between field seasons. Gravid female rattlesnakes should also be unaffected by any declines in prey, since they rarely, if ever, feed during gestation (e.g. Macartney and Gregory 1988). Given the similarity of study years, I expected a lack of annual effects on the condition of non-gravid females and males, and on the growth rates of reproductive females, non-reproductive females, and males.

Human disturbance did not appear to affect the condition or growth rates of Eastern Massasauga Rattlesnakes in Killbear Provincial Park, but these findings must be accepted with caution. Since none of the snakes used in these analyses were implanted with transmitters, their exposure to human disturbance could not be accurately determined. Thus, some of the snakes captured in Site A may have had little exposure to humans, and conversely, those found in Site B may have originated from more heavily disturbed areas.

Brood Size and Offspring Size

In this study, brood size was positively correlated with female snout-vent length. This finding was not entirely unexpected, because many authors have reported similar results for a variety of other snake species (e.g. Seigel and Ford 1987, King 1993, Graves and Duvall 1993). More surprising was the finding that Eastern Massasauga Rattlesnakes in Killbear Provincial Park apparently produce larger broods than American conspecifics (cf. Seigel 1986, Table 3).

Snake populations are subject to year-to-year variation in both average brood size (Seigel and Fitch 1985, Seigel and Ford 1987) and average offspring size (Seigel and Ford 1987). However, because of the similarity of field seasons during this study (see above) I expected a lack of significant annual effects. For the most part, this expectation was met. However, offspring born to females found in the undisturbed study site were significantly longer in 1995 than those born in 1996. This is perhaps because gravid females were found to be in significantly better condition in 1995 than in 1996. Several authors have shown that female size can affect offspring size (Seigel and Ford 1987).

The surgical implantation of radio transmitters can cause gravid females to reabsorb developing follicles, though the likelihood declines as the active season progresses (Graves and Duvall 1993). In this study, transmitter implantation did not affect brood size, probably because no gravid female received a transmitter before late June, at least midway through the snakes' active season. However, of females found in the undisturbed study site in 1995, those implanted with transmitters produced significantly longer young than without transmitters. I can offer no plausible explanation for this effect.

Human disturbance did not affect brood size or offspring size. However, given the small sample sizes, and the concomitant low power of the statistical tests (always < 0.50 and often < 0.15) these results must be interpreted with caution.

Parturition Date

I expected human disturbance to disrupt the thermoregulation of gravid females, and because the development rate of embryonic snakes is temperature-dependent (Saint Girons 1985), I predicted that parturition dates in disturbed areas would be later than those in undisturbed areas. However, human disturbance did not affect average body temperatures, so I was not surprised to find that parturition dates were unaffected.

Summary

Eastern Massasauga Rattlesnakes in Killbear Provincial Park appear to respond to people as potential predators. Presumably to reduce their risk of detection, gravid females become less visible, and the average distance moved per day by gravid females, non-gravid females, and males declines with increasing exposure to human disturbance. These results have several interesting implications.

First, despite the common perception that snakes are simply "instinctive machines" (Ford and Burghardt 1993), this study suggests that perceived predation risk can affect snake behaviour. In fact, there is increasing evidence that individual behavioural responses to ecological factors result in significant intraspecific variation in thermoregulation, patterns of movement and habitat use in snakes (Shine 1987). However, few researchers have explicitly examined the effects of predators on snake activity patterns (Gibbons and Semlitsch 1987).

Second, this study suggests that snakes may respond to even apparently benign human activities, and cautions that the responses may be subtle, and thus easily-overlooked. Given the growing use of parks and wilderness areas, identification of the impacts of human disturbance on wildlife will likely become an increasingly important aspect of protected areas management, especially with regards to rare or endangered species.

Eastern Massasauga Rattlesnakes in Killbear Provincial Park should be particularly vulnerable to human disturbance, because any opportunities for foraging or reproduction lost during July and August, the park's period of heaviest human use, would be difficult to make good before hibernation in October. However, mark-recapture results revealed no effects of human disturbance on snake condition or growth rates, or on the brood size, offspring size, or parturition date of gravid females. Nevertheless, the conclusion that snakes do not suffer fitness costs as a result of human disturbance must be viewed with caution. Several other effects, not assessed in the course of this study, may be operative.

For example, increased crypsis in areas subject to heavy human disturbance could decrease individual male reproductive success by disrupting the long distance movements inherent in mate searching behaviour. 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-structure.

Finally, the results of this study suggest that further research into snake predator avoidance tradeoffs would prove rewarding. For example, in areas subject to human disturbance, many ectotherms become active mainly at night (e.g. Van Dyke et al. 1986, McLellan and Shackleton 1988). However, such temporal avoidance may not be feasible for Temperate Zone snakes, because even during mid-summer, low temperatures may preclude nocturnal activity. How snakes respond to human disturbance where activity period shifts are not constrained by thermoregulatory considerations (e.g. in the tropics) remains an interesting question.

