Journal of Herpetology, Vol. 40, No. 3, pp. 335–342, 2006 Copyright 2006 Society for the Study of Amphibians and Reptiles

# Microhabitat Selection of Five-Lined Skinks in Northern Peripheral Populations

KATE C. QUIRT, GABRIEL BLOUIN-DEMERS, BRIAR J. HOWES, AND STEPHEN C. LOUGHEED 1,3

ABSTRACT.—Identifying microhabitat preferences is important in understanding distributions of organisms and crucial to focusing conservation efforts. The Five-Lined Skink (Eumeces fasciatus) is a rock-dwelling diurnal lizard that, in Canada, is considered a species of "special concern" under the recently passed Species at Risk Act (SARA). In this study, we examined the early-season diurnal retreat site selection preferences of the Five-Lined Skink at the northern limit of its range. To determine preferences we compared dimensions, thermal properties, and other associated microhabitat characteristics of rocks under which skinks were found to randomly selected rocks in two populations. A matched-pairs logistic regression revealed that individuals of E. fasciatus prefer longer than average cover rocks located in areas with few trees. We also found that, compared to other available cover element-substrate combinations, rocks lying on a bedrock substrate afford the best opportunities for skinks to achieve preferred body temperatures. These retreat site preferences are likely driven both by the necessities of thermoregulation and protection from predators.

Habitat selection is a central theme in ecology and conservation biology. Choice of habitat

involves interplay of such factors as thermal ecology, food and mate acquisition, and protection from predators (Huey, 1991; Downes and Shine, 1998; Downes, 2001). Within a habitat, these factors can be further optimized to the needs of the organism through microhabitat

<sup>&</sup>lt;sup>1</sup>Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada

<sup>&</sup>lt;sup>2</sup>Department of Biology, University of Ottawa, Ottawa, Ontario, K1N 6N5, Canada

 $<sup>^3</sup>$ Corresponding Author. E-mail: lougheed@biology.queensu.ca

choice (Huey et al., 1989; Kearney, 2001; Compton et al., 2002)

Temperature is an important aspect of habitat selection for all animals (Webb and Shine, 1998; Blouin-Demers and Weatherhead, 2001; Chruszcz and Barclay, 2002). However, the importance of thermoregulation is most obvious in ectotherms that adjust microhabitat use to maintain core body temperature within an optimal range (Huey, 1991; Kearney and Predavec, 2000; Shah et al., 2004). Thermoregulation is well studied in reptiles because of the particularly strong link between temperature and physiological processes (Huey and Slatkin, 1976; Huey, 1991; Chen et al., 2003; Zhang and Ji, 2004). Studies examining microhabitat selection afford an opportunity to observe preferences for a certain subset of thermal regimes available within a particular habitat. For example, in a classic paper Huey et al. (1989) found that garter snakes (Thamnophis sirtalis) select cover rocks with intermediate thickness because this enables them to achieve their preferred body temperature for greater durations over the course of a day. However, microhabitat selection may not be exclusively driven by thermoregulatory requirements. An experimental study of possible factors relevant to microhabitat selection for the Thick-Tailed Gecko (Nephrurus milii) revealed that protection from predators was a primary concern in addition to thermoregulation (Shah et al., 2004). The often-conflicting demands of protection from predators and foraging can compromise thermal preferences (Downes and Shine, 1998; Downes, 2001). For example, when predator scent was present, Garden Skinks (Lampropholis guichenoti) opted for safer microhabitats despite the suboptimal foraging and thermoregulatory opportunities they provided (Downes, 2001). Studying the structural and thermal properties of selected sites may provide valuable insight into a variety of ecological factors influencing microhabitat selection.

