

**Habitat selection in the Common Five-lined Skink near the northern
extent of its range**

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Abstract

The study of habitat selection is vital to identify potential threats and to conserve species at risk. The consequences of living in a particular habitat can influence processes beyond the individual with observable effects on populations, species interactions, assembly of ecological communities, and the origin and maintenance of biodiversity. Northern populations of the Common Five-lined Skink (*Plestiodon fasciatus*) occur primarily in open areas within the eastern deciduous forest of North America. One of two Canadian populations of the Five-lined Skink, the Carolinian population, is currently listed as endangered. The comparative use of macrohabitat types available in northern populations has not been formally described. Furthermore, the relative importance of canopy structure (and associated thermal environment for skinks) when compared to other habitat factors is not well understood. My study asks (1) what macrohabitats are used most by skinks, (2) which habitat factors best predict occupancy, and (3) whether skinks show a gradual or a threshold response to increasing forest canopy cover. I conducted my study at Rondeau Provincial Park in southwestern Ontario. To measure macrohabitat use I completed visual surveys of coverboards placed in four main terrestrial habitat types available at the study site. I compared expected to observed use in each habitat type. To measure how occupancy might be affected by multiple habitat parameters, I completed visual surveys of coverboard transects and collected habitat measurements in the field and using GIS. I used Poisson regression analysis and Akaike Information Criteria to determine which variables contributed to the prediction of site occupancy. I then analysed the same data set using piecewise regression to test for abrupt changes in the relationship between site use and canopy cover. Skinks preferred dune habitat of the main terrestrial habitats available. Skink habitat use was affected most by temperature, canopy cover and moisture. Skinks exhibited a negative threshold response to canopy cover >50% for much of the active season. Habitat loss and the rate of natural succession are concerns for the remaining Endangered Carolinian populations of the Five-lined Skink. Understanding which habitats are used most by this species may assist targeted management efforts to preserve existing isolated populations and to restore areas for future translocations.

Lay Summary

Wildlife typically occur over the landscape unevenly, with species occupying only a small proportion of habitats available to them. For conservation of wildlife to be effective it is important to determine if available habitats are capable of supporting species of interest. I studied habitat use of the Common Five-lined Skink near the northern extent of its range. Specifically, I investigated whether skinks were evenly abundant in dune, savannah, forest and human altered habitats. I also investigated what habitat factors best determined if skinks were present at a location. Finally, I investigated whether skinks responded to increasing forest cover abruptly, and if so, where this occurs. I found that skinks showed an overall preference for dune habitat during much of the time they are active. I found that temperature, canopy and moisture were the factors most important in determining whether skinks would be present at a site. I also discovered that skinks responded abruptly to increasing forest cover and that they were not likely to use locations with greater than 50% forest cover. My findings may assist targeted management efforts to preserve currently isolated populations as well as to restore areas for skink translocation.

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Chapter 1: General Introduction

The study of how and why organisms select particular habitats has a history as long as any integrative topic in ecology (Huey 1991, Rosenzweig 1991) and continues today to be a central focus of evolutionary ecologists and conservation biologists alike (Morris et al. 2008). The term *habitat* is often used to describe the area in which an animal lives, fulfilling all necessary aspects of its life. However, the exact meaning of the term tends to vary depending on the life history of the animal and the goal of the researcher (Stamps 2012). Morris (2003a) defines habitat as a spatially bounded area with a subset of physical and biotic conditions, within which the density of interacting individuals and at least one of the parameters of population growth are different from adjacent areas. Habitats are therefore species-specific and are ultimately best defined by the distributional patterns of the organism concerned (Stamps 2012). Habitats typically vary in quality and extent, making the selection of the best of available habitats essential for maximizing a species' fitness (Rosenzweig 1974, 1981; Morris 1987). Habitat selection in its simplest form can be defined as the process whereby individuals preferentially use, or occupy, a non-random set of available habitats (Morris 2003a).

Selection can be viewed as a hierarchical process (i.e. coarse to fine-grained patch choice) by which an organism selects a general place in which to live (macrohabitat) and then makes subsequent decisions about the use of different patches, search modes it employs, and its responses to specific objects and conditions that it encounters (microhabitat) (Johnson 1980, Orians and Wittenberger 1991). Patterns of use and complexity are often varied at micro- and macrohabitat scales and consequently, the scale at which selection occurs is important when

assessing habitat use (Morris 1987). Defining the scale of habitats which organisms use is difficult and may vary depending on the context of the organisms seasonal behaviours, heterogeneity of available environmental factors, and the focus of the researcher. Macrohabitat can be defined as a location capable of supporting an individual's biological requirements during a period of activity (Morris 1987) such as a zone of vegetation (e.g. bog, woodland, grassland). Microhabitat can be defined as a location an organism engages in specific activities such as breeding, foraging and resting and individuals are expected to utilize multiple microhabitats to during any period of activity (Stamps 2012).

To appropriately assess and mitigate species losses managers require accurate assessments of populations and detailed information pertaining to environmental constraints and habitat/species interactions (Bradshaw 2012). At a time when many species face local extirpation through habitat loss, knowledge on habitat requirements is vital to the success of conservation initiatives. Conservation efforts, if misdirected, can lead to wasted resources that otherwise could be put to valuable scientific or conservation initiatives (Manly et al. 2002, Pike et al. 2011). Researchers seeking to explore and answer questions of habitat use are therefore charged with identifying determinant factors of habitat selection as well as providing meaningful interpretation of their findings for those seeking to implement successful management strategies.

Ectotherms can be relatively more sensitive to changes in structural microhabitat elements than endotherms and, as such, available structures comprising a local habitat can often directly influence microclimatic conditions important for thermoregulation (Pianka 1973, Heatwole 1977, Huey 1991, Smith and Ballinger 2001). Several studies have demonstrated effects of

habitat use on the life history traits of lizards, with implications for individual fitness (See: Smith and Ballinger 2001). Many factors can act on the strength of habitat selection in lizards, including substrate composition, canopy structure, moisture, predation and anthropogenic disturbance (Huey 1991, Hecnar 1994, Garden et al. 2007, Watson 2008, Lopez and Martin 2013). The direct physiological influence that habitat structure has on lizard functionality makes these organisms suitable for exploring the effects of habitat type and structure on occupancy. This is particularly true of lizard species at the northern limits of their range in Canada, where they must respond to relatively cooler and shorter periods of activity relative to other regions within their range (Powell and Russell 2007).

Preferred body temperatures in lizards often coincide with optimal performance temperatures for physiological requirements (Dawson 1975, Huey and Bennett 1987) and overall fitness (Huey and Kingsolver 1989). Thermoregulation is particularly important for reptiles in northern environments because temperatures are often far from a species' optimum (Blouin-Demers and Weatherhead 2001, Powell and Russell 2007).

Describing habitat selection beyond critical levels of change is important for understanding gradual population declines in relation to habitat loss and fragmentation (Cunningham and Johnson 2012). Looking beyond directional responses of species to habitat characteristics, the identification of ecological thresholds is of particular interest for conservation efforts (Cunningham and Johnson 2012). Ecological thresholds can be characterized as abrupt changes in a response variable as a consequence of continuous change in an independent variable (Muradian 2001), or similarly one or more zones at which relatively rapid change occurs from

one ecological condition to another (Bennett and Radford 2003). Attaining knowledge of ecological thresholds can help define sensitivity of species to threatening processes such as the loss, simplification and fragmentation of habitat (Hugget 2005).

The Five-lined Skink (*Plestiodon* [formerly *Eumeces*] *fasciatus*) is a small, diurnally active but secretive, semi-fossorial lizard that occurs in eastern North America (Conant and Collins 1998). Although its range highly overlaps with the distribution of the eastern deciduous forest (Braun 1950), *P. fasciatus* tends not to occur in dense forest but in associated open and edge habitats (Fitch 1954). Habitat descriptions of *P. fasciatus* vary throughout its relatively large range (Fitch 1954, Hecnar 1991, Seburn 1993, Quirt et al. 2006, Watson and Gough 2012), with evidence suggesting southern populations occur in more closed canopy/wooded areas, while more northerly populations occur in relatively more open habitats (Fitch 1954, Hecnar 1991, Watson and Gough 2012, Quirt et al. 2006).

An essential habitat component for this species is the presence of suitable microhabitat (woody or rock debris) that provides refuge cover in open macrohabitats (Fitch 1954, Hecnar 1991, 1994). Five-lined Skinks spend about 90 percent of their time under cover objects and make short foraging forays into surrounding areas (Fitch 1954, Fitch and von Achen 1977) where they search for arthropod prey (Judd 1962, Hecnar et al. 2002, Brazeau et al. 2015). Individuals tend to congregate beneath the same microhabitat debris (Fitch 1954; Hecnar 1991, 1994; Seburn 1993). Aside from some agonistic behaviour among wandering males during breeding season, skinks are non-territorial, somewhat social, have shifting home ranges (Fitch 1954) and do not seem to be limited by density dependent effects (Hecnar 1991).

Plestiodon fasciatus do not occupy fixed home ranges but instead use a succession of cover objects moving up to a maximum of just over 100 meters in a year (Fitch 1954; Seburn 1990, 1993). Detailed mark-recapture studies by Fitch (1954) showed that *P. fasciatus* may move distances of up to 207 m from points of original capture (average 18 m, $n = 323$). Time between captures ranged from one day to 47 months. The activity level of *P. fasciatus* varies considerably throughout the year and between sexes (Fitch 1954). Skink activity in Ontario appears to show two peaks of activity: during May, when males are searching for females, and during July, when females brood their eggs (Hecnar 1991, Seburn 1993). In fall, hatchlings and juveniles are actively foraging to build fat reserves for winter. Few details regarding hibernation are known, but there is evidence that skinks in Ontario hibernate in their home ranges either singly or in groups underground or in debris that provides protection from freezing or flooding (Hecnar et al. 2012a). During breeding season, males develop a bright red suffusion of the jaws and actively search for mates, while females and juveniles are actively foraging to build fat reserves (during this time egg development occurs). This red suffusion is an indicator that mating season is at or near its peak, and indicates that a majority of the population is active either in seeking mates or in foraging. Following this period of heightened activity, males will often retreat to underground refugia and females will search for nesting sites. Juveniles remain active throughout their first full season to build up fat reserves and prepare for hibernation (Fitch 1954).

Five-lined Skinks in Canada occur in two designated units, the Carolinian Population (southwestern Ontario), and the Great-Lakes – St. Lawrence/Southern Shield Population (central Ontario; COSEWIC 2007). These two populations were separated into two distinct groups based

on genetic divergence and isolation (Howes et al. 2006, COSEWIC 2007, Howes and Lougheed 2008). The Great Lakes St. Lawrence population, currently designated as "Special Concern," is comprised of 84 sub-populations spread over a relatively small geographic area. Current spatial structure allows for sufficient connectivity to facilitate dispersal between populations, but human development of infrastructure threatens to increase isolation (Wick 2004, COSEWIC 2007).

