
Activity Patterns of Garter Snakes, *Thamnophis sirtalis*, in Relation to Weather Conditions at a Fish Hatchery on Vancouver Island, British Columbia

Author(s): Kari J. Nelson and Patrick T. Gregory

Source: *Journal of Herpetology*, Mar., 2000, Vol. 34, No. 1 (Mar., 2000), pp. 32-40

Published by: Society for the Study of Amphibians and Reptiles

Stable URL: <https://www.jstor.org/stable/1565235>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/1565235?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Herpetology*

JSTOR

Activity Patterns of Garter Snakes, *Thamnophis sirtalis*, in Relation to Weather Conditions at a Fish Hatchery on Vancouver Island, British Columbia

KARI J. NELSON¹ AND PATRICK T. GREGORY

Department of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria,
British Columbia, Canada, V8W 3N5

ABSTRACT.—Temperature is one of many factors that may have an important influence on activity of ectotherms. We investigated the influence of weather conditions on activity of common garter snakes, *Thamnophis sirtalis*, at a fish hatchery on Vancouver Island where the water in which they forage is cold (<14°C). We used reduced major axis regression to partition the relationship between air temperature and number of snakes seen into subsets, and the uppermost subset of data was used to describe the upper boundary of the overall relationship. At the hatchery site, the maximum number of snakes observed increased in relation to maximum daily air temperatures, with the highest numbers of snakes being observed on days when maximum daily air temperatures exceeded 25°C. By contrast, at a nearby reference site where snakes do not consume fish, the maximum number of snakes observed decreased in relation to maximum daily air temperatures, with very few snakes being observed on days with high maximum daily air temperatures. Radiotagged snakes were observed swimming in hatchery channels only on days when maximum daily air temperatures were high. Body temperatures of these snakes decreased extremely rapidly when the snakes entered the water, and remained low while they were in the hatchery channels. The body temperature of one snake that captured a fish while swimming in the channels was just over 14°C. We hypothesize that hot weather conditions permit snakes at hatchery sites to achieve high body temperatures rapidly subsequent to foraging activity.

Activity patterns of reptiles are closely tied to thermal conditions. Many species of snakes change their diel patterns of activity in response to seasonal differences in environmental temperatures. Activity in some snakes is typically diurnal during cool seasons, but becomes nocturnal during the hottest time of the year (Heckrotte, 1962; Landreth, 1973; Moore, 1978; Mushinsky et al., 1980; Saunders and Jacob, 1980; Patterson and Davies, 1982). Even in strictly diurnal species, timing of activity is dependent on daily temperatures and weather conditions (e.g., most activity occurring at midday during cool weather conditions, and in the early morning and evening during hot weather conditions; Stewart, 1965; Platt, 1969). Although timing of activity has been documented for many species of snakes, few studies do much more than simply describe these patterns (Gibbons and Semlitsch, 1987).

Season, time of day, and weather conditions all influence the range of thermal conditions present in the environment, which in turn determines the potential for body temperature variation in snakes (Peterson et al., 1993). Behaviors that are highly dependent on body tem-

perature therefore will be restricted to periods when favorable body temperatures can be achieved. For example, encounter probabilities of actively foraging snakes and their prey will be influenced by body temperature (Huey, 1982), as will capture probability (Greenwald, 1974).

The common garter snake (*Thamnophis sirtalis*) is an inefficient predator on fish (Drummond, 1983) and normally feeds on amphibians and earthworms (Fitch, 1965; Gregory, 1978; Kephart, 1982). This species, however, becomes highly piscivorous in situations in which fish are abundant (e.g., in hatcheries or rearing facilities; Lagler and Salyer, 1945; Gregory and Nelson, 1991) or otherwise easily caught (e.g., in drying pools in intermittent streams; Fitch, 1941; Carpenter, 1952; White and Kolb, 1974; Kephart and Arnold, 1982). However, water at hatcheries can be quite cold and this presents a potential obstacle to foraging for fish. Even fairly large endotherms may experience marked and rapid declines in body temperature while foraging in cold water (Kruuk et al., 1997), but this problem is exacerbated for small ectotherms such as garter snakes, in which body temperatures rapidly reach ambient levels in water (Hailey and Davies, 1987). Although swimming speeds are relatively unaffected by low temperatures, crawling speeds of snakes are signifi-

¹ Corresponding Author. Present Address: 1895 Sea Lion Crescent, Nanoose Bay, British Columbia, Canada, V9P 9J3.

cantly reduced at low body temperatures, and snakes emerging from cold water may be especially vulnerable to predation while their body temperatures remain low (Stevenson et al., 1985).

At hatchery sites on Vancouver Island, British Columbia, garter snakes (*Thamnophis sirtalis*) consume fish almost exclusively (Gregory and Nelson, 1991). The water in which these snakes capture fish is cold (maximum monthly mean 12.5°C; Mundie and Traber, 1983). We predicted that snakes at hatchery sites would be limited in their activity to periods when they can rapidly achieve high body temperatures when out of the water. At nearby reference sites, where snakes do not consume fish (Gregory and Nelson, 1991), activity patterns should be similar to those documented for other species of diurnal, temperate-zone snakes (i.e., retreating to cover during the warmest part of clear, hot days) (cf. Stewart, 1965). In this paper, we test our prediction by comparing the upper limits of the relationship between number of snakes observed per hour of search time and maximum daily air temperatures at a hatchery site and an adjacent reference site. Using data on body temperature variations and movements of individuals, we discuss alternative explanations for the observed patterns.