The Five-Lined Skink (Eumeces fasciatus) offers excellent opportunities for investigating thermal aspects of microhabitat selection. These lizards spend most of their time within retreat sites, such as logs, rocks, or leaf litter depending on the nature of their habitat (Fitch, 1954; Fitch and von Achen, 1977). Microhabitat selection should be particularly important in Ontario because environmental temperatures are, on average, far from the optimum for reptiles (Row and Blouin-Demers, 2006); thus, careful choice of retreat sites is necessary for skinks to maintain their body temperatures within the range that affords maximum performance.

In Canada, the Five-Lined Skink is considered to be of "special concern" under the newly

passed Species at Risk Act (SARA) primarily because of declining numbers and a decrease in number of populations (Committee on the Status of Endangered Wildlife in Canada, Status Assessments, http://www.cosewic.gc.ca/eng/ sct0/index\_e.cfm, 2005). Decreasing abundance in southwestern Ontario is attributable to conversion of habitat to agricultural lands and recreational development and to loss of suitable woody debris that provides cover for these small lizards (Hecnar and M'Closkey, 1998). The more northerly Canadian skink populations are found on granite outcrops covered with loose rock that provides cover (Patch, 1934), and indeed, it is proportion of available rock cover that best predicts microsite selection in these populations (Howes and Lougheed, 2004). In this study, our objective was to expand upon these previous results and examine the physical and thermal attributes that may be important in cover rock selection in two northern populations of Five-Lined Skinks.

### MATERIALS AND METHODS

We focused on two populations on the southern edge of the Canadian Shield in Ontario, Canada. The first study site (Frontenac County, 44°N, 76°W) consists of two parallel granite ridges embedded within a matrix of coniferous/deciduous forest. The second site (Lennox and Addington, 44°N, 77°W) consists of granite outcrops sloping upward from a small lake again surrounded by coniferous/deciduous forests. We cannot release more specific locality information because of concerns over illegal collection of skinks for the pet trade. Both sites are comprised of < 2 km<sup>2</sup> of exposed granite. The exposed granite is covered partly by herbaceous plants (grasses, small bushes, leaf litter), moss (Andreaea spp., Ceratodon spp.), fruticose lichens, bare soil, and loose cover rock ranging from pebbles to large slabs over 60 cm thick. The climate of the region is continental temperate with mean daily minimum and maximum air temperatures (in C°) ranging from the mid-20 s in July to several degrees below freezing in January (Environment Canada, Canadian Climate Normals, http://www. climate.weatheroffice.ec.gc.ca/climate\_normals, 2005).

Microhabitat Selection.—Howes and Lougheed (2004) showed that cover rocks play an important role in microsite selection for Five-Lined Skinks in Canadian Shield populations but investigated neither physical dimensions nor thermal properties of selected cover rocks. To further examine the role cover rocks play in habitat selection of skinks, we compared size, thermal properties, and other associated micro-

| Variable | Radius (m)   | Description   |  |  |  |
|----------|--------------|---|--|--|--|
| LROCK    |              | Length of focal rock (cm)   |  |  |  |
| WROCK    | _            | Width of focal rock (cm)  |  |  |  |
| TROCK    | _            | Thickness of focal rock (cm)  |  |  |  |
| ANGLE    | 10           | Slope angle (degrees) of granite bedrock in immediate region of focal rock  |  |  |  |
| ASPECT   | 10           | Slope aspect (degrees) of granite bedrock in immediate region of focal rock |  |  |  |
| CANCLO   | $45^{\circ}$ | Canopy closure (%) within a 45° vertical cone centered on the focal rock    |  |  |  |
| DEDGE    | 50           | Distance (m) to nearest edge  |  |  |  |
| %ROCK    | _            | Coverage (%) of rock under focal rock                                       |  |  |  |
| %SOIL    | _            | Coverage (%) of bare soil under focal rock                                  |  |  |  |
| %VEG     | _            | Coverage (%) of vegetation under focal rock                                 |  |  |  |
| %TREE5   | 5            | Coverage (%) of trees within plot centered on focal rock                    |  |  |  |
| %ROCK5   | 5            | Coverage (%) of exposed rock within plot centered on focal rock             |  |  |  |
| %MOSS5   | 5            | Coverage (%) of mosses within plot centered on focal rock                   |  |  |  |
| %HERB5   | 5            | Coverage (%) of herbs within plot centered on focal rock                    |  |  |  |