The Carolinian Population of Five-lined Skinks in Canada is listed as "Endangered" (COSEWIC 2007, Environment Canada 2014) because of historical decline resulting from habitat loss, habitat degradation, isolation from extreme habitat fragmentation and other threats. The distance between extant populations in the Carolinian Zone vastly exceeds the dispersal capabilities of the species (Hecnar, unpublished data). Knowledge of the habitat relationships, general ecology, and status of local *P. fasciatus* populations is vital for future regional species recovery (Seburn 2010). Further, an improved understanding of the similarities or differences in habitat preference among extant populations is essential to guide strategies and methodologies for future regional restoration efforts. Carolinian habitats are so-named because they are characteristic of areas in the southeastern United States and include a variety of ecosystems such as forests, prairies, and wetlands. They are restricted in their Canadian distributions to southern Ontario in areas that have been mostly converted to agriculture (Allen et al. 1990). Because people are generally unaware of the existence of a lizard in Ontario, the Five-lined Skink provides the public with insight into the biodiversity of Canadian fauna. The charismatic nature and attractive colouration of *P. fasciatus* is appealing to most people, and the use of the skink as a „flagship“ as well as an „umbrella“ species encourages public increase awareness and understanding of Ontario reptiles as a whole (COSEWIC 2007).

The isolated skink population in Point Pelee National Park (PPNP; 41°57' N, -81° 31' W), southwestern Ontario, is the only Carolinian population for which detailed ecological and biological knowledge is available (COSEWIC 2007, Seburn 2010). Over a quarter century of study has revealed that the highest skink densities occur in open habitats such as stabilized dune and cedar savanna associated with the dynamic shoreline of Lake Erie and open, old-field, anthropogenic, and relictual tallgrass prairie patches in the PPNP interior (Hecnar 1991, 1994; Hecnar and M'Closkey 1998; Hecnar and Hecnar 2013). Hecnar and M'Closkey (1998) observed that loss of microhabitat at PPNP was one of the leading causes of a decline in population size, and further research and active management at PPNP showed that open habitats could be restored by adding suitable woody debris (Hecnar and M'Closkey 1998, Hecnar and Hecnar 2011). Individuals of *P. fasciatus* prefer relatively large logs of >17cm diameter and boards of >1,700 cm² area that provide microhabitat (Hecnar and M'Closkey 1998, Seburn 1993).

Rondeau Provincial Park (RPP; 42°17' N, -81° 52' W), near Morpeth, Ontario, is located on Lake Erie (Figure 1.1) on a rounded, 35-km² cusped peninsula approximately 7 km long, 0.5 km across at the narrowest and most northern extent, and gradually widening to a maximum of 2 km across at the southern extent. RPP contains one of the largest continuous remaining tracts of Carolinian Forest in Canada. The park is surrounded by water and areas of intensive agricultural and urban development, making the peninsula a functional island of terrestrial natural habitat. RPP was founded in 1884 and has been managed at various levels over the last century (Mann and Nelson 1980). The Lake Erie Lowlands region, in which RPP and PPNP are both located, is

one of the warmest regions in Canada, with a mean annual temperature of $\sim 8^{\circ}\text{C}$, mean summer temperature of 18°C and a mean winter temperature of -2.5°C . Precipitation from a neighbouring weather station (Ridgetown, ON. 23 km north of RPP) for June, July and August of 2013 was 102.3mm, 78.3mm and 53.2 mm respectively (233.8 mm total), and for June, July and August of 2014 was 48 mm, 130 mm and 35.8 respectively (213.8 mm total).

RPP likely contains the second largest of eight known extant, relictual populations in the Carolinian Zone of Canada (unpublished data). Historically, at least fifty populations or localities of *P. fasciatus* were documented in southwestern Ontario (Ontario Herpetofaunal Summary, Ontario Nature Reptile and Amphibian Atlas). However, few details regarding skinks at RPP have been documented (see Judd 1962, Gillingwater and Piraino 2002, Farmer 2007) and its status in the park remains unknown. Analysis of population trends at PPNP by Hecnar and Hecnar (2009) suggest a risk of extirpation due to inherent variability in abundance. Seburn (2010) suggested that other Carolinian sub-populations may similarly be at risk. In much of the rest of *P. fasciatus*' range temperatures in Ontario are more varied and on average cooler (Powell and Russell 2007).

Coarse-scale macrohabitat selection by *P. fasciatus* has never formally been described. Reports of non-random use of habitats is mostly anecdotal and based on general observations (Fitch 1954, Fitch 1977, Seburn 1993). Microhabitat preferences focusing on characteristics of refugia have been better explored (Hecnar 1991, Hecnar 1994, Seburn 1993, Howes and Loughheed 2004, Quirt et al. 2006). Currently, few studies have examined factors that comprise the immediate environment used by *P. fasciatus* (see Watson and Gough 2012, Quirt et al. 2006). Further still,

the relationship between canopy structure and its associated microclimate with habitat use by *P. fasciatus* has never formally been assessed in the northern portion of its range.

Due to the small size and endangered status of the Five-lined Skink populations in Ontario, identification of individuals is preferably non-invasive, making many traditional methods for marking lizards unfeasible (e.g. toe-clipping). Further, due to the semi-fossorial nature of these animals, and regular ecdysis, non-invasive markings are often short-lasting and unreliable (Hecnar, pers. comm.). For these reasons, I chose to sample individuals without an intention to recapture and to employ exclusively visual searches to assess relative abundance. The sampling methods I employed for this study are based on, in part, protocols that Hecnar and Hecnar (2012b) have been using for 25 years at Point Pelee National Park. These are essentially activity indices representing a minimum number of individuals known to be alive at a particular time. Activity indices can be calibrated with true density (see Hecnar and M'Closkey 1998).

Many of the effective yet simple sampling methods in herpetological field research use some type of trap or attraction device to increase capture rates or to target secretive species. Although much of the previous work on *P. fasciatus* and other Plestiodontid species has focused on the searches of natural debris (Fitch 1954, Hecnar and Hecnar 2011, Tietje 1997, Howes 2006), a number of studies have successfully implemented coverboards to increase encounter rates (Tietje 1997, Pike et al. 2008, Cavalieri and Fox 2010, Hecnar and Hecnar 2011). Availability of suitable microhabitats has been described as a potential limiting factor for *P. fasciatus* (Hecnar and M'Closkey 1998, Howes and Loughheed 2004), and the use of coverboards exploits this fact. Coverboards are a type of active trap that serves as an attractant to the study animal but allows its

free movement to and from the trap. Coverboards can yield high capture rates of target species and can be useful for assessing patterns of abundance over time or space (Wilson 2009, Halliday and Blouin-Demers 2015). Furthermore, coverboards and other active traps have several practical advantages, including less maintenance, simple sampling protocols and decreased chance of causing mortality when compared to other trap methods. Because of a lack of sufficient natural woody debris within open habitats of the park (pers. obs., Brazeau and Hecnar 2012) coverboards also provide crucial microhabitat for *P. fasciatus* and other fauna within the park (Hecnar and Hecnar 2013). The exclusive use of coverboards for analysis greatly reduces variation in capture rates associated with the range of natural cover object variation. This is particularly true when cover is incorporated into the modeling process (see Quirt et al. 2006).

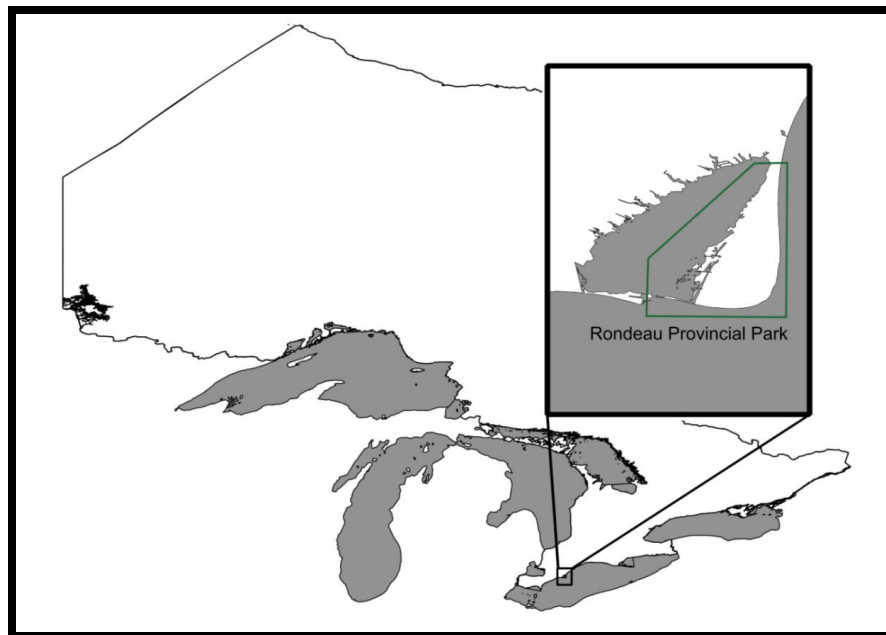


Figure 1.1: Map of the study location, Rondeau Provincial Park, Ontario on the northern shore of Lake Erie. Map data from Statistics Canada (2006).

In this thesis I attempt to characterize previously unexplored aspects of *P. fasciatus* habitat use near its northern range using a multifaceted approach with increasing resolution at sequentially finer scales. Results of this thesis will aid in the identification of factors that may act to limit population persistence and be useful for effective conservation.

My specific questions were:

- 1) What are the macrohabitat preferences of *P. fasciatus* in Carolinian portion of its range? (Chapter II)
- 2) What environmental variables measured at the microhabitat scale best predict site occupancy by *P. fasciatus*? (Chapter III)
- 3) Can the relationship of *P. fasciatus* with increasing tree canopy cover best be described as a threshold response? What is the thermal quality of available forest canopy? (Chapter IV)

Understanding the relationship between canopy cover and quality of skink habitat is of fundamental importance for critical habitat management. This is especially important in the northern portions of the skink range, where forest encroachment is replacing prairie remnant habitat with tree cover (Fitch 2006a, 2006b). Forest clearing, as well as prescribed burn programs are being used as habitat management to conserve relictual prairie habitat and create habitat mosaic structure at the landscape scales.

Chapter 2: Macrohabitat selection in the Common Five-lined Skink (*Plestiodon fasciatus*) near its northern range limits

2.1. Introduction

The study of how and why organisms select particular habitats has a history as long as any integrative topic in ecology (Rosenzweig 1991) and continues today to be a central focus for both evolutionary ecologists and conservation biologists. Habitat selection can be defined as the process whereby individuals preferentially use, or occupy, a non-random set of available habitats (Morris 2003a). Habitats within a landscape tend to vary in quality and extent, with selection of the ideal habitat being essential to maximize individual fitness (Fretwell and Lucas 1970, Stamps 2009). The consequence of habitat selection on individuals can manifest itself through differences in predation, availability of food resources, and limitations imposed by physiology (Huey 1991, Smith and Ballinger 2001). The consequences of living in a particular habitat can influence processes beyond just the individual, with observable effects on population regulation, species interactions, assembly of ecological communities, and the origin and maintenance of biodiversity (Smith and Ballinger 2001, Manly et al. 2002, Morris 2003b). Understanding and maintaining preferred habitats used by individuals, at multiple scales, is thus essential to enhance knowledge of species distributions. Further, variation in habitat selection can be used as an index that aids in determining whether protected areas are functioning in a way to provide the critical habitats required to support the species they harbour.

Animals use available habitat features in a non-random way to meet basic physiological, locomotory, behavioural, and ecological needs. Ectotherms are relatively more sensitive to

changes in structural microhabitat elements than endotherms (Pianka 1973, Huey 1991, Smith and Ballinger 2001). The structures composing a local habitat can often directly influence microclimatic conditions important for behavioural thermoregulation (Heatwole 1977). For example, Row and Blouin-Demers (2006) observed that the temperatures of open and edge habitats deviated less from preferred temperatures than forest habitats of the Eastern Milk snake (*Lampropeltis triangulum triangulum*).