MATERIALS AND METHODS

Study Site.—We conducted this study in 1989 and 1990 at the Robertson Creek Hatchery, located 15 km west of Port Alberni, British Columbia (124°58'W, 49°15'N). The six open rearing channels (hatchery channels) at Robertson Creek are each approximately 20 m long and 3 m wide. Coho fry (*Oncorhynchus kisutch*) were present in three of these channels for the entire year, and chinook fry (*O. tshawytscha*) were present in the remaining channels for three months in the spring of each year. Natural forest vegetation in the immediate vicinity of the channels had been cleared, and grasses, which are periodically cut by hatchery staff, lined the sides of the channels. The diet of snakes at this hatchery site consists almost exclusively of fish (prey type in 86% of snakes with food; Gregory and Nelson, 1991).

To compare activity of snakes at hatchery sites to those of snakes at a site where fish are not as readily available (i.e., not as abundant), we established a reference site about 200 m from the hatchery site. The reference site ran along a creek, up to some rearing channels and a small pond. A variety of shrubs and mixed stands of deciduous and evergreen trees lined the edges of the creek and the pond. Fish (coho fry and sculpins, *Cottus*) were present in the creek and rearing channels at the reference site, but not

notably abundant. In the spring of 1989 and 1990, chinook fry were reared in one channel at the reference site. These fish were released in the latter half of May, prior to the time when most of our observations of activity were made. The diet of snakes at this reference site consisted primarily of earthworms and amphibians (prey types in 71% of snakes with food, Gregory and Nelson 1991).

Hatchery personnel, using a mercury thermometer suspended in the water, monitored water temperatures in the hatchery channels twice daily. Water temperatures were maintained under 14°C by pumping cold water from the bottom of a lake into the reference-site creek, which supplies water to the hatchery channels. Water temperatures in the creek and in hatchery channels were thus similar (mean = 13.3°C, SD = 1.88°C, range = 5.5°C–17.7°C; data from April to September 1989 and 1990, collected by hatchery personnel).

Activity.—We measured levels of activity for snakes at each site by counting the number of individuals observed (captured, missed, and seen but previously captured) during each search effort. In 1989, we made no attempt to randomize the timing of these searches, although we did attempt to sample each site at all times of day during different weather conditions. To standardize search efforts for comparison, we divided the total number of snakes observed by the total amount of time we spent searching at each site on each day and then calculated the number of snakes observed per 60 min of search effort. To account for time spent handling snakes, we subtracted two minutes for each snake captured from the total amount of time spent searching. In 1989, we sampled 24 d between early May and the end of August, and in most cases, we searched each site two to three times per day, although on three days only one site was searched.

In 1990, we randomly selected one-hour search periods in either the morning or afternoon of alternate days. Random selection of search periods was made without replacement, so that all time intervals (0700 to 1800 h) would be represented during the sampling period. Twenty-eight days were sampled from mid-July to the end of September. No snakes were observed at either site during searches conducted between 0700 and 0800 h, or 0800 and 0900 h. In 1989, no searches were conducted before 0900 h, so to facilitate comparisons between years, searches conducted before 0900 h in 1990 were excluded from subsequent analysis.

Captured snakes were given an individual mark based on a numerical system of clipping subcaudal scutes (Blanchard and Finster, 1933). These marks allowed us to identify recaptured

individuals and to detect movements of individuals. Some snakes had been captured and marked in a previous study conducted in 1987–1988, and we included these in our analysis of movements. Presence or absence of food was determined by gentle palpation. To minimize disruption of regular patterns of foraging activity, and to ensure that snakes were handled no more than once during each three-to-four day sampling period, we marked snakes on the head with a color of nail polish specific to each sampling period.

Our aim was to determine whether there is a relationship between activity levels of snakes and environmental conditions. That is, as weather becomes warmer or colder, do we see more or fewer animals? One problem is that, although weather may limit the maximum number of animals that we are likely to see, other (unmeasured) factors may limit the number we actually see. Therefore, even in apparently optimal weather conditions, we sometimes may see very few or no snakes, resulting in a distribution of observations in which there is a large amount of scatter below the upper limit. Such situations are common in ecology and present challenges in terms of statistical analysis (Blackburn et al., 1992; Thomson et al., 1996; Scharf et al., 1998). What we sought to do was to determine the nature (e.g., positive linear relationship) of the upper boundary of the overall scatter of points and test the statistical significance of that boundary relationship. Given sufficiently large samples, the best way to determine the upper limit is probably the quantile regression technique suggested by Scharf et al. (1998). However, because our samples were modest in size, we used a method suggested by Thomson et al. (1996). In Thomson et al.'s method, the overall data set is divided in two by regression, and the two subsets of data thus created are subdivided by further regression. This process of regression and subdivision can be repeated through a number of such cycles. The uppermost subset of data so produced is then used to describe the upper boundary of the overall relationship. Because of the nature of our data, we used reduced major axis (or geometric mean) regression, which also has the useful property of scale-invariance, rather than least-squares regression (see Ricker, 1984).