Table 1. Structural variables used in the analysis of habitat selection by Five-Lined Skinks in Ontario with associated abbreviations and sampling radii.

habitat characteristics of rocks under which skinks were found (occupied rocks) to rocks under which no skinks were found (random rocks). This approach has been used successfully in other studies (Schlesinger and Shine, 1994; Compton et al., 2002).

Data were collected between 8 May 2005 and 3 June 2005 between 1000 h and 1600 h EST. Mean daily temperatures over this period were 5–24°C. The Frontenac County and Lennox and Addington County sites were visited seven and four times, respectively. During each visit, a team of three to five observers systemically lifted all cover rocks found on the exposed granite except rocks requiring more than two people to lift, and rocks deeply embedded (> 15 cm) within the substrate. The exclusion of the larger and embedded rocks could bias our sampling toward those that were more easily turned. However, a previous study indicated that the preferred dimensions of occupied rocks were typically smaller than the maximum dimensions of rocks that two or more people could lift (Howes and Lougheed, 2004). When a skink was found beneath a rock, it was handcaptured and classified as juvenile, female, or male depending on size and coloration. For each rock under which we found a skink, we chose a rock at random for comparison. The random rock was one that a skink could potentially use, closest to a point determined by walking a randomly determined distance (from the roll of a 20-sided die that determined the number of paces from the occupied rock) in a randomly chosen direction (from the random spin of a compass bearing dial).

For each occupied and random rock, we recorded 14 structural habitat variables (Table 1). We visually estimated the percent coverage of the various land covers to the nearest 5%. We calculated the slope angle of the granite

in the immediate region of the rock from the inverse tangent of the vertical height gained per horizontal distance (< 2 m). We measured the slope aspect in degrees from magnetic north. The canopy closure was evaluated by lying horizontally next to the focal rock and looking upward through a piece of 2-cm radius tubing with cross-hairs at one end. The tubing was aimed haphazardly by the observer within a  $45^{\circ}$  vertical cone. The tubing was aimed 20 times and each time the observer noted whether canopy intercepted the cross-hairs (a hit). The percent canopy closure was calculated by multiplying the number of hits by five.

To analyze microhabitat selection based on habitat characterization, we used matched-pairs logistic regression where each skink location is compared to its paired random location to control for variations in environmental conditions through time and to ensure that the random locations were available to the individual (Compton et al., 2002; Keating and Cherry, 2004). In matched-pairs logistic regression, the estimated coefficients are interpreted the same way as in standard logistic regression. For a coefficient  $\beta_i$ , an *n*-unit increase in the habitat variable corresponds to an  $e^{n\beta i}$  increase in the odds ratio. Because the presence of a skink is a low probability event, the odds ratio estimates the relative risk, which is the ratio of the probability of x (the presence of a skink) given A (variables measured at the skink location) to the probability of x given B (variables measured at the random location; Breslow and Day, 1980; Compton et al., 2002). Also, because in the paired design the variables are differences in values between skink and random observations, the model is interpreted as differences in the habitat and not as absolute measured values.

Based on preliminary univariate and multivariate analyses, we selected candidate models.

We chose these models conservatively and included only variables most likely to account for the differences between skink and random locations. Single members of groups of highly correlated variables were included in the candidate models to avoid masking of the effects of important variables. Candidate models were compared against each other using Akaike's Information Criterion (AIC; Burnham and Anderson, 1994). The linearity of the final models was tested using design variables based on the quartiles of each original variable (Hosmer and Lemeshow, 2000).