Several studies have demonstrated effects of habitat use on the life history traits of lizards (for review see: Smith and Ballinger 2001) with implications for individual fitness. Many factors may act on the strength of habitat selection of lizards including substrate composition, canopy structure, moisture and predation (Huey 1991, Garden et al 2007, Watson 2008, Lopez and Martin 2013). Although all species are intimately linked to the environment, the direct physiological influence that habitat structure has on lizard functionality makes these organisms ideal to explore the effects of habitat type and structure on macrohabitat selection. This is particularly true of lizards or other reptiles at the northern limits of their range in Canada, with behavioural responses required to cope with relatively cooler and shorter periods of activity, compared to other regions within their range (Powell and Russell 2007).

My objective was to determine the general pattern of macrohabitat selection in an isolated population of *Plestiodon fasciatus* (Common Five-lined Skink) in a protected area near the northern limits of the species range. This population is one of several relictual isolates of the endangered Carolinian Population of the species in Canada (COSEWIC 2007). My goal was to also provide information on the populations realized and potential distribution to aid in the

understanding of habitat selection and provide information on critical habitat for effective conservation and management of this species at risk.

2.2. Methods

2.2.1. Study Area

Rondeau Provincial Park (RPP; 42°17' N, -81° 52' W), is located adjacent to Lake Erie near Morpeth, Ontario, Canada (Figure 1.1). RPP is a 35 km² cusped peninsula with flora of the Carolinian forest region (see Chapter 1 for details).

2.2.2. Data Collection

I chose four broadly defined, distinct habitat categories for the study: stabilized dune (hereafter referred to as dune), savannah, anthropogenic, and forest (Figure 2.1). These are the four main terrestrial habitats in the park and are known to be used by skinks. Habitats were delineated first using detailed Ecological Land Classification maps (ELC; provided courtesy of Ministry of Natural Resources and Forestry) and reassessed with ground truthing prior to board placement. Sites with strong anthropogenic influence were selected based on the constructed category for the ELC maps, with four additional sites located in areas of high use by staff and residents. All anthropogenic sites were directly adjacent to cottage or park infrastructure. Potential problems identified by ground truthing included: the potential of some areas for flooding, high likelihood of human disturbance within the period of study, inaccessibility of some areas in the park, or unsuitable habitat (e.g. marsh). Open beach, seasonally flooded and open marsh areas were excluded because of the tendency for Five-lined Skinks to be negatively associated with the

storm surge zone of open beaches (Hecnar 1991, Hecnar and Hecnar 2012) and wet habitats (Fitch 1954, Ussher and Cook 1979). Logistics and lack of permission from some leaseholders limited site selection for the anthropogenic treatment.

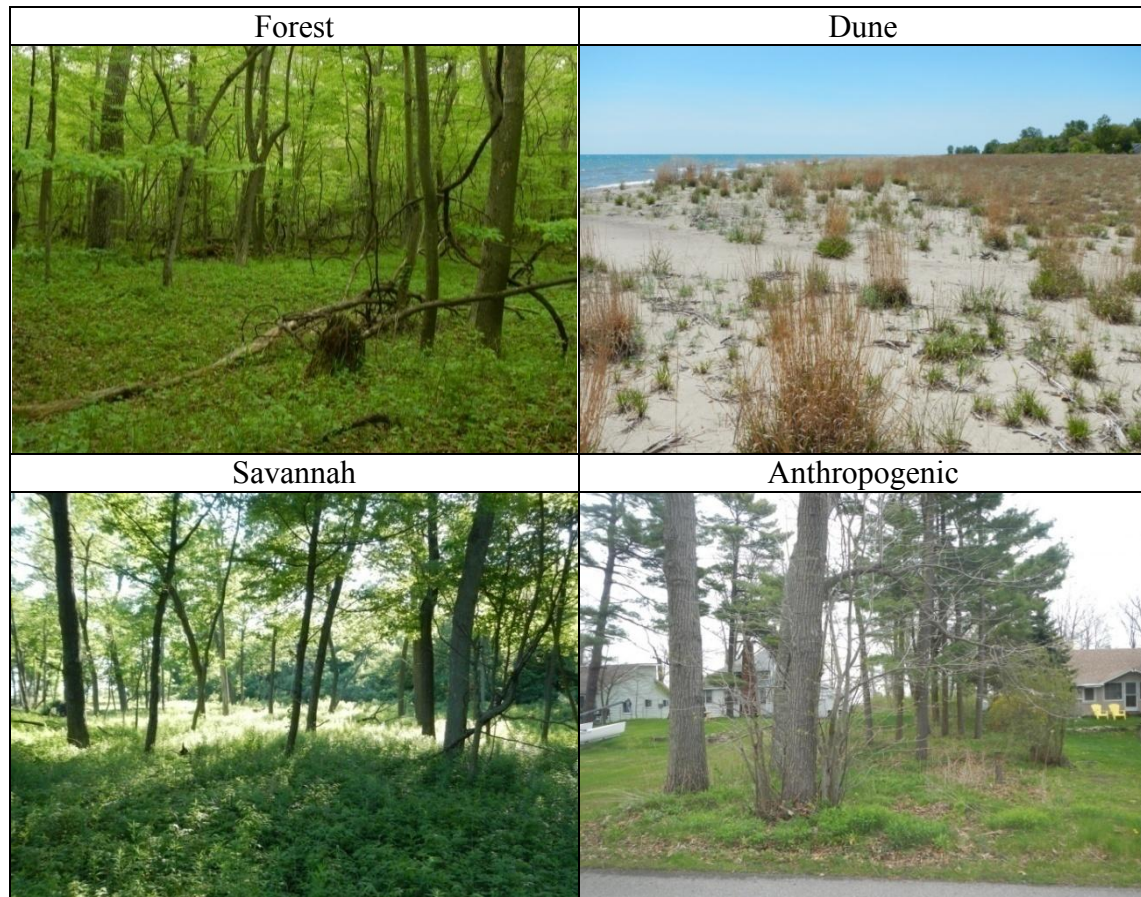


Figure 2.1: Photos of the four habitat categories: dune, forest, savannah and anthropogenic.

I used visual surveys of cover boards, to sample the RPP skink population. Visual surveys are the primary method of sampling for *P. fasciatus* (e.g. Fitch 1954, Hecnar 1994, Hecnar and M^cCloskey 1998; Howes and Loughheed 2004, Quirt et al. 2006). I placed untreated spruce cover boards of preferred size (120 cm x 11.25 cm = 3,484 cm²; >2,300 cm² [Hecnar and M^cCloskey 1998]) within each habitat type (Figure 2.2). Boards were in pairs 2m apart with sites spaced 40

m apart where possible. I raked the area under board locations to remove vegetation and flatten the site of placement so that thermal and moisture conditions remained as stable as possible (Hecnar 1991). I selected 147 sites for board placement in the four sampled habitat types, with a nearly equal design as follows: forest-40 sites; savannah-37-sites; anthropogenic-30 sites; stabilized dune-40 sites. I surveyed all cover boards 15 times in 2013 (June 2- Sept 3) and 42 times in 2014 (May 2-Oct 10). These dates spanned the duration of the skink activity season in each year.

For sampling I lifted boards, checking for presence of skinks and then replacing the board in its original configuration. Care was taken replacing boards to avoid harming resident animals. When possible, age-class and sex were recorded. I distinguished age-class as hatchling, juvenile, or adult, based on size and colouration. I distinguished sex based on the presence of a red suffusion and the wide jaws of males. Individuals were not marked; counts represented an activity density or relative abundance of all individuals for each survey. This work fully complied with the Canadian Council on Animal Care (CCAC) guidelines and was approved by the Lakehead University Animal Care Committee. Permits were provided by RPP, Ontario Parks, MNRF district, and an exclusion to the Endangered Species Act of Ontario was obtained.

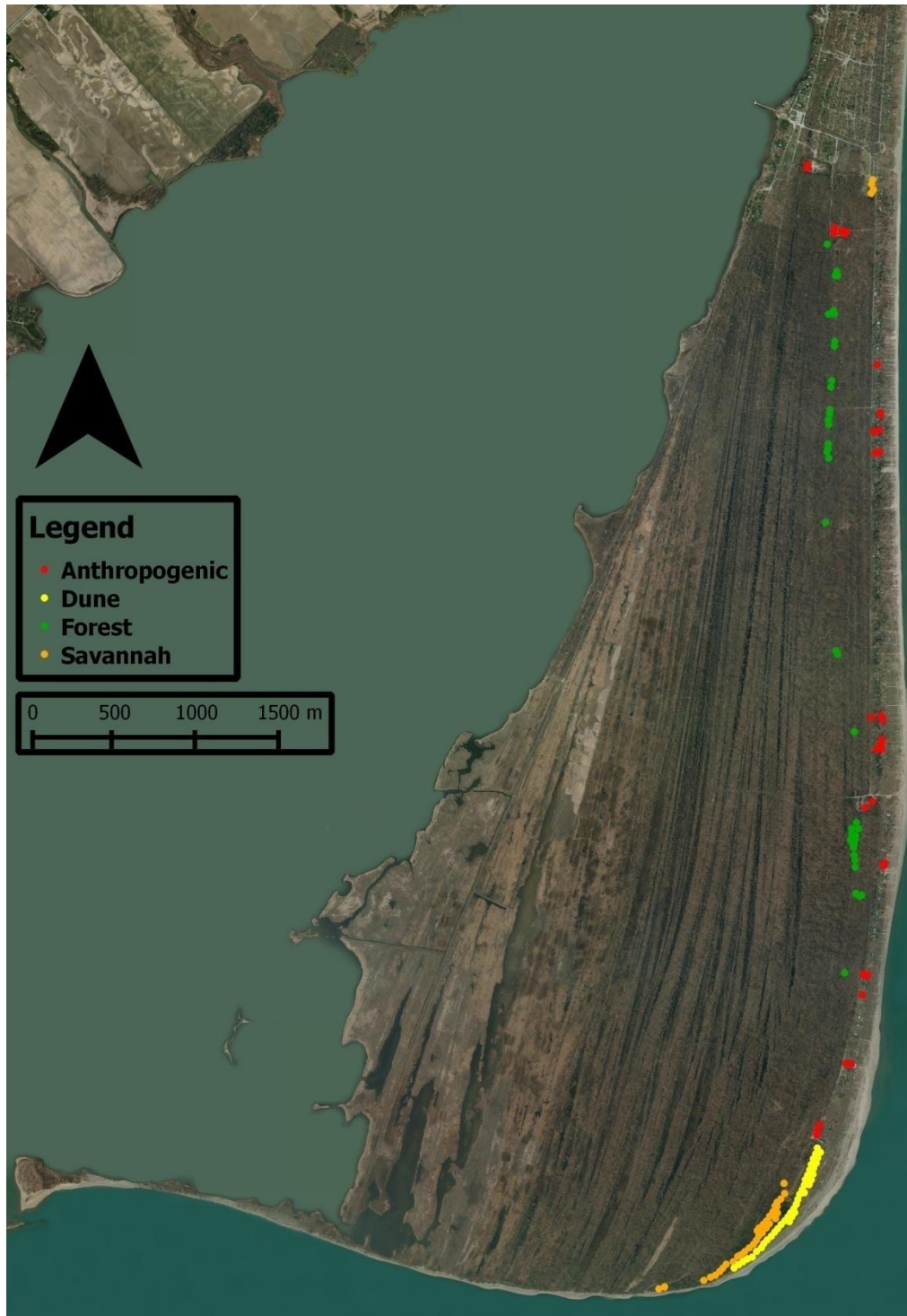


Figure 2.2: Map of site selection and final board placement. Site locations for the habitats sampled are included: anthropogenic (red, 30), dune (yellow, 40), savannah (orange, 37) and forest (green, 40). Map constructed using data from the Southwestern Orthophotography project (2010).