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IMAGE EVALUATION
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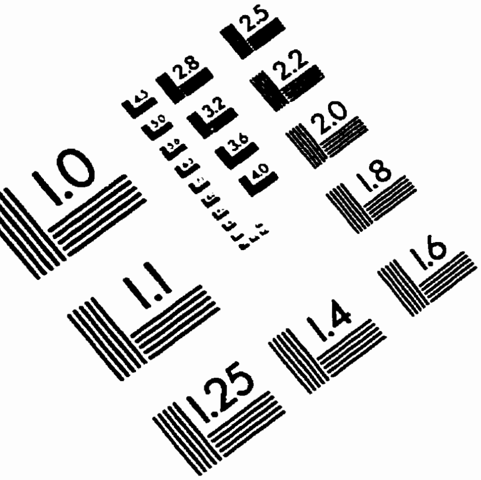

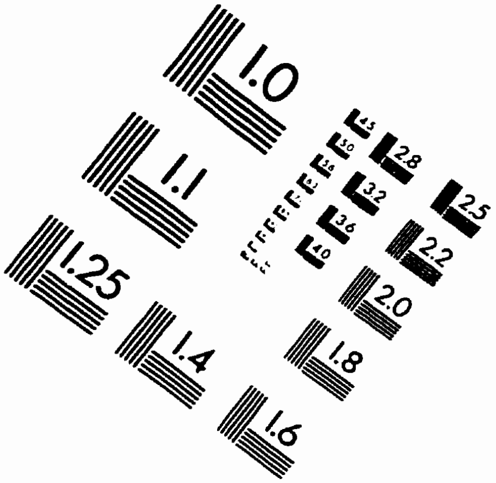

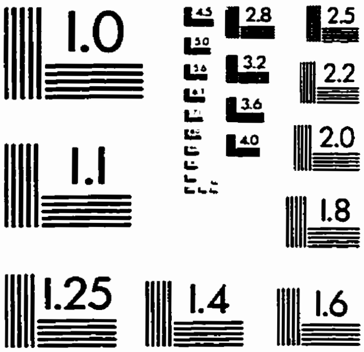

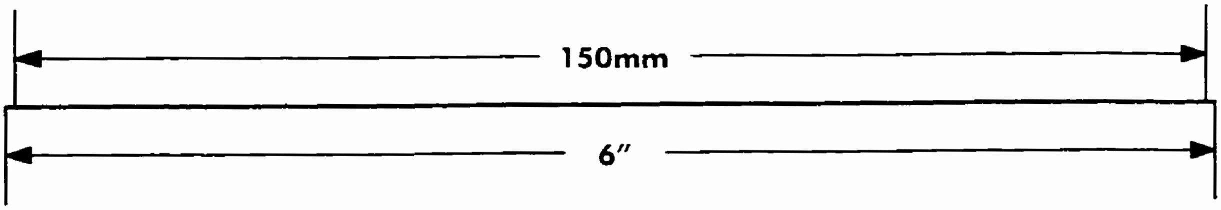

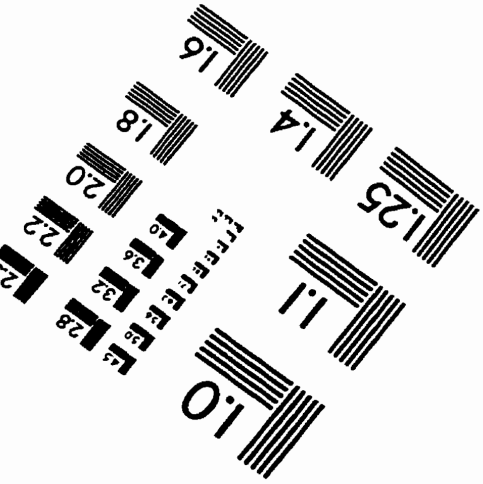

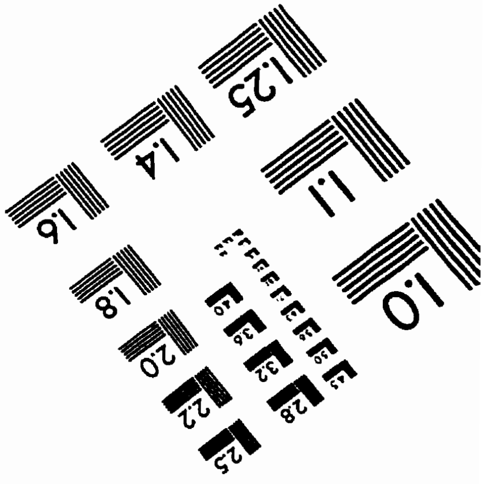

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