The best measure of physical conditions from a snake's perspective is operative temperature (Bakken and Gates, 1975), which may be obtained from thermoconforming models (Peterson et al., 1993). We did not have model temperature data for all of the search intervals in 1989 and 1990, and sample sizes were too small to use these data to determine the upper boundaries of the relationship between snake activity

and environmental conditions. We therefore used maximum daily air temperatures as an index of environmental conditions. We recognize that air temperature data are limited in terms of describing conditions potentially available to snakes at the actual time of the search, but previous studies have generally shown air temperatures to be positively correlated with body temperatures of snakes (e.g., Gregory, 1984). In any case, when we plotted the few operative temperatures that we had against number of snakes seen, we obtained the same trends for the two sites that we obtained using maximum air temperatures (see Results). Thus, maximum air temperature provides a satisfactory index of environmental conditions that is consistent between sites and between years and therefore appropriate for comparative purposes.

Weather data were recorded on-site by hatchery personnel for Canada's Atmospheric Environment Service (AES). Maximum and minimum air temperatures were recorded in the morning and again in the afternoon using maximum-minimum thermometers located inside a weather station provided by the AES. We compared maximum temperatures recorded in the afternoon of the day on which the search was conducted with those recorded in the morning of the following day to obtain maximum daily air temperatures for each search interval.

Telemetry.—We monitored activity, body temperatures and movements of individual free-ranging snakes using temperature-sensitive radiotransmitters (Model CPH-2P, Telonics Co., 3.4×1.7 cm, approx. 6.0 g). We calibrated the transmitters prior to implantation using a water bath that ranged in temperature from 5° to 40°C . Because of battery failure and transmitter malfunction, we were unable to re-calibrate the transmitters at the end of the study to account for potential "drift", which may affect the actual values for snake body temperatures that we present. However, the degree of variation in estimated snake body temperatures over the short time periods that we present is so large that drift would have had to be very substantial ($>20^{\circ}\text{C}$) and occurring continuously to have influenced our main conclusions. Furthermore, estimates of body temperatures for snakes known to be in the water consistently matched water temperature levels, indicating that readings were accurate.

Transmitters were implanted in four female snakes (610–660 mm SVL; 78.4–86.4 g) and one male snake (580 mm SVL, 76 g) captured at the hatchery channels. The transmitters were fairly large for the snakes we studied (7–8% of snake body mass), but behavior and locomotory ability of snakes with transmitters did not differ in any obvious way from those of snakes we saw

without transmitters. In fact we observed one of our radiotagged snakes engaged in mating activity on several occasions in late August and September 1990. Snakes were anesthetized using Metofane (Methoxyflurane, Pitman-Moore, Inc., Washington Crossing, NJ; Aird, 1986), and surgical procedure followed that of Weatherhead and Anderka (1984). Animals were held in the laboratory for at least two days to ensure recovery prior to release, and were allowed two days to acclimatize in the field before we commenced recording body temperatures.

We monitored body temperatures of as many of the radio-tagged snakes as possible every fifteen minutes for six hours in either the morning (0700 to 1300 h) or afternoon (1300 to 1900 h) of alternate days, although readings were sometimes taken at mid-day (0930 to 1330 h, 1000 to 1400 h, or 1030 to 1430 h). In total, we monitored between one and three snakes on a total of 43 d (72 snake days), resulting in 252.25 h of observation (402.25 snake hours). All of the times reported are Pacific Daylight Savings Time.

Statistical Analysis.—For each cycle of partitioning of the data on snake activity vs. maximum daily air temperature, we calculated reduced major axis (geometric mean) regressions from least squares regressions (obtained using Microsoft® Excel for Windows™ Version 5.0), as outlined by Ricker (1984). We examined residuals to split the data into subsets (above or below the line), and the data were divided twice, resulting in four subsets of data. The significance of the uppermost regression line for the resulting subset of data was tested using the product-moment correlation coefficient (Ricker, 1984). All statistical tests were considered significant at $\alpha = 0.05$.

RESULTS

Activity.—The bivariate distributions of number of snakes observed per hour in relation to maximum daily air temperatures at both hatchery and reference sites reveal the large amount of variation present in these data (Fig. 1). That there are other factors besides maximum daily temperatures operating to determine snake activity levels is illustrated by the fact that at both sites, days when zero snakes were observed occurred across a wide range of maximum daily temperatures. By partitioning the data using major axis regression, we were able to describe the ceilings of these distributions, which give us a better indication of the upper limits to snake activity imposed by maximum daily air temperatures.