2.2.3. Statistical Methods

I used *G*-tests to determine if habitat use was disproportionate to its availability in each of the four categories. Habitats being used more than expected would provide evidence of preference or selection (Johnson 1980). To generate the expected frequency of individuals for each habitat type I multiplied the total number of skinks observed by the proportion of boards available in each habitat type. Significantly higher observed than expected frequency indicates selection (Hecnar 1991, Hecnar and Hecnar 2012). I used Biomstat 10.0 for computations, following Sokal and Rohlf (2012), and used Williams' correction for the most accurate approximation of the Chi-squared distribution (McDonald 2014). Data for surveys were first pooled to determine overall trends in observations among habitats. A heterogeneity *G*-test was then completed to determine if surveys differed significantly from one another. I then completed all analyses for data pooled by the skink activity seasons sampled: mating (May-June), nesting (July), and post-hatching (August-October). This was done to determine if use or selection differed among seasons.

Initially I planned a second parallel analysis of the habitat selection data by a repeated measures ANOVA with skink abundance as the dependent variable, habitat types as category, and survey as the repeated measure. However, both raw and transformed data violated the assumptions of ANOVA. Instead I used a non-parametric equivalent for repeated measures ANOVA, Quade's test without replication, which also allows for post-hoc tests (Sokal and Rohlf 2012, Systat 12). I randomly selected sites within each habitat type to equalise sample size, and data and site locations were pooled for each survey. I first analysed the data pooled across sex and age classes and then each separately. Pooled data included all skink observations, some of those of unknown

age and sex. The two survey years, 2013 and 2014, were analysed separately because of the large difference in sample size and inclusion of additional, biologically relevant seasons in 2014. Cool spring weather in 2013 slightly delayed initiation of skink activity, making it also logical to analyse the survey years separately. Because of the extended survey season during a post-hatching period in 2014, new hatchlings were included in a separate age and sex class for analysis.

Results

2.2.4. General patterns

I observed 1342 skinks (308 during 15 surveys in 2013, and 1034 during 42 surveys in 2014; Table 2.1). They included 263 males, 397 females, and 374 juveniles, 224 hatchlings and 84 individuals of unknown age. Observation rates for each survey were 20.5 and 24.6 skinks/survey in 2013 and 2014 respectively. During the peak of the active season (nesting) I observed on average 11.4 and 18.5 adults in 2013 and 2014 respectively. During the same period I observed on average 10.08 and 8.93 juveniles in 2013 and 2014 respectively.

Table 2.1: Summary of skink observations for all habitat types by sex and age-class during the 2013 and 2014 RPP field seasons.

2013 Survey (N=15)		Time Period				2014 Survey (N=42)		Time Period		
Sex/ Age-class	Habitat	Mating (n=6)	Nesting (n=6)	Post-Hatching (n=3)	2013 totals (N=15)	Emergence (n=8)	Mating (n=8)	Nesting (n=7)	Post-Hatching (n=19)	2014 totals (N=42)
Male (263)	Anthropogenic	2	5	2	9	13	11	5	3	32
	Dune	29	13	0	42	12	28	21	25	86
	Forest	2	2	0	4	1	4	6	1	12
	Savannah	5	6	0	11	14	14	24	15	67
Female (397)	Anthropogenic	6	7	5	18	28	22	20	25	95
	Dune	27	22	2	51	18	50	56	63	187
	Forest	4	1	0	5	0	4	2	1	7
	Savannah	4	2	2	8	8	7	4	7	26
Juvenile (374)	Anthropogenic	4	10	0	14	36	30	9	15	90
	Dune	26	60	0	86	6	14	60	30	110
	Forest	0	3	0	3	2	1	4	2	9
	Savannah	4	14	11	29	5	11	5	12	33
Hatchling (224)	Anthropogenic	NA	NA	9	9	NA	NA	NA	52	52
	Dune	NA	NA	8	8	NA	NA	NA	115	115
	Forest	NA	NA	0	0	NA	NA	NA	1	1
	Savannah	NA	NA	1	1	NA	NA	NA	38	38
*Unknown (84)	Anthropogenic	1	1	0	2	0	1	2	8	11
	Dune	1	3	0	4	0	1	12	35	48
	Forest	0	0	1	1	0	1	2	0	3
	Savannah	0	2	1	3	4	2	1	5	12
Totals		115	151	42	308	147	201	233	453	1034

*Individual age-class and sex not identified

2.2.5. 2013 Results

The number of skink observations in 2013, pooled across age, sex class and season varied significantly among habitats. When pooled across the active, season skink observations in dune habitat were twice that of the expected frequency with fewer than expected skinks observed in all other habitats ($G=203.5$, $df=3$, $P<0.001$; Figure 2.3). Similarly, Quade's analysis detected a highly significant effect of habitat type on observed use ($F_{3,42}=10.48$, $P<0.001$). Quade's pairwise comparisons of the pooled data identified significant differences in the number of skinks observed for all habitat type comparison's ($P<0.05$), with the exception of savannah and anthropogenic habitats (Table 2.2). Heterogeneity testing revealed a highly significant result between all surveys ($n=15$, $G=84.1$, $df=3$, $P<0.001$; Figure 2.3), whereas Quade's did not ($F_{41,123}=1.26$, $P>0.05$).

Concurrent results occurred when seasons were analysed separately, with twice as many skink observations in dune habitat and less than half what was expected in other habitats, both for mating ($G=102.98$, $df=3$, $P<0.001$) and for nesting ($G=111.15$, $df=3$, $P<0.001$) seasons. Habitat use remained significantly different during post-hatching season ($G=22.48$, $df=3$, $P<0.001$), but with observations in dune below the expected level and savannah and anthropogenic habitats higher than expected use (Figure 2.3).

Analogous patterns to pooled data occurred for the separate sex and age classes, with significant differences in habitat use for males ($G=42.11$, $df=3$, $P<0.001$), females ($G=56.39$, $df=3$, $P<0.001$) and juveniles ($G=107.25$, $df=3$, $P<0.001$). There was twice as many skink observations

as expected in dune habitat for all sex and age classes. Use was less than expected for all other habitats for males and juveniles, whereas female use of anthro habitat was greater than expected but still significantly less than dune ($P < 0.05$).

Table 2.2: Quade's pairwise comparisons of observed use in habitats for 2013. Included are pooled data of age classes and sex, as well as pooled data for all surveys of juveniles, males and females. Significantly different comparisons ($P < 0.05$) are in bold.

Age-class	Habitat	Anthropogenic	Dune	Forest	Savannah
Pooled	Anthro	0.00			
	Dune	164.00	0.00		
	Forest	-113.00	-277.00	0.00	
	Savannah	-11.00	-175.00	102.00	0.00
Juveniles	Anthro	0.00			
	Dune	159.75	0.00		
	Forest	-81.75	-241.50	0.00	
	Savannah	60.00	-99.75	141.75	0.00
Males	Anthro	0.00			
	Dune	138.50	0.00		
	Forest	-37.00	-175.50	0.00	
	Savannah	24.50	-114.00	61.50	0.00
Females	Anthro	0.00			
	Dune	124.00	0.00		
	Forest	-126.50	-250.50	0.00	
	Savannah	-101.50	-225.50	25.00	0.00

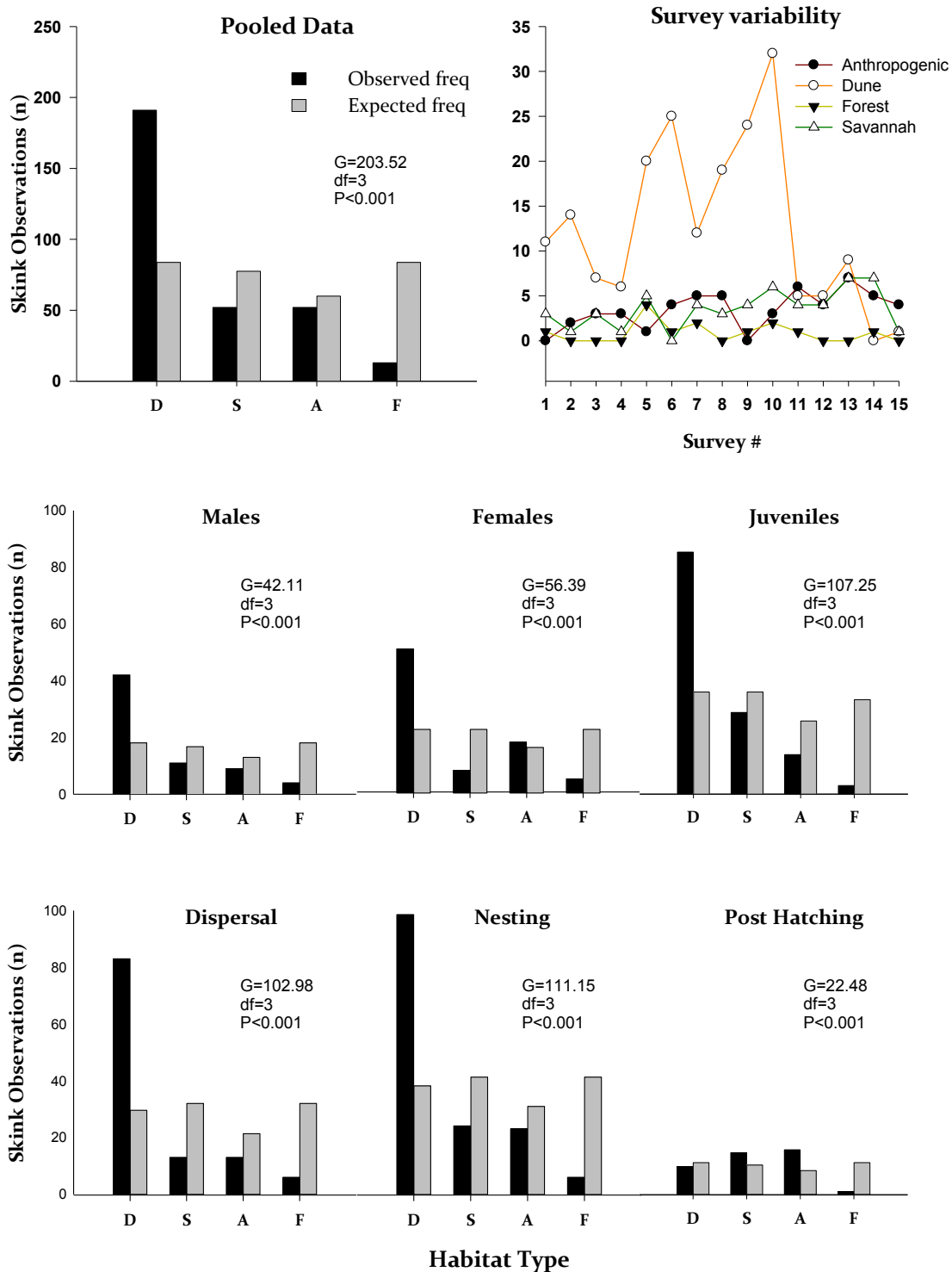


Figure 2.3 Observed use (black) and expected use (grey) in 2013 for all pooled data, seasonal periods and separate sex and age-class.