Thermal Profiles.—The second part of this study examined the thermal profiles of occupied rocks compared to other cover elements available over a two-week period at our Frontenac County site. We wished to determine whether the rocks used by skinks had thermal profiles that would lead to body temperatures closer to the optimum for performance than other types of cover elements. The site was visited seven times between 8 May 2005 and 24 May 2005. During each visit, we searched as many potential cover rocks as possible and particularly those where a skink had been found on previous occasions. At the end of this period, we selected six rocks (lying on bedrock) that were occupied on at least two visits. We selected one unoccupied rock (lying on bedrock) at random for each of the six focal occupied rocks (as above). For further comparison, we chose three other categories of possible cover elements (under which we have never found skinks during our intensive surveys over the last four years): two rocks lying on a humus substrate in forest, two logs (> 40 cm diameter) on bedrock, and two logs that were relatively large (> 40 cm diameter) and moderately decayed (according to Hecnar, 1994) within forest, again on a humus substrate. Under all 18 cover elements, we placed an iButton temperature data logger (DS1921, Dallas Semiconductor, Sunnyvale, CA) as close to the center as possible. The loggers were programmed to measure the temperature on the hour for the duration of the field study, from 0100 h on 27 May 2005 to 2400 h on 10 June 2005.

For the purpose of statistical analyses, temperatures collected prior to 1000 h and after 1600 h were excluded because we do not know whether skinks exhibit the same retreat site

preferences outside of this time frame. Preferred body temperature for Five-Lined Skinks (T<sub>set</sub>) is between 28°C and 36°C (Fitch, 1954), and we employ this range here. For each temperature recorded for each cover element, we calculated the thermal quality index (d<sub>e</sub>) of Hertz et al. (1993): the deviations of environmental temperatures from the preferred temperature range in absolute values. For each cover element, we averaged all values of d<sub>e</sub> across the 15 days for which we had data (N = 135 for each element). We compared the average de under the occupied and random rocks with a paired *t*-test. This test was one-tailed because we predicted that mean d<sub>e</sub> should be higher for unoccupied rocks. We did not conduct formal statistical analyses for the other cover elements because of small sample sizes and instead focused on the thermal properties of skink preferred microsites, rock on rock (Howes and Lougheed, 2004). We simply plotted values for each of the five cover element-substrate combinations.

Statistical Analyses.—All statistical analyses were performed with R (R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, R Development Core Team, Vienna, Austria, 2004) and JMP version 5 (SAS Institute, Inc., Cary, NC). We inspected box plots to determine whether assumptions of normality and homogeneity of variance were upheld. We reported all means  $\pm$  1 SE and accepted significance of tests at  $\alpha$  = 0.05.

#### RESULTS

Microhabitat Selection.—We characterized the habitat at a total of 88 skink rocks (32 females, 10 males, and 46 juveniles) and 88 random rocks. Because our sample sizes were modest for each reproductive group, we pooled data for all reproductive classes in our analyses. This should make our tests more conservative because age and sex differences may alter retreat-site selection preferences. We selected the model with the lowest AIC value. The best model had two variables (LROCK and %TREE5) and was significant (AIC = 68.9,  $R^2$ = 0.27, Wald<sub>2</sub> = 21.6, P < 0.001). Based on the odds ratios, skinks used longer than average rocks that were in areas with few trees: a 1-cm increase in LROCK resulted in a 6% increase in the probability of selection and a 1% increase in

Table 2. Paired logistic regression model of microhabitat selection for Five-Lined Skinks in Ontario.

| Variable | Coefficient       | SE    | Increase | Odds ratio | 95% CI (OR)  |
|----------|-------------------|-------|----------|------------|--------------|
| LROCK    | $0.065 \\ -0.047$ | 0.015 | 1 cm     | 0.94       | (1.04, 1.10) |
| %TREE5   |                   | 0.021 | 1%       | 1.05       | (0.92, 0.99) |

%TREE5 resulted in a 5% decrease in the probability of selection (Table 2). Rocks used by skinks were  $55.2 \pm 2.1$  cm long on average, whereas unoccupied rocks were  $33.5 \pm 1.7$  cm long on average. Similarly, the 5-m area surrounding occupied rocks had canopy closures that average  $7.2 \pm 1.2$ %, whereas the 5-m area surrounding unoccupied rocks had canopy closures that averaged  $16.5 \pm 2.5$ %.