At the hatchery site, there was a significant positive relationship between the maximum numbers of snakes observed and maximum dai-

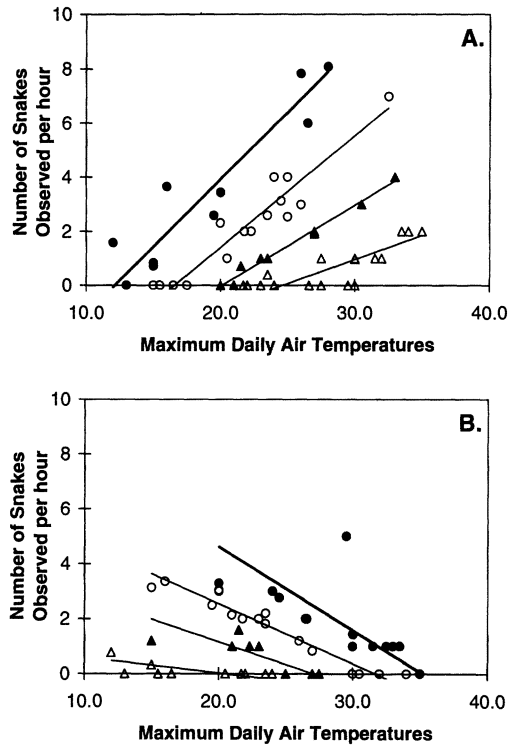


FIG. 1. Two-cycle partitioned regression of number of snakes observed per hour vs. maximum daily air temperatures for a) Hatchery and b) Reference sites. Reduced major axis regression was used to divide the overall data set into two sets of points (represented by circles and triangles). These subsets of data were subdivided again by reduced major axis regression, resulting in four sets of points (represented by open and closed circles and triangles). Lines plotted are reduced major axis regression lines for the resulting four subsets of data.

ly air temperatures [Fig. 1a; equation of uppermost line, $Y = -6.04 + 0.50(X)$; $P(r_s \geq 0.93) < 0.001$]. We observed the highest numbers of snakes at the hatchery site on days when maximum daily air temperatures exceeded 25°C. At the reference site, there was a significant negative relationship between maximum numbers of snakes observed and maximum daily air temperatures [Fig. 1b; equation of uppermost line, $Y = 10.70 - 0.30(X)$; $0.01 < P(r_{11} \geq |-0.66|) < 0.02$]. An outlier in this relationship (Fig. 1b) represents one instance in which maximum daily air temperatures did not accurately describe general conditions at the time of the search. This search took place between 1000 and 1100 h when heavy morning fog moderated temperatures on a day that later became sunny and very hot. However, inclusion or exclusion of this data point does not affect our conclusion.

In 1989 and 1990, 40 snakes were captured at

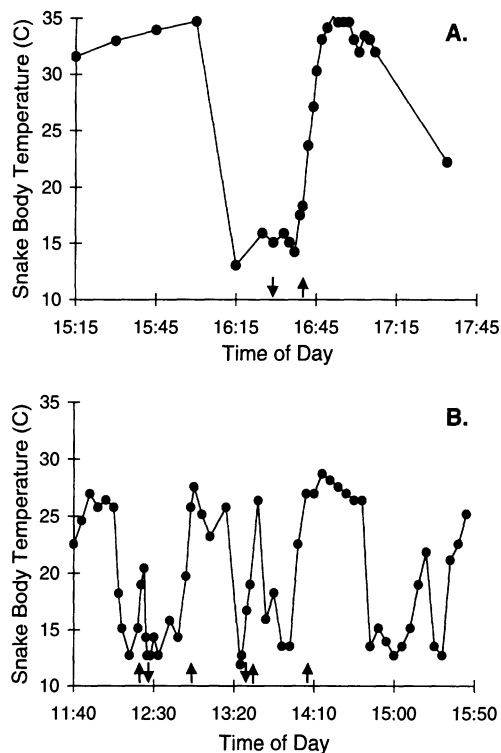


FIG. 2. Body temperatures records for snakes observed foraging in hatchery channels: a) R8L7, August 1, 1990; b) R5L10, August 2, 1990. Arrows represent times when the snake was observed on shore (arrow pointing away from axis) or in the water (arrow pointing toward axis).

hatchery channels with fish in their stomachs. The fish in 17 of these snakes were undigested and therefore probably consumed the day the snake was captured. Maximum air temperatures on these days ranged from 16° to 32°C (mean = 26.7°, SD = 3.91, N = 17).

Telemetry.—During the 43 d of observation (72 snake days), radiotagged snakes were observed in hatchery channel water on only five days, and we obtained data on body temperature variations on four of these days (Figs. 2, 3). Three records of body temperature variation were obtained from one snake (Figs. 2b, 3a, b). All of the records were obtained in the afternoon (between 1200 and 1800h) of sunny days when maximum daily air temperatures ranged from 27.0° to 34.0°C.

On each occasion, we monitored the behavior of the snake as closely as possible while it was in the vicinity of the channel. No predators were observed in the area on these occasions, and because snakes at the hatchery site were consuming fish (Gregory and Nelson, 1991), we assumed that the main reason for snakes to be in hatchery channel water was to obtain food.