2.2.6. 2014 Results

Analysis of pooled data for 2014 produced results similar to those of 2013, with the number of skink observations (pooled across age, sex class and season) significantly different among habitats ($G=605.93$, $df=3$, $P<0.001$) and observations in dune habitat twice that expected (Figure 2.4). Similarly, Quade's analysis detected a highly significant effect of habitat type ($F_{3,123}=56.82$, $P<0.001$). Observations in anthropogenic habitat indicated an increase from 2013 with greater than expected use, while observations in savannah and forest habitats were less than expected. Quade's pairwise comparisons of the pooled data identified significant differences in skink observations for all habitat type comparisons ($P<0.01$; Table 2.3). Heterogeneity testing identified a highly significant difference among all surveys ($n=42$, $G=309.12$, $df=123$, $P<0.001$; Figure 2.5), whereas Quade's did not ($F_{41,123}=1.26$, $P>0.05$).

Results were concurrent for the majority of seasons and observations in habitats were significantly different from expected for mating ($G=94.27$, $df=3$, $P<0.001$), nesting ($G=154.68$, $df=3$, $P<0.001$), and post-hatching seasons ($G=345.4$, $df=3$, $P<0.001$), with observations in dune habitat nearly twice that expected (Figure 2.4). Habitat use was highly significant during emergence ($G=113.63$, $df=3$, $P<0.001$), but observations were less than expected in dune habitat and more than twice that expected in anthro habitat. Observations within forest habitat were consistently the lowest of all habitat types, with less than 25% expected use for all seasons.

Analogous patterns to pooled data occurred when observations were analysed by separate sex and age classes. The number of skinks observed in the four habitats was significantly different for

males ($G=70.71$, $df=3$, $P<0.001$), females ($G=272.58$, $df=3$, $P<0.001$), juveniles ($G=144.65$, $df=3$, $P<0.001$) and hatchlings ($G=152.52$, $df=3$, $P<0.001$) and observations in dune habitat were greater than expected for all classes. Additionally, there was greater than expected use of anthropogenic habitat by females, juveniles and hatchlings, and greater than expected use of savannah habitat by males (Figure 2.6-2.7).

Table 2.3: Quade's pairwise comparisons of observed use in habitats for 2014. Included are pooled data of age classes and sex, as well as pooled data for all surveys of juveniles, males and females. Significantly different comparisons ($P<0.05$) are in bold.

Age-class	Habitat	Anthropogenic	Dune	Forest	Savannah
Pooled	Anthro	0.00			
	Dune	630.25	0.00		
	Forest	-1734.00	-2364.25	0.00	
	Savannah	-627.25	-1257.50	1106.75	0.00
Juveniles	Anthro	0.00			
	Dune	82.50	0.000		
	Forest	-1343.50	-1426.00	0.00	
	Savannah	-755.000	-837.50	588.50	0.00
Males	Anthro	0.00			
	Dune	1061.50	0.00		
	Forest	-434.50	-1496.00	0.00	
	Savannah	860.00	-201.50	1294.50	0.00
Females	Anthro	0.00			
	Dune	457.50	0.00		
	Forest	-1487.25	-1944.75	0.00	
	Savannah	-1233.25	-1690.75	254.00	0.00
Hatchlings	Anthro	0.00			
	Dune	123.50	0.00		
	Forest	-266.50	-390.00	0.00	
	Savannah	-88.00	-211.50	178.50	0.00

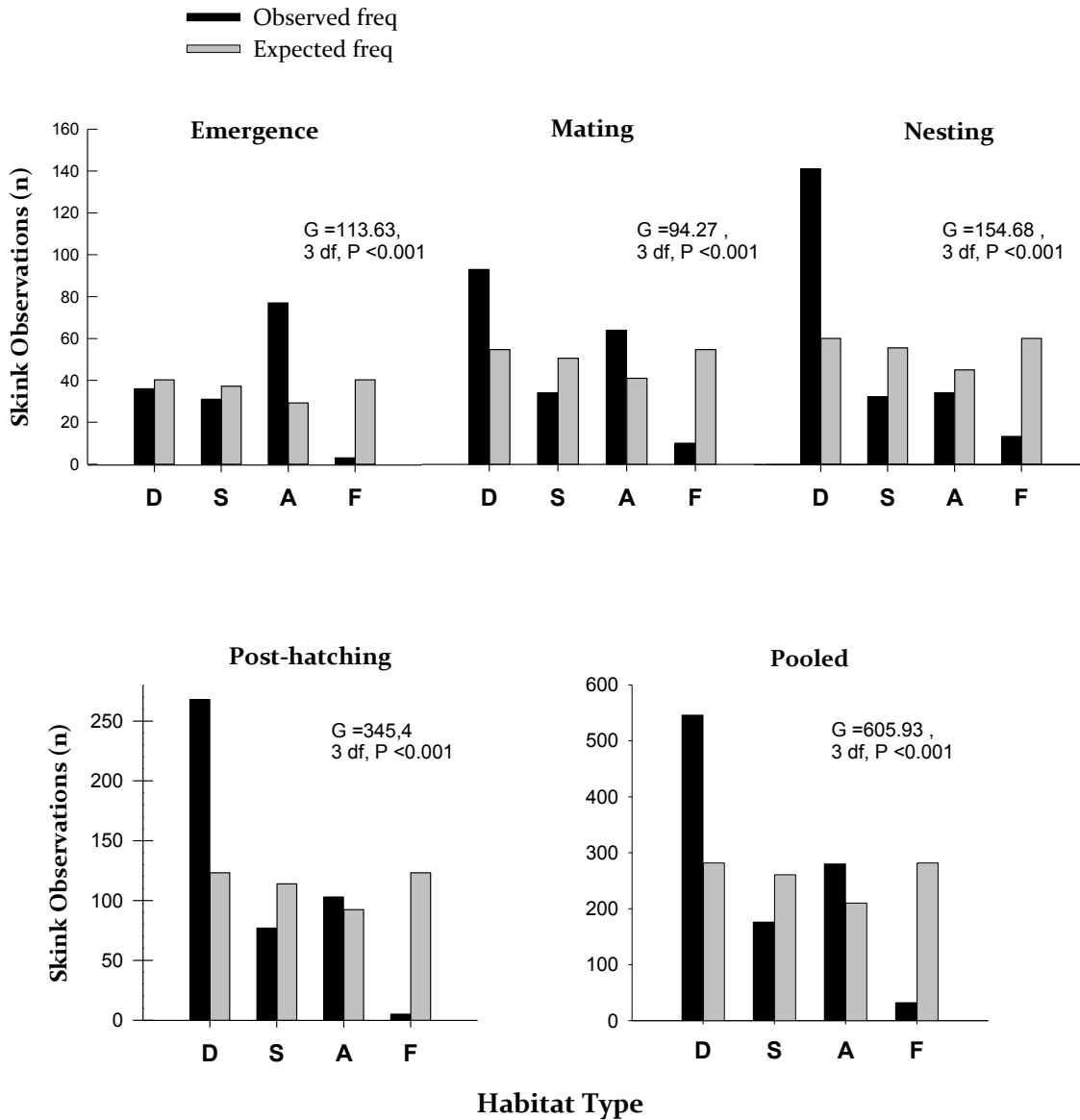


Figure 2.4: Observed use (black) and expected use (grey) in 2014 for four periods of skink activity and pooled data. Dune (D), savannah (S), anthropogenic (A) and forest (F).

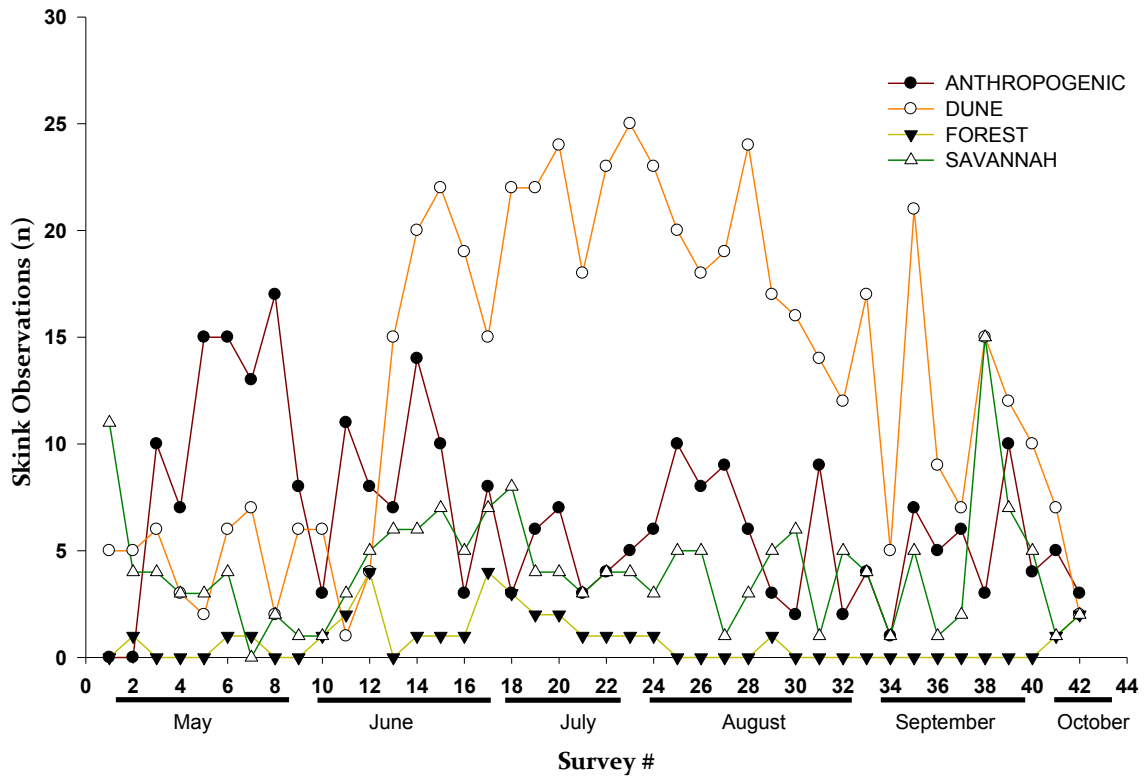


Figure 2.5: Skink observations in 2014 within the four habitat types across all surveys and seasons.