Thermal Profiles.—The mean deviation from the preferred temperature range across 15 days was  $1.99 \pm 0.65$ °C for occupied rocks and  $4.33 \pm 2.11$ °C for unoccupied rocks. Our paired *t*-test (N=5 pairs because one data logger failed) indicated that this difference was marginally significant ( $t_{(4)}=2.173,\ P=0.047$ ). Cover elements in forest showed the highest mean temperature deviations from the preferred range, and the rocks under which we found skinks showed the lowest (Fig. 1).

Rocks on bedrock selected by skinks show little variation in their thermal profiles. Each affords a period between 1100 h and 1900 h in which substrate temperatures are within the range of preferred body temperatures (Fig. 1). Rocks unoccupied by skinks exhibit greater variation in their thermal profiles. Some rocks fail to reach temperatures within the preferred range and some may become hotter (Fig. 1). It is clear that logs within forest, logs on bedrock, and rocks within a forest are too cool and seldom reach preferred body temperatures (Fig. 1).

## DISCUSSION

Our study shows that individuals of *E. fasciatus* in two northern populations select a subset of available cover elements and that longer than average rocks lying on a bedrock substrate afford the best opportunities for Five-Lined Skinks to achieve preferred body temperatures early in the active season. These findings can provide insight into factors that limit the distribution of this species, and have implications for the conservation of these northern Canadian populations that are of conservation concern.

Quantifying the structural and thermal aspects of selected microsites provides valuable information regarding a variety of ecological factors that influence microhabitat selection, such as thermal benefits, social advantages, and avoidance of predators (Downes and Shine, 1998). Our results show that individuals of *E. fasciatus* prefer cover rocks that were longer, on average, than unoccupied cover rocks. Other studies have shown that cover dimensions are important structural elements for microsite selection in lizards (Schlesinger and Shine,

1994; Webb and Shine, 1998; Kearney, 2001) potentially providing a number of benefits. Shah et al. (2004) showed that the Thick-Tailed Gecko (N. milii) actively selected shelter sites that offered a high degree of concealment from predators. Larger cover rocks may also expose lizards to a greater thermal gradient, thereby allowing individuals to exploit different thermal regimes over the diurnal cycle without traveling to a new site and risking predation (Huey et al., 1989). Longer cover rocks may also correspond to a greater likelihood of encountering prey items or conspecifics (Seburn, 1993). This factor may be especially important during the breeding season when adults are searching for mates or during nesting season when female adults of E. fasciatus show aggregated nesting behavior (Fitch, 1954; Seburn, 1993; Hecnar, 1994; B. J. Howes and S. C. Lougheed, pers. obs.). Important to consider is the unavoidable bias arising from excluding rocks that are too large to turn over. Inclusion of these data would have likely indicated whether there exists a limit to preferred rock length.

Individuals of *E. fasciatus* also showed preferences for cover rocks that were located in more open (few trees) microsites than unoccupied cover rocks. This retreat site feature relates to how exposed the cover rock surface is to solar radiation and how much granite bedrock surrounds the microsite and, thus, may ultimately be important in determining the thermal profile of a cover rock. In other areas of Ontario like Point Pelee, degree of shading may be less significant in microhabitat selection of E. fasciatus because it is not indicative of a specific type of substrate (Seburn, 1993). Individuals in the populations that we studied selected rocks offering thermal conditions that most closely matched their preferred body temperature range, presumably to maximize time within temperatures at which physiological processes are maximized (Huey, 1991; Chen et al., 2003). Numerous other studies of saxicolous reptiles show that they selectively use microhabitats where their preferred T<sub>b</sub>s are most easily attainable (Thamnophis elegans, Huey et al., 1989; Oedura lesueurii, Schlesinger and Shine, 1994; Hoplocephalus bungariodes, Webb and Shine, 1998; Christinus marmoratus, Kearney, 2001).