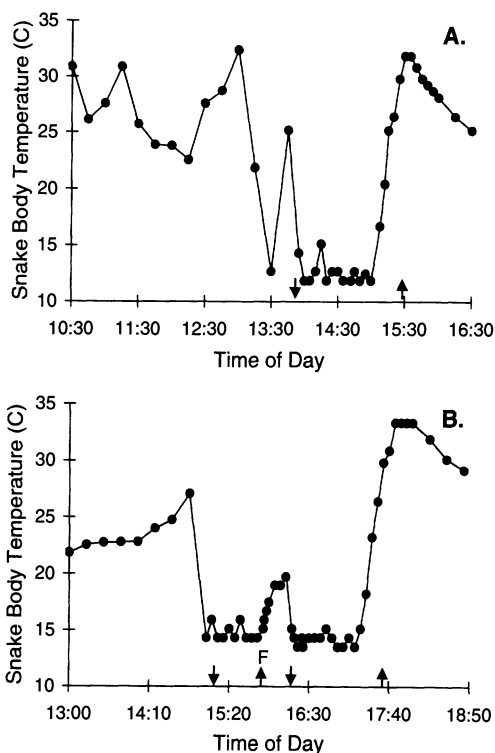


FIG. 3. Body temperatures records for snakes observed foraging in hatchery channels: a) R5L10, August 5, 1990; b) R5L10, August 12, 1990. Arrows represent times when the snake was observed on shore (arrow pointing away from axis) or in the water (arrow pointing toward axis). "F" above arrow in d) refers to point at which the snake was observed returning to shore with a fish in its mouth.

In most cases, we did not actually observe snakes entering the water at hatchery channels, but we were always able to locate the snake in the channel following a dramatic decrease in body temperature between telemetry readings (arrows pointing toward axis in Figs. 2, 3). On one occasion (Fig. 2b), the snake was observed entering and leaving the hatchery channel water several times, with corresponding decreases and increases in body temperature. The body temperature of this snake declined 7.8°C in two minutes (3.87°C/min) when it was observed moving from the bank of the hatchery channel into the water (Fig. 2b).

On the three other occasions when radiotagged snakes were observed in the hatchery channel water (Figs. 2a, 3a, b), they remained along the edge of the channel, often on top of floating mats of grass, for 30 min to one hour after entering the water. Body temperatures of snakes while they were in the hatchery channel ranged from 12°C (equal to the water temperature) to

16°C (when they were basking on grass at the edge of the channel).

One snake was observed capturing a salmonid fry in the hatchery channel (Fig. 3b). This snake was in the water at the edge of the channel for 48 min before it was observed swimming out to the middle of the channel. It disappeared under the water for about a second, and returned to shore with a fish in its mouth. The body temperature of this snake was 14.3°C at the time the fish was captured. The snake's body temperature rose slightly while it consumed the fish on the bank, and then it returned to the edge of the channel where it remained for approximately one hour.

When the snakes monitored by telemetry left the hatchery channel water, they all raised their body temperatures to high levels (28 to 35°C) by basking. Heating rates ranged from a low of 0.56°C/min on 12 August (Fig. 3b) to a high of 1.50°C/min on 1 August (Fig. 2a).

Movements.—Between June 1987 and September 1990, we captured 106 new snakes and made 63 captures of previously marked snakes at the hatchery channels. Three snakes originally captured at the hatchery channels were recaptured 1 to 3 years later, 87 to 180 m away from the channels. Another two snakes originally captured at the channels were recaptured 84 and 94 m away, 8 and 30 d later, respectively. Two snakes originally captured away from the vicinity of the hatchery channels were recaptured at the channels. One snake was recaptured after 57 d, 37 m from its original capture location. The other snake was recaptured over one year later, 85 m from its original location. There were no records of movements between the reference and hatchery sites.

Of the five snakes studied by telemetry, only one snake (R5L10 in Figs. 2b, 3) remained in the vicinity of the hatchery channels for the entire summer. One snake remained in the vicinity of the channels from the time it was released on 30 June until 17 July, but could not be located after that date.

The other three snakes moved away from the channels within several days of their release. One individual moved away by 1 July, and was found dead of an unknown cause 92 m away on 13 July. Another snake released at the channels on 21 July moved away from the channels immediately, and was not located until 28 July, under power lines, approximately 215 m away from the channels. We recaptured this snake on 30 July, and re-released it at the channels. It immediately moved 59 m away and remained at this location until 9 August, when it began to move back toward the power lines. By 12 August it was located back in the area where it had originally been recaptured.

Another individual (R8L7 in Fig. 2a) that moved away from the vicinity of the channels after it was released on 30 June was located later the same day along a creek 169 m away. The snake remained in this area until 26 July, when we captured it and re-released it at the channels. It moved back to the same location along the creek after release. The snake was subsequently observed on two occasions in the vicinity of the hatchery channels, returning each time to its previous location along the creek.

When radiotagged snakes were not moving or observed in the channels, they remained under cover for extensive periods of time, in both sunny and cloudy weather conditions.

DISCUSSION

Despite certain advantages over endotherms (Pough, 1980), ectotherms are necessarily limited in their activity patterns by environmental temperatures, except in some tropical habitats (Shine and Madsen, 1996). Behavioral thermoregulation, by which ectotherms maintain a more-or-less constant body temperature, often conflicts with other necessary activities (Gregory et al., in press) and may not be possible at all in some situations (Huey and Slatkin, 1976). Thus, in the temperate zone, ectotherms are frequently faced with constraints and tradeoffs, and may be forced at times to "accept" suboptimal thermal conditions. Our study illustrates such a tradeoff.