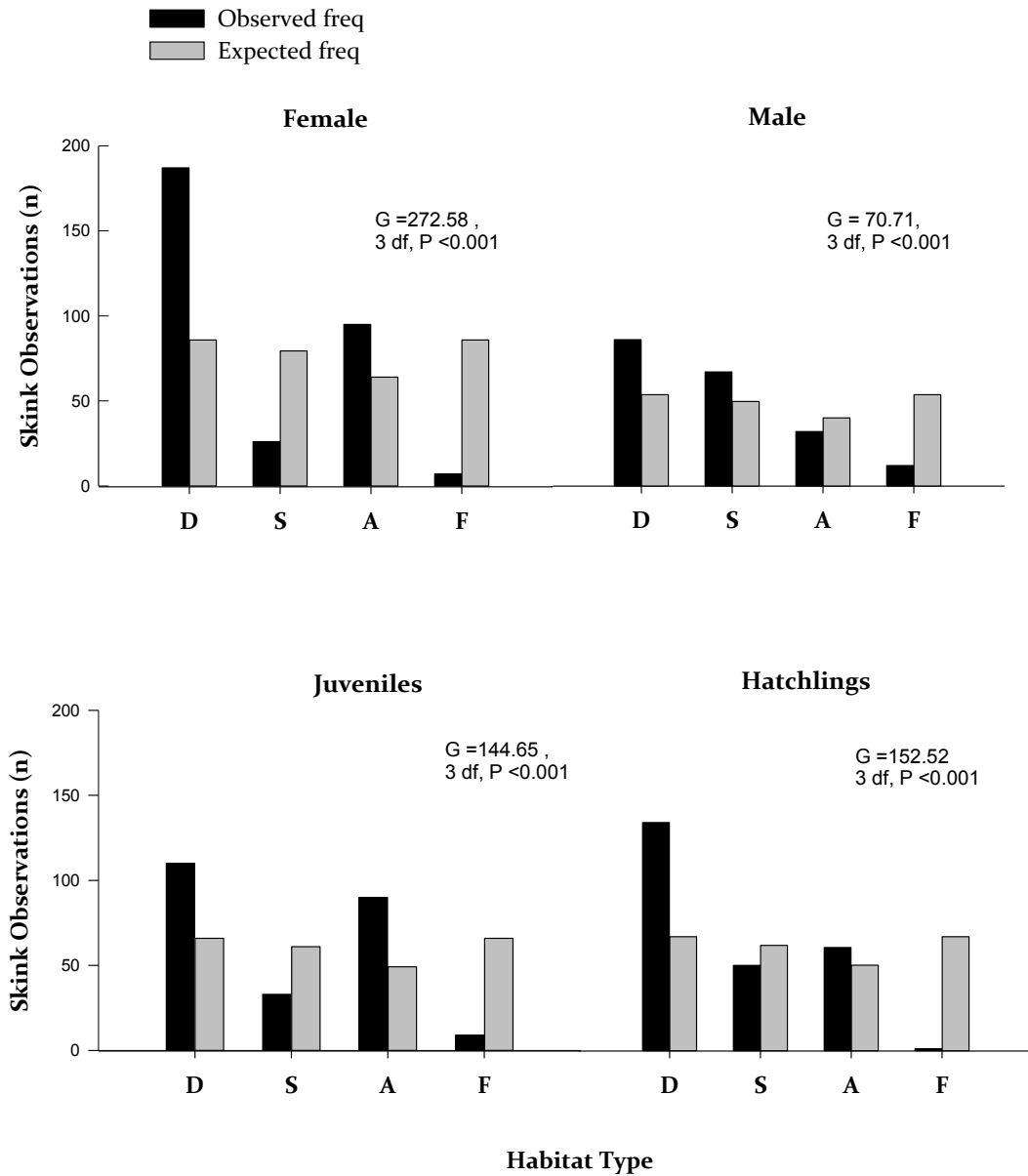


Figure 2.6: Habitat selection of all sex and age classes in 2014. Dune (D), anthropogenic (A), forest (F), and savannah (S) habitats.

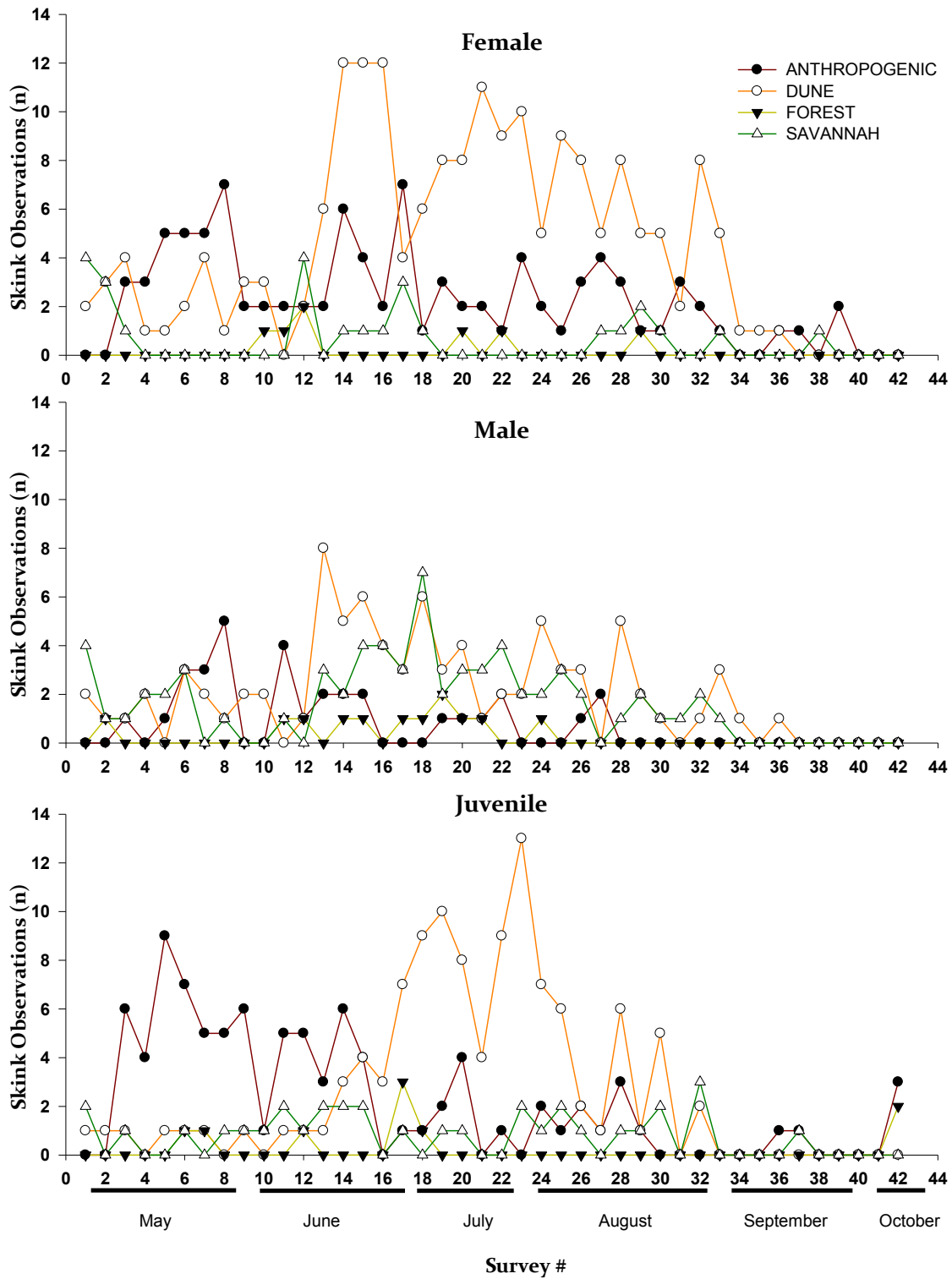


Figure 2.7: Skink observations in the four habitat types through time for female, male and juvenile *P. fasciatus* in 2014.

2.3. Discussion

My study demonstrates habitat selection by *P. fasciatus* among the four main terrestrial habitat types in Rondeau Provincial Park with a clear overall preference for stabilized dune habitat. This overall preference is consistent for males, females and juveniles individually and for mating and nesting seasons for both 2013 and 2014. Results of the post-hatching surveys in August of 2013 and 2014 and the emergence survey in 2014 showed equal to greater use of anthropogenic and savannah habitats over dune habitat. This latter pattern suggests that these two habitats should not be overlooked as important skink habitat and may be of seasonal importance for hibernation sites. Further, this study strongly contrasts with behaviours and habitat preferences observed in the southern part of this species range, where Five-lined Skinks compete with other sympatric Plestiodontid species, and used closed canopy habitat in a warmer environment (Watson and Gough 2012).

The variability of skink habitat preferences I identified during spring emergence and hibernation when compared to the peak of the active season identifies several potentially important trends in the behaviour of *P. fasciatus*. Skink observations from the end of August for both 2013 and 2014 indicated a sharp seasonal decrease in the use of dune habitat by both juveniles and adults. During this same period observations within savannah and anthropogenic habitats remained at relatively the same level. Savannah and anthropogenic habitats may be more conducive to continued or increased activity prior to hibernation. Further, although no comparison for the 2013 emergence period was available, 2014 observations indicated an overall seasonal preference for anthropogenic habitat. The preference of anthropogenic habitats directly following emergence from hibernation suggests a possible use of human infrastructure for hibernation. This

trend was particularly evident for juveniles in 2014 suggesting a potential association of hatchlings to this habitat to in the 2013 season. Fitch's (1954) mark-recapture studies demonstrated that individuals were often recaptured closely to the area of first capture, and instances of large movements were not explained by any noticeable ecological requirement. Large seasonal differences in habitat preferences is suggestive of seasonal migrations during those time periods. Little is known regarding habitat selection of hibernation sites for *P. fasciatus*, but previous observations suggest that individuals hibernate within their home range (Fitch and von Achen 1977). Further, in a habitat study completed on Western Skinks (*Eumeces skiltonianus*) and Alligator Lizards (*Elgaria coerulea*), Rutherford and Gregory (2003) found nothing suggestive of seasonal migrations among habitats. In the neighbouring skink population at Point Pelee National Park, some individuals likely hibernate in their late-season home range and individuals are sometimes observed inside buildings (Hecnar et al. 2012, Hecnar and Hecnar 2012). The RPP study site may promote individual migration behaviour which has not been previously observed in other parts of *P. fasciatus* range, or in other lizards at similar latitudes. My observations at the end of the active season for 2013 and the beginning and end of 2014 suggest that individuals either decrease surface activity more quickly in dune habitat, or that they do not use dune habitat during hibernation site selection. The potential avoidance of dune habitat for hibernation may be due to the inhospitable nature of coastal dune habitats during winter storms and ice surge, which hibernating individuals would be helpless to avoid.

In spite of an abundance of surrounding microhabitat availability in anthropogenic habitats at RPP skinks used dune sites much more frequently during late spring and early summer, during the peak of the active season. Skinks may be avoiding habitats of greater human influence during

this period. The presence of cottagers at RPP peaks midsummer which corresponds with the peak of skink activity and cottagers as well as park staff may engage in activities that disturb skinks such as seasonal maintenance (lawn mowers, power tools) and recreation. Repeated disturbance of debris may result in nest abandonment by females (Hecnar and M'Closkey 1998) and may over time lead to avoidance behaviour by some individuals. Additionally, pets (potential predators) may impact skink behaviour, although pets are supposed to be closely monitored by cottagers. Management at the study location, (RPP) ensures that destruction and encroachment from cottages to adjacent property (potential skink habitat) is often prevented or limited. If disturbance to debris or cover boards is not the cause of lower densities for periods of the active season, there may be an indirect factor associated with anthropogenic structures not previously identified. Reptile response to urban environments, particularly low disturbance environments, has not been well explored (Germaine and Wakeling 2001), but declines of lizard populations within anthropogenic and urban settings is most often associated with the loss of habitat (Pike and Rosnik 2009). Skinks are generally not known to occur in urban environments and appear to be restricted to areas with some natural habitat. However when such 'natural' habitat exists around anthropogenic structures, skinks can potentially thrive (COSEWIC 2007).