Our results also provide clues as to factors that may determine the northern range limits of *E. fasciatus*. At the northern edge of the species' range, *E. fasciatus* is less generally distributed than it is further south and seems to be restricted to open rock outcrops that have greater thermal quality than surrounding habitats (Fitch, 1954). Individuals of *E. fasciatus* in our northern study populations selected micro-

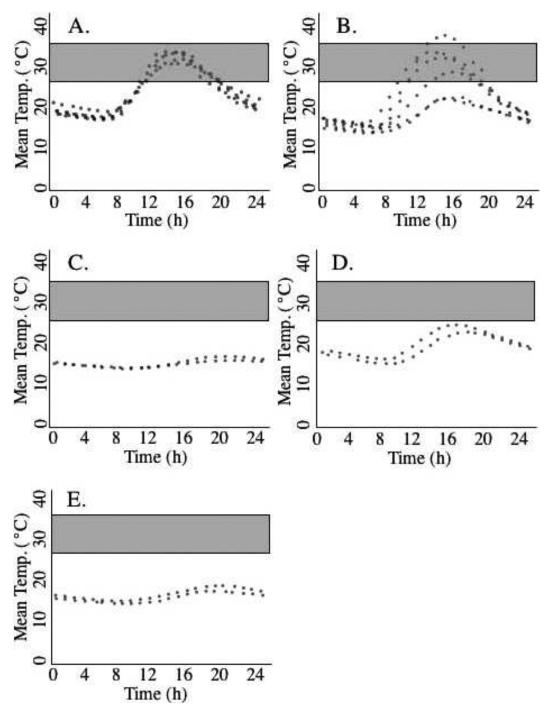


Fig. 1. Average 24-h temperature profiles of each iButton temperature data logger for each of the six cover element type/substrate combinations. The grey rectangle shows the preferred temperature range of *Eumeces fasciatus*. (A) occupied rock on bedrock, (B) unoccupied randomly selected rock on bedrock, (C) log on forest floor, (D) log on bedrock, (E) rock on forest floor.

sites with high thermal quality that closely matched their preferred body temperature range. It is possible that the northern distribution of *E. fasciatus* is limited by inadequate thermal properties of microsites beyond the current distribution of the species. Examining adult or juvenile (i.e., second year) thermal preferences during daylight hours during the breeding season is one aspect of the thermal ecology for this species. Additionally, range limits may arise as a result of thermal limitations during other parts of their life cycle or annual cycle such as during hibernation or egg development. Rosen (1991) proposed that the selection of suitable hibernacula is essential to the persistence of populations of Coluber constrictor foxii in cold climates and, thus, may dictate the northern range limit of the species. St. Clair and Gregory (1990) suggested that low temperatures in Painted Turtle (Chrysemys picta) nests may exceed the thermal tolerance of the species in some years and, therefore, may determine the northern range limit of the species in southern British Columbia. Likewise, because the egg is a highly vulnerable stage in the life cycle of oviparous reptiles (Packard and Packard, 1988) temperature constraints on egg incubation may also influence the range limit. For example, Muth (1980) suggested that the geographical range of the lizard Dipsosaurus dorsalis may be limited by the climatic restrictions on egg incubation rather than on adult physiology. Similarly, the differences in altitude ranges of Sceloporus occidentalis and Sceloporus graciosus may be a result of different thermal constraints on egg physiology (Adolph, 1990). Undoubtedly, additional environmental factors also influence the geographic range of E. fasciatus. Ussher and Cook (1979) suggested that moisture level and drainage was important in determining the northeastern range limit of the species in Ontario. Soil moisture was found to be an important physical factor in microsite selection of nests for individuals of *E. fasciatus* in southwestern Ontario (Hecnar, 1994), further supporting the notion that environmental factors other than temperature may contribute to the range limits of the species.