We reach three main conclusions: (1) fish hatcheries, although a source of abundant prey that make foraging there worthwhile, nonetheless significantly constrain foraging activity of snakes; (2) because hatchery water is so cold, snakes can afford to forage in it only when air temperature is sufficiently high that snakes can raise their body temperatures rapidly when out of the water; (3) because of the influence of foraging in cold water, snakes at hatcheries have a different pattern of activity in relation to environmental temperature than do snakes at the reference site, where snakes do not eat fish.

An important assumption that underlies our conclusions is that counts of snakes are good indices of snake activity. We can think of two potential criticisms of our approach:

- (1) "Active" snakes at any given moment either may have been in the open or hidden; because density of vegetation was higher at the reference site, there may have been more animals in the latter category than at the hatchery.
- (2) On warm days, snakes presumably were faster and more likely to move into vegetation before they could be spotted, whereas on cooler days, they could not move so fast or

were more likely to be in the open, warming up, in the first place.

Both of these are valid criticisms. To counter the first, we point to the fact that the activity index at the reference site changed (decreased) in relation to maximum daily air temperatures. That difference might be accounted for by the second criticism; radiotelemetry of snakes at both sites under all weather conditions would be needed to test whether the decrease in activity we observed at the reference site was due merely to increased mobility of snakes when air temperatures were higher. However, other researchers have reported that snakes are rarely observed in the open during the hottest part of the day in summer (Stewart, 1965; Scott et al., 1982; Hammerson, 1987; pers. obs.), so that snakes at the reference site appear to exhibit a "typical" pattern of activity.

In any case, neither of these criticisms can be applied as easily to snakes at the hatchery site, where visibility was very high. Therefore, regardless of any effect at the reference site, our observation that maximum levels of activity for snakes at the hatchery site increased with increases in maximum daily air temperatures remains unchanged.

Daily activity of snakes may be related to many factors, including thermoregulation, predator avoidance, searching for mates, and foraging (Gibbons and Semlitsch, 1987). Previously, we found that the diet of snakes at our two sites differed significantly, with snakes at the hatchery site consuming fish almost exclusively, whereas snakes at the reference site consumed earthworms and amphibians (Gregory and Nelson, 1991). In this study, we found that snakes at the hatchery site that had fresh fish in their stomachs were captured primarily on hot days, and that radiotagged snakes entered hatchery channel water (presumably to forage) only on hot days. These factors suggest that the increased levels of activity demonstrated by hatchery-site snakes during hot weather are related to their aquatic foraging behavior.

Several hypotheses might explain this trend toward increasing levels of activity of snakes at hatchery sites on days with high maximum air temperatures. Hot weather conditions may allow snakes at hatchery sites to raise their body temperatures prior to foraging above some threshold level at which foraging activity is more efficient. However, high cooling rates of radiotagged snakes entering cold hatchery channel water, our observation of a snake catching a fish when its body temperature was just over 14°C, and the fact that *T. sirtalis* engages in inefficient open-mouth searching behavior while foraging aquatically (Drummond, 1983; K. Nel-

son, pers. obs.), suggest that at hatchery sites at least (where prey densities are extremely high), high body temperatures are not required for aquatic foraging activity. Furthermore, Stevenson et al. (1985) showed that swimming performance of the related *T. elegans* was high over a broad range of temperatures.

If hot weather conditions confer no advantage on snakes during foraging activity itself, perhaps they are important in allowing snakes to achieve high body temperatures subsequent to foraging activity. All snakes monitored by telemetry engaged in basking behavior after emerging from the water and, as a result, raised their body temperatures to high levels. This not only may help increase digestion rates (Skoczylas, 1970; Naulleau, 1983), but also may be important to snakes in the vicinity of channels in reducing the risk of predation from other fish- and snake-eating predators such as mink (*Mustela vison*) and heron (*Ardea herodias*), especially given that vegetation and other cover is sparse. On one occasion in 1990, we observed a mink pursuing a snake that had been located at the edge of a hatchery channel. The snake had to move extremely rapidly to escape. Movement patterns of radiotagged snakes away from channels suggest that hatcheries are not suitable sites for snakes when they are not foraging. Recaptures of snakes away from channels also indicate that most snakes do not remain in the vicinity of hatchery channels for extended periods, but move there just to forage, and then move away to other areas with more protective cover. In this study, we observed radiotagged snakes at the hatchery on only 5 of 72 snake days of monitoring. When they were not moving, or at the hatchery channels, radiotagged snakes remained under cover for extended periods, in both cool and hot weather.

Prey abundance is high at salmonid hatcheries, but there evidently are tradeoffs for snakes that use such sites for feeding. The main one is the restriction of their activity to hot weather conditions. Although we did not measure them, there may be additional risks of predation in the open areas near hatchery channels. This hypothesis is supported by the observation that individual snakes only briefly visited the hatchery, but spent most of their time elsewhere where the vegetation was more dense; whether such movement patterns are typical for *T. sirtalis* in this area or specific to hatchery-feeding snakes remains to be determined. Interactions between feeding, thermoregulation, and other activities presumably are widespread in ectotherms (e.g. Gregory et al., in press) and should be expected to underlie many local variations in their ecology.