Fitch (1954) reported the highest densities of Five-lined Skinks in wood piles/debris associated with anthropogenic structures. I observed similar behaviour at Rondeau with some of the largest observed aggregations of skinks, particularly during nesting, within undisturbed piles of debris placed adjacent to RPP cottage lots (Brazeau pers. obs. 2013, 2014). Furthermore, high densities of the related Northern Prairie Skink (*P. septentrionalis*) occur at anthropogenic sites in remnant prairie sites of southwestern Manitoba (Danielsen et al. 2014). Similarly, Pike et al. (2007) found

that the Sand Skink (*Plestiodon reynoldsi*) was able to persist in human altered landscapes, provided that the appropriate soil structure was maintained. The lower overall use of savannah, in relation to dune, suggests that subsets of what could be considered relatively open and undisturbed habitats are preferred over others. In this case, the variation in sub-canopy cover, grasses and other low lying herbaceous plants may have a greater impact on skink presence than previously observed or displayed. Further, Fitch (2006b) found that *P. fasciatus* persisted around anthropogenic structures (laboratories and research residences) despite being locally extirpated by ecological succession. During storm events at RPP in 2013 and 2014 cover boards and debris in some areas of dune habitat were shifted and moved out of place while debris in anthropogenic habitat were left unaffected (Brazeau pers. obs. 2013, 2014) suggesting that the structure of anthropogenic habitats (presence of houses and brick fences) or elevation was protective. Furthermore, there may be fewer aerial predators in anthropogenic habitats. Myschowoda (2015) found that increased visitor activity at Point Pelee National Park was correlated with a decrease in avian predators and frequency of tail breaks (caudal autotomy).

My observations also indicated high seasonal variability in habitat use between sex and age classes. Explaining this variability is difficult without the aid of marking to recapture and identification of individuals. By the end of August, nearing the end of the active season, fewer adults were present and presumably moving to subterranean or better protected locations. Surface activity for adult males typically decreases early in skink populations with individuals burrowing deeper in substrate after breeding, whereas female and juvenile activity decreases soon after hatching occurs (Fitch 1954; Hecnar 1991, 1994). Genetic research on populations of *P. fasciatus* in the Great Lakes/St. Lawrence Region (Wick 2004) suggests that there is no

variation in dispersal distance by age or sex classes. This interpretation is supported in part by mark recapture studies by Fitch (1954) that did not indicate large variance in maximum dispersal distance between sex and age classes.

Variability in the activity level among sex and age classes has been observed in several other studies (Fitch 1954, Fitch and von Achen 1977, Seburn 1993). Juveniles have been observed shifting to new areas more frequently (Fitch 1954), and females commonly aggregate during nesting season (Seburn 1993, Hecnar 1994). Females have also been observed migrating from post emergence home ranges to locate nesting sites (Seburn 1993). Inherent variation of female and male activity patterns may bias the observed variation in habitat use. For example, during the nesting period over the 2013 and 2014 field seasons at RPP, I observed twice as many females as males. Males appear to be less specific than females in their habitat use, occupying multiple habitats in relatively high frequency for the duration of the active season. However, male observations showed a strong increase in savannah habitat from 2013 to 2014. This does not appear to be related to mate searching or guarding because females utilized savannah habitat in relatively lower frequency throughout the active season. Males may be foraging in alternate habitats throughout the active season. Differences in habitat use of females from males and juveniles may be attributed to selection of suitable nesting sites. Females preferred dune overall during nesting and used anthropogenic habitats (more than expected) considerably more than savannah habitats. Pregnant or gravid female lizards often modify habitat use to maintain a body temperature that is different from those of males or non-pregnant females (Smith and Ballinger 2001). Further, colder incubation temperatures can produce poorer quality offspring in some lizards (Qualls and Andrews 1999) suggesting that females are selecting dune habitats because

they are thermally ideal for nesting sites. There is a greater overall availability of debris on and near cottage properties in the form of stored or discarded construction materials and other debris (pers. obs. 2013, 2014). The reliability and abundance of this debris near human habitation may make anthropogenic habitat more attractive relative to savannah habitat for nest site selection.

The high use of dune habitat by hatchlings suggests that dune habitats are also ideal for the peak of hatchling activity. Because females have been observed to leave their home range to nest, Wick (2004) suggested that hatchlings are the dispersers of this species. Maximum yearling movement recorded in a Carolinian population was 107 m (Seburn 1993), suggesting this age class is capable of dispersal to optimal habitat from nesting sites within the restraints of a single season.

Powell and Russell (2007) consider that populations of Canadian lizards are limited by density independent effects such as overwintering mortality, reproduction success and mortality caused by climatic variation. Such effects may put populations of *P. fasciatus* at risk where management is not acting effectively to mitigate losses of ideal habitat. Further, because ectotherms achieve body temperature through behavioural interactions with their environment, the selection of ideal habitat is often related to the thermal structure of the habitat (Huey 1991, Blouin-Demers and Weatherhead 2002). In many cases, lizards are capable of passive thermoregulation (Smith and Ballinger 2001), but the range of temperatures that *P. fasciatus* experiences at RPP, just over 350 km from its northern maximum, would require relatively high levels of thermoregulatory behaviour to maximize the relatively short activity period. It is likely that the strength of selection for dune habitat is a result of a behaviour to optimize such thermal requirements.

Future research should focus on attaining comprehensive temperature data, relative to canopy cover and habitat structure. These data should aid in understanding the importance of thermoregulatory requirements and behaviour of lizards in colder regions of their range. A better understanding of why relatively fewer *P. fasciatus* occur in savannah and anthropogenic habitats should also be explored because these habitats may provide unforeseen elements important for local persistence. Specifically, whether anthropogenic and savannah habitats provide some relief from stochastic events (e.g. storm events, localized flooding, frost penetration) or alternatively represent preferred hibernation sites should be further explored at RPP. Without a mark-recapture design, I am unable to determine if this variation was caused by an increase in overall population size (through increased survivorship of juveniles or increased recruitment in a habitat or both), shifts in individual habitat use, variation in the time required to find boards in the different habitats, or by other unforeseen variables.

Chapter 3: The relative effect of multiple spatial and microclimate variables in determining microhabitat selection by the Common Five-lined Skink (*Plestiodon fasciatus*)

3.1. Introduction:

The scale at which habitat selection occurs is an important consideration (Morris 1987) with patterns of use and complexity of interactions often varied at micro- and macrohabitat scales. Habitat selection can be viewed as a hierarchical process by which an organism selects a general place in which to live (a given habitat type or macrohabitat) and then makes subsequent decisions about the use of different patches, the search modes it employs, and its responses to specific objects and conditions that it encounters at the microhabitat scale (Johnson 1980, Orians and Wittenberger 1991).

Ectotherms can be relatively more sensitive to changes in structural microhabitat elements than endotherms and structures in a habitat can often directly influence microclimatic conditions important for behavioural thermoregulation (Pianka 1973, Heatwole 1977, Huey 1991, Smith and Ballinger 2001). The effect of habitat structure on microclimate is of particular relevance for reptile species at the northern limits of their range, where individuals are required to respond to relatively cooler and shorter periods of activity (Powell and Russell 2007). Many factors may act on the extent of habitat selection in lizards, including substrate composition, canopy structure, moisture, predation, and anthropogenic disturbance (Huey 1991, Hecnar 1994, Garden et al. 2007, Watson 2010, Lopez and Martin 2013). Several studies have demonstrated effects of habitat use on the life history traits of lizards (Smith and Ballinger 2001).

Microhabitat preferences of *P. fasciatus* have been explored in considerable detail for Carolinian populations (Hecnar 1991, 1994; Seburn 1993) and similarly in the Great Lakes-St. Lawrence populations (Howes and Loughheed 2004, Quirt et al. 2006). The definition of microhabitat can vary greatly depending on context of the research question. This is especially true of semi-fossorial species such as *P. fasciatus*, for which one can measure characteristics of a refuge site, which is often referred to as the microhabitat. Alternatively, one could measure characteristics of the environment directly surrounding and associated with refuge sites. Both of these perspectives imply an organism-specific definition of the environment, which is important when studying habitat selection (Stamps 2012). For the purposes of this study, microhabitat will refer to the immediate environment in and surrounding refuge sites. Habitat selection studies of *P. fasciatus* have largely focused on the availability and quality of the refuge itself (Hecnar 1991, 1994; Seburn 1993; Howes and Loughheed 2004; Quirt et al. 2006). Few studies, and none in the Carolinian Population, have studied the link between macrohabitat characteristics with microhabitat factors and the subsequent outcome on habitat selection by skinks (see Watson and Gough 2012, Quirt et al. 2006).

Several habitat factors have been identified as potential indicators of *P. fasciatus* occupancy including canopy cover, temperature (Quirt et al. 2006, Watson and Gough 2012), moisture (Ussher and Cook 1979, Hecnar 1994), anthropogenic habitat (Fitch 1954) and roadways (Farmer 2012). However, the relative importance of these factors has not been formally tested. The RPP study site provides a unique assemblage of habitat types with varied levels of disturbance and habitat structure making it an ideal location to test the relative effects of environmental variables on skink occupancy. My objective in this chapter was to identify the

relative effect of spatial landscape factors and microclimate variables on microhabitat selection by *P. fasciatus*.

3.2. Methods

3.2.1. Study Area

Rondeau Provincial Park (RPP; 42°17' N, -81° 52' W), is located adjacent to Lake Erie near Morpeth, Ontario, Canada (Figure 1.1). RPP is a rounded 35 km² cusped peninsula with flora of the Carolinian forest region (see Chapter 1 for details).

3.2.2. Data Collection

I used visual surveys of cover boards to collect data as outlined in Chapter II. Transect locations were chosen randomly within cottage property rights of way (ROW) using GIS software and boards were placed 15 m apart in pairs. A total of 134 sites were chosen comprising 15 transects (Figure 3.1). Habitat measurements including canopy cover, moisture, and distance variables were recorded in 2013, whereas temperature was measured in 2014. Canopy cover readings were measured using a convex spherical densitometer (Forest Densitometers, Model-A) to provide percent canopy cover for each site. Soil measurements were taken using a moisture and pH soil probe (Kelway, Model HB-2). Two moisture measurements were taken under each of the two boards and averaged for the site. Spatial variables including distance to anthropogenic structure, shoreline and roads were measured using 2010 orthophotographic maps of RPP in QGIS. Distance to natural debris was calculated using a laser range finder (Tasco, 600 Rangefinder) when distances exceeded 2 m. Only debris of sufficient size to conceal a skink (>10cm in width)

from previous studies were included in analysis (Hecnar 1991, Seburn 1993, Hecnar and M'Closkey 1998).