To better address whether the structural and thermal features of retreat sites are involved in determining the northern range limits of *E. fasciatus* further research is required. Comparing the thermal profiles of occupied cover rocks observed in our populations with cover rocks of similar dimensions located in similar habitat beyond the known species range may shed light on this question. If few cover rocks provided opportunities for individuals of *E. fasciatus* to achieve their preferred body temperature range, we could intuit that the northern limit of the

species range is influenced, at least in part, by thermal properties of microsites. We could also examine the structural and thermal features of nest sites for individuals in these northern populations. These properties could directly influence successful egg development and perhaps ultimately, successful recruitment of individuals into the population. Additionally, it would be interesting to track individuals throughout their entire diurnal and seasonal cycle as retreat site selection in lizards may change across temporal scales (e.g., *Christinus marmoratus*; Kearney, 2001).

Finally, our results have important conservation implications for these northern populations of *E. fasciatus* that are considered to be at risk in Canada. Hecnar and M'Closkey (1998) showed that *E. fasciatus* are sensitive to the removal of suitable microhabitat. Between 1990 and 1995, there was a fivefold decrease in the skink population at Point Pelee National Park, Ontario, Canada, as a result of microhabitat loss. It is likely that removal or destruction of cover elements in Canadian Shield populations will result in similar population declines. A better understanding of habitat selection within this northern range limit would help focus conservation efforts. Conservation techniques such as the use of artificial rocks on degraded rocky outcrops have proven to be successful in restoring suitable microhabitats for the snake Holocephalus bungaroides and lizard Oesoutheastern dura lesueurii in Australia (Webb and Shine, 2000) and may prove to be effective in restoring E. fasciatus habitat on the Canadian Shield if local population extinction occurs.

Acknowledgments.—This research would not have been completed without the enthusiastic and dedicated field help of J. Agostino, P. Jiang, and R. Dakin, nor without the logistical support of B. Montgomerie. Thanks to G. Smith, S. Hecnar, and an anonymous reviewer for suggestions for improvement of this manuscript. We are also grateful to J. Row for statistical advice and to G. Bulté for programming the data loggers. NSERC and CFI/OIT provided funding for this work, and OMNR issued the required permits.

#### LITERATURE CITED

ADOLPH, S. C. 1990. Influence of behavioural thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology 71:315–327.

BLOUIN-DEMERS, G., AND P. J. WEATHERHEAD. 2001. Habitat use by Black Rat Snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. Ecology 83: 2882–2896.