Acknowledgments.—We thank Don Lawseth for permission to undertake this study and for providing us with weather data collected by hatchery personnel. This research was made possible by a Natural Sciences and Engineering Research Council (NSERC) of Canada Postgraduate Scholarship to K.J.N., and was supported by an Operating Grant from NSERC to P.T.G.

LITERATURE CITED

- AIRD, S. D. 1986. Methoxyflurane anesthesia in *Crotalus*: comparisons with other gas anesthetics. *Herpetol. Rev.* 17:82–84.
- BAKKEN, G. S., AND D. M. GATES. 1975. Heat transfer analysis of animals: Some implications for field ecology, physiology, and evolution. In D. M. Gates and R. B. Schmerl (eds.), *Perspectives of Biophysical Ecology*, pp. 255–290. Springer, New York.
- BLACKBURN, T. M., J. H. LAWTON, AND J. N. PERRY. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. *Oikos* 65:107–112.
- BLANCHARD, F. N., AND E. B. FINSTER. 1933. A method of marking living snakes for future recognition, with a discussion of some problems and results. *Ecology* 14:334–347.
- CARPENTER, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis sauritis*), and the Butler's garter snake (*Thamnophis butleri*). *Ecol. Monogr.* 22: 235–258.
- DRUMMOND, H. 1983. Aquatic foraging in garter snakes: comparison of specialists and generalists. *Behaviour* 86:1–30.
- FITCH, H. S. 1941. The feeding habits of California garter snakes. *California Fish and Game* 27:2–32.
- . 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. *Univ. Kansas Publ. Mus. Nat. Hist.* 15:351–468.
- GIBBONS, J. W., AND R. D. SEMLITSCH. 1987. Activity Patterns. In R. A. Seigel, J. T. Collins and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 396–421. MacMillan Publishing Co., New York.
- GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture in gopher snakes. *Copeia* 1974:141–148.
- GREGORY, P. T. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. *Can. J. Zool.* 56:1967–1974.
- . 1984. Correlations between body temperature and environmental factors and their variations with activity in garter snakes (*Thamnophis*). *Can. J. Zool.* 62:2244–2249.
- , AND K. J. NELSON. 1991. Predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. *Can. J. Zool.* 69:988–994.
- , AND ———. 1992. Erratum: predation on fish and intersite variation in the diet of common garter snakes, *Thamnophis sirtalis*, on Vancouver Island. *Can. J. Zool.* 70:2501.
- , L. H. CRAMPTON, AND K. M. SKEBO. *In press*. Conflicts and interactions among reproduction, thermoregulation, and feeding in viviparous reptiles: are gravid snakes anorexic? *J. Zool. (Lond.)* 247.
- HAILEY, A., AND P. M. C. DAVIES. 1987. Activity and thermoregulation of the snake *Natrix maura*. 1. r and K thermoregulation. *J. Zool. (Lond.)* 213:71–81.
- HAMMERSON, G. A. 1987. Thermal behavior of the snake *Coluber constrictor* in west-central California. *J. Therm. Biol.* 12:195–197.
- HECKROTTE, C. 1962. The effect of environmental factors in the locomotory activity of the plains garter snake (*Thamnophis radix radix*). *Anim. Behav.* 10: 193–207.
- HUEY, R. B. 1982. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12., pp. 25–91. Academic Press, London.
- , AND M. SLATKIN. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51:363–384.
- KEPHART, D. G. 1982. Microgeographic variation in the diets of garter snakes. *Oecologia* 52:287–291.
- , AND S. J. ARNOLD. 1982. Garter snake diets in a fluctuating environment: a seven-year study. *Ecology* 63:1232–1236.
- KRUUK, H., P. T. TAYLOR, AND G. A. T. MOM. 1997. Body temperature and foraging behaviour of the Eurasian otter (*Lutra lutra*), in relation to water temperature. *J. Zool. (London)* 241:689–697.
- LAGLER, K. F., AND J. C. SALYER III. 1945. Influence of availability on the feeding habits of the common garter snake. *Copeia* 1945:159–162.
- LANDRETH, H. F. 1973. Orientation and behavior of the rattlesnake *Crotalus atrox*. *Copeia* 1973:26–31.
- MOORE, R. G. 1978. Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado desert sidewinder (*Crotalus cerastes laterorepens*). *Copeia* 1978:439–442.
- MUNDIE, J. H., AND R. E. TRABER. 1983. Carrying capacity of an enhanced side-channel for rearing salmonids. *Can. J. Fish. Aquat. Sci.* 40:1320–1322.
- MUSHINSKY, H. R., J. J. HEBBARD, AND M. G. WALLEY. 1980. The role of temperature on the behavioral and ecological associations of sympatric water snakes. *Copeia* 1980:744–754.
- NAULLEAU, G. 1983. The effects of temperature on digestion in *Vipera aspis*. *J. Herpetol.* 17:166–170.
- PATTERSON, J. W., AND P. M. C. DAVIES. 1982. Predatory behavior and temperature relations in the snake *Natrix maura*. *Copeia* 1982:472–474.
- PETERSON, C. R., A. R. GIBSON, AND M. E. DORCAS. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*, pp. 241–314. McGraw-Hill, New York.
- PLATT, D. R. 1969. Natural history of hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. *Univ. Kansas Publ. Mus. Nat. Hist.* 18:253–420.
- POUGH, F. H. 1980. The advantages of ectothermy for tetrapods. *Amer. Natur.* 115:92–112.
- RICKER, W. E. 1984. Computation and uses of central trend lines. *Can. J. Zool.* 62:1897–1905.
- SAUNDERS, J. S., AND J. S. JACOB. 1980. Thermal ecology of the copperhead (*Agkistrodon contortrix*). *Herpetologica* 37:264–270.
- SCHARF, F. S., F. JUANES, AND M. SUTHERLAND. 1998.

- Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* 79:448–460.
- SCOTT, J. R., C. R. TRACY, AND D. PETTUS. 1982. A biophysical analysis of daily and seasonal utilization of climate space by a montane snake. *Ecology* 63: 482–493.
- SHINE, R., AND T. MADSEN. 1996. Is thermoregulation unimportant for most reptiles? an example using water pythons (*Liasis fuscus*) in tropical Australia. *Physiol. Zool.* 69:252–269.
- SKOCZYLAS, R. 1970. Influence of temperature on gastric digestion in the grass snake, *Natrix natrix* L. *Comp. Biochem. Physiol.* 33:793–804.
- STEVENSON, R. D., C. R. PETERSON AND J. S. TSUJI. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* 58:46–57.
- STEWART, G. R. 1965. Thermal ecology of the garter snakes *Thamnophis sirtalis concinnus* (Hallowell) and *Thamnophis ordinoides* (Baird and Girard). *Herpetologica* 21:81–102.
- THOMSON, J. D., G. WEIBLEN, B. A. THOMSON, S. ALFARO, AND P. LEGENDRE. 1996. Untangling multiple factors in spatial distributions: lilies, gophers and rocks. *Ecology* 77:1698–1715.
- WEATHERHEAD, P. J., AND F. W. ANDERKA. 1984. An improved radio transmitter and implantation technique for snakes. *J. Herpetol.* 18:264–269.
- WHITE, M., AND J. A. KOLB. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. *Copeia* 1974:126–136.

Accepted: 11 October 1999.

Journal of Herpetology, Vol. 34, No. 1, pp. 40–46, 2000
Copyright 2000 Society for the Study of Amphibians and Reptiles

Differences in Diet among Frogs and Lizards Coexisting in Subtropical Forests of Australia

ALBERTINA P. LIMA,¹ WILLIAM E. MAGNUSSON,¹ AND DAVID G. WILLIAMS²

¹Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia, CP. 478, 69011-970 Manaus Am, Brasil

²Applied Ecology Research Group, University of Canberra, P.O. Box 1, Belconnen ACT 2616, Australia

ABSTRACT.—This study investigates predator size and prey type as potential proximal causes of differences among diets of three lizard species (family Scincidae) and three frog species (subfamily Limnodynastinae) that coexist in wet subtropical forest in eastern Australia. Frogs eat smaller prey than lizards having the same gape size and there were significant differences in the types of arthropods eaten by frogs and lizards. Differences among species within frogs and lizards were small and not statistically significant. Frogs ate more amphipods, mites, and ants than the lizards, and lizards ate more termites, millipedes, isopods, and orthoptera than the frogs. Other categories were eaten in similar quantities by both frogs and lizards.

The degree of specialization in types and sizes of prey often changes with the body size of a predator. Change of diet with ontogeny has been related to changes in prey size in lizards (Schoener and Gorman, 1968; Rose, 1976; Domínguez and Salvador, 1990; Magnusson and Silva, 1993). Frogs change both prey type and prey size as they grow (Pengilley, 1971; Labanick, 1976; Christian, 1982; Donnelly, 1991; Simon and Toft, 1991; Wiggins, 1992). The latter authors suggested that the change in prey types is a result of the shift in prey size, because different types of arthropods have different mean sizes. However, diet composition differs among species in some assemblages of frogs (Lima and Magnusson, 1998) and lizards (Magnusson and Silva, 1993), and the shift in prey types with growth is more than a passive effect of selection for larger prey in seven species of leaf-litter

frogs of Central Amazônia (Lima and Moreira, 1993; Lima, 1998). Caldwell and Vitt (1999) showed consistent differences between species of lizards and species of frogs in one Amazonian locality, but there are no other published studies of differences in diet between syntopic lizards and frogs.

In this study, we make use of extensive collections of subtropical lizards and frogs in the Australian Museum to investigate the effects of predator size and species identity on diet composition within and between three species of lizards (family Scincidae) and three species of frogs (subfamily Limnodynastinae) that coexist in subtropical rainforest in eastern Australia.

MATERIALS AND METHODS

The frogs and lizards were collected during a New South Wales National Parks and Wildlife