- Breslow, N. E., and N. E. Day. 1980. Statistical Methods in Cancer Research. Lyon, France.
- Burnham, K. P., and K. P. Anderson. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75:1780–1793.
- CHEN, X. J., X. F. Xu, AND J. XIANG. 2003. Influence of body temperature on food assimilation and locomotor performance in White-Striped Grass Lizards, *Takydromus wolteri* (Lacertidae). Journal of Thermal Biology 28:385–391.
- CHRUSZCZ, B. J., AND R. M. R. BARCLAY. 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices. Functional Ecology 16:18–26.
- Compton, B. C., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.
- Downes, S. 2001. Trading heat and food for safety: costs of predator avoidance in a lizard: Ecology 82:2870–2881.
- Downes, S., and R. Shine. 1998. Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities: Animal Behaviour 55:1387–396.
- FITCH, H. S. 1954. Life history and ecology of the Five-Lined Skink, *Eumeces fascitus*. University of Kansas Publications Museum of Natural History 8:1– 156
- FITCH, H. S., AND P. L. VON ACHEN. 1977. Spatial relationships and seasonality in the skinks *Eumeces fasciatus* and *Scincella laterale* in northwestern Kansas. Herpetologica 33:303–313.
- HECNAR, S. J. 1994. Nest distribution, site selection, and brooding in the Five-Lined Skink (Eumeces fasciatus). Canadian Journal of Zoology 72:1510–1516.
- HECNAR, S. J., AND R. T. M'CLOSKEY. 1998. Effects of human disturbance on five-lined skink, *Eumeces fasciatus*, abundance and distribution. Biological Conservation 85:213–222.
- Hertz, P. E., R. B. Huey, and R. D. Stevenson. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. American Naturalist 142:796–818.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. 2nd ed. John Wiley and Sons, Inc., New York.
- Howes, B. J., and S. C. Lougheed. 2004. The importance of cover rock in northern populations of the Five-Lined Skink (*Eumeces fasciatus*). Herpetologica 60:287–294.
- Huey, R. B. 1991. Physiological consequences of habitat selection. American Naturalist 137: S91–S115.
- HUEY, R. B., AND M. SLATKIN. 1976. Cost and benefits of lizard thermoregulation. Quarterly Review of Biology 51:363–384.
- HUEY, R. B., C. R. PETERSON, S. J. ARNOLD, AND W. P. PORTER. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by the garter snakes and its thermal consequences. Ecology 70:931–944.

- KEARNEY, M. 2001. Hot rocks and much-too-hot rocks: seasonal patterns of retreat-site selection by nocturnal ectotherm. Journal of Thermal Ecology 27:205–218.
- KEARNEY, M., AND M. PREDAVEC. 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. Ecology 81:2984–2996.
- KEATING, K. A., AND S. CHERRY. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.
- Muth, A. 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. Ecology 61:1335–1343.
- PACKARD, G. C., AND M. J. PACKARD. 1988. The physiological ecology of reptilian eggs and embryos. *In C.* Gans and R. B. Huey (eds.), Biology of the Reptilia. Vol. 16, pp. 523–606. Academic Press, New York.
- Patch, C. L. 1934. *Eumeces* in Canada. Copeia 1934:50–51.
- ROSEN, P. C. 1991. Comparative ecology and life history of the racer (*Coluber constrictor*) in Michigan. Copeia 1991:897–909.
- Row, J. R., and G. Blouin-Demers. 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milksnakes. Oecologia 148:1–11.
- Schlesinger, C. A., and R. Shine. 1994. Choosing a rock: perspectives of a bush-rock collector and saxicolous lizard. Biological Conservation 67:49–56.
- SEBURN, C. N. L. 1993. Spatial distribution and microhabitat use in the Five-Lined Skink (Eumeces fasciatus). Canadian Journal of Zoology 71:445– 450
- SHAH, B., R. SHINE, S. HUDSON, AND M. KEARNEY. 2004. Experimental analysis of retreat-site selection by Thick-Tailed Geckos Nephrurus milii. Austral Ecology 29:547–552.
- St. Clair, R. C., and P. T. Gregory. 1990. Factors affecting the northern range limit of painted turtles (*Chrysemys picta*)—winter acidosis or freezing. Copeia 1990:1083–1089.
- USSHER, R. D., AND F. R. COOK. 1979. Eastern limit of the Five-Lined Skink, *Eumeces fasciatus*, in Ontario. Canadian Field Naturalist 93:321–323.
- Webb, J. K., and R. Shine. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. Biological Conservation 86:233–242.
- 2000. Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? Biological Conservation 92:92–99.
- ZHANG, Y. P., AND X. Ji. 2004. The thermal dependence of food assimilation and locomotor performance in southern grass lizards, *Takydromus sexlineatus* (Lacertidae). Journal of Thermal Biology 29:45–53.

Accepted: 20 April 2006