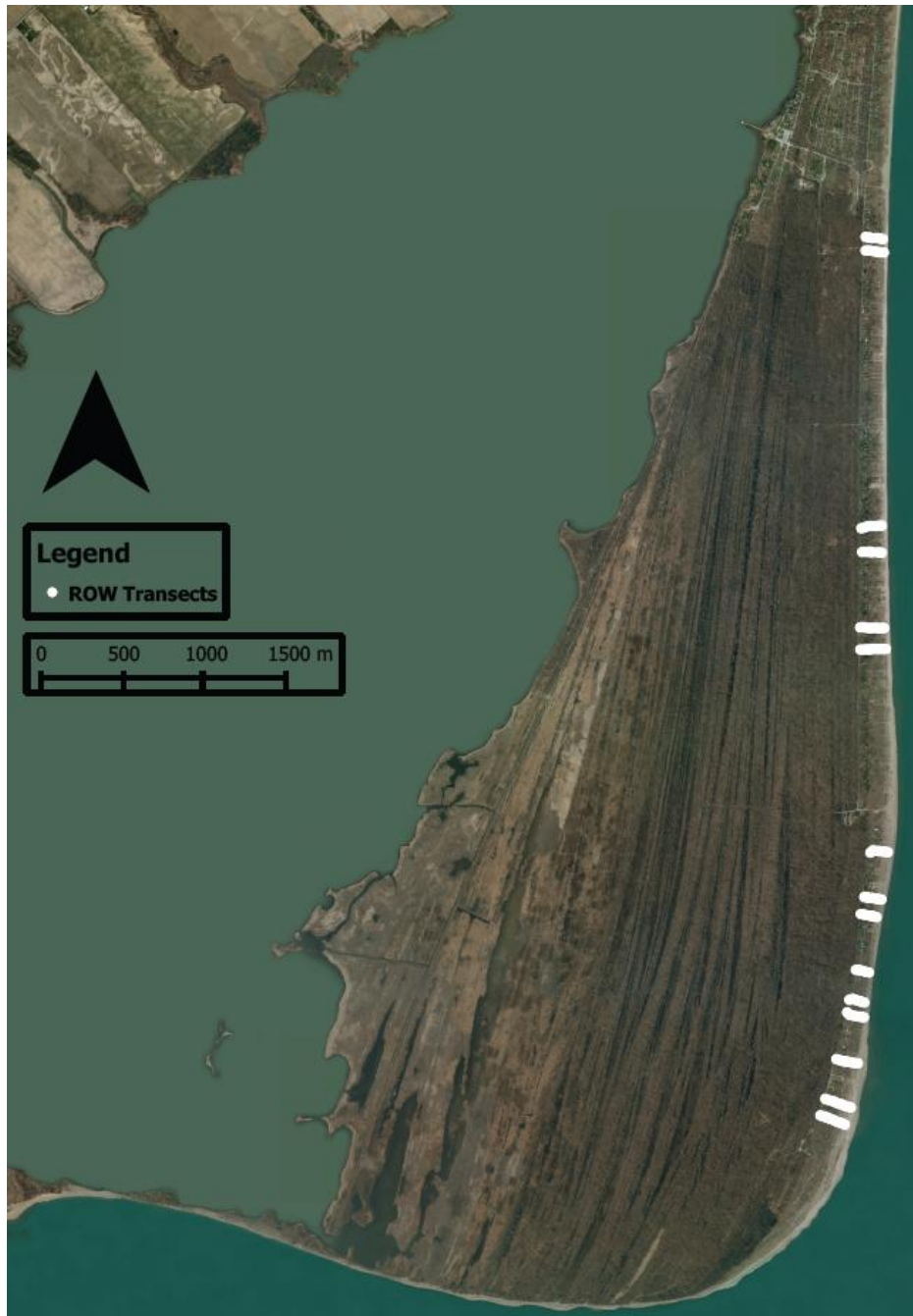


Figure 3.1: Locations for the 15 transects of 134 cover board sites used for Chapter 3 and Chapter 4 analyses. Geospatial data from the Southwestern Orthophotography Project (2010).

I used temperature data loggers (Thermochron I-button, DS1921KI) to measure temperature of each site. I placed data loggers under a monitoring board and an ambient location at each site. I chose the ambient location for each site at random from one of the four cardinal directions. To prevent movement or animal thievery ambient temperature loggers were attached to the board with a piece of metal wire (30cm in length). The under-board location was placed as close to the centre of the board as possible while avoiding burrows, ant colonies and other confounding characteristics. Data loggers were placed at all ROW sites (n=134) so that temperature could be incorporated into the GLM (Generalized Linear Model) and compared to 2013 analysis. Because of limited numbers of I-buttons this was completed in four rounds, with data collected at each site for three days. I calculated a correction factor to account for temperature variation between sampling periods using logger data from 15 sites that remained stationary for the entirety of the study.

3.3. Statistical Methods

To explore how skink site use was affected by microhabitat variables I utilized three techniques: Pearson correlation matrix, Poisson regression and Akaike Information Criterion. Because soil moisture was measured only in 2013 it was excluded from 2014 models, and temperature was excluded from 2013 models because it was only measured in 2014. A total of six and seven independent variables were used in 2013 and 2014 analyses respectively. Parameter IDs were assigned to each variable (Table 3.1). Analysis for all model exploration (2013 and 2014) was completed on total observations at each site pooled across the peak of activity at RPP, the nesting season (Hecnar and Brazeau 2014, 2015). I assumed that changes in moisture were relative and that sites of high moisture would consistently maintain higher moisture levels. Because I

sampled soil moisture only once in 2013 inference cannot be made regarding specific moisture requirements, but rather on whether individuals prefer site of relatively higher or lower moisture.

Table 3.1: Description of all predictor variables used in microhabitat analyses for 2013 and 2014.

	Variable	Variable Description
2013	CANOPY	Tree canopy cover, percentage occupied
	MOIST	Soil moisture, percentage saturation
	ROAD	Distance (m) to road (Lakeshore Rd)
	ANTHRO	Distance (m) to anthropogenic structure
	MICRO	Distance(m) to the nearest cover object
	WATER	Distance(m) to lake shoreline
2014	CANOPY	Tree canopy cover, percentage occupied
	ROAD	Distance (m) to road (Lakeshore Rd)
	ANTHRO	Distance (m) to anthropogenic structure
	MICRO	Distance(m) to the nearest cover object
	WATER	Distance(m) to lake shoreline
	Max.1	Maximum temperature (°C) underneath the cover board
Max.2	Maximum ambient temperature (°C) adjacent cover board	

I first used a Pearson Correlation as a preliminary analysis to explore the strength and direction of correlation using Systat (12.0). Because count data are typically zero-inflated, I used Poisson regression to eliminate overdispersion (McCullagh and Nelder 1989, Bolker et al 2009). The Poisson regression analysis was completed using the glm function in the R stats package (R core team 2014). I tested for multicollinearity in the global model using the vif (variance inflation factor) function in the car (companion to applied regression) package (Fox and Weisberg 2011). To determine the relative affect of individual variables on skink observations I then used the AICmodavg package (Mazzerole 2013) to generate model selection tables based on the Akaike Information Criteria (AIC) as well as to calculate overdispersion. QAIC values were used to account for remaining overdispersion not removed by the Poisson distribution. When models

competed for first place ($\Delta_i < 2$) I used model averaging (a.k.a. multimodal inference) and included all models except those including interactions (see Burnham and Anderson 2002). Coefficient estimates as well as 95% confidence intervals (CI) were used to determine the relative magnitude and direction of effect of individual parameters on skink observations. Akaike weights were then used to determine the best of the single parameter models, with evidence ratios calculated to identify the magnitude of differences. A pseudo r-squared measure used for GLM's, the McFadden R^2 , was calculated using the pscl package in R (Jackman 2012) to assess model fit, with a value of 0.2-0.4 indicating good fit (McFadden 1977).

Results

In 2013 Nesting period surveys I observed 183 skinks over six surveys (31 skinks per survey).

The 2014 Nesting period surveys showed a marked increase in the number of observations, with 378 skinks over seven surveys (54 skinks per survey).

3.3.1. 2013 Results

Skink use was positively correlated with ROAD and MICRO ($r = 0.10 - 0.02$) and negatively related with CANOPY, MOIST and WATER ($r = 0.37 - 0.14$; Table 3.2) as revealed in initial Pearson Correlation analyses.

Pearson Correlation largely agreed with the findings of QAIC and the subsequent model exploration. Skink use was best predicted by the model that included CANOPY, MOIST and ANTHRO (model 9; Table 3.3). QAIC provided three models with substantial evidence for first place ($\Delta_i < 2$; Table 3.3). All three models were highly significant ($P < 0.001$) had comparable fit

($R^2=0.23$), and included CANOPY, MOIST and ANTHRO (models 9, 17 and 4) with one also including MICRO (model 4). Within the top model, CANOPY, MOIST and ANTHRO were all significant ($P<0.01$) for the top three models, while MICRO was not ($P> 0.05$; see Appendix-Table 6.1 for full model list).

The 95% CI of the QAIC model averaged estimates indicated that skink observations were negatively correlated with CANOPY (-0.0426, -0.0128), MOISTURE (-0.0684, -0.0113) and ANTHRO (-0.021, -0.0044; Table 3.5). Model averaging indicated that site occupancy was best predicted by MOIST (-0.0399) followed by CANOPY (-0.0277) and ANTHRO (-0.0127). Individual parameter models obtained from QAIC as well as model fit identified CANOPY ($R^2=0.15$; $P<0.001$) as the best single parameter model with the evidence ratio indicating that it was 17.8 times more likely than MOIST ($R^2=0.12$, $P<0.001$), which was 230 times more likely than WATER. McFadden R^2 values were consistent with rankings obtained from the evidence ratios for all 2013 parameters.

Table 3.2: Pearson Correlation Matrix of 2013 and 2014 nesting observations and selected variables. Significant correlations ($P < 0.05$), using the Bonferroni correction, are in bold font.

Variables	2013 Nesting	2014 Nesting	Max.1	Max.2	CANOPY	MOIST	ROAD	MICRO	ANTHRO	WATER
2013 Nesting	1									
2014 Nesting	0.499	1								
Max.1	NA	0.353	1							
Max.2	NA	0.43	0.698	1						
CANOPY	-0.371	-0.379	-0.757	-0.679	1					
MOIST	-0.316	NA	-0.51	-0.493	0.483	1				
ROAD	0.102	0.107	0.264	0.265	-0.468	-0.576	1			
MICRO	0.016	-0.072	0.159	0.084	-0.203	-0.114	0.19	1		
ANTHRO	0.061	0.031	0.276	0.276	-0.532	-0.487	0.903	0.194	1	
WATER	-0.142	-0.274	-0.273	-0.304	0.302	0.58	-0.675	-0.175	-0.52	1

Table 3.3: Predictive models and QAIC results of skink observations for the 2013 nesting period. Models are listed in decreasing order of likelihood as calculated by QAIC. All models identified as very unlikely ($\Delta_i > 10$) are excluded. McFadden's R^2 is included.

Models	Model #	K	QAICc	Delta QAICc	QAICc Wt	Quasi.LL	R^2
~CANOPY+MOIST+ANTHRO	9	5	187.53	0.00	0.29	-88.53	0.23
~CANOPY*MOIST+ANTHRO	17	6	188.37	0.84	0.19	-87.85	0.23
~CANOPY+MOIST+MICRO+ANTHRO	4	6	189.17	1.65	0.13	-88.26	0.23
~CANOPY*MOIST+MICRO+ANTHRO	13	7	190.12	2.59	0.08	-87.61	0.23
~CANOPY+MOIST+MICRO+ANTHRO+ROAD	2	7	191.19	3.67	0.05	-88.15	0.23
~CANOPY*MICRO+MOIST+ANTHRO	21	7	191.19	3.67	0.05	-88.15	0.23
~CANOPY+MOIST+MICRO+ANTHRO+WATER	3	7	191.27	3.75	0.04	-88.19	0.23
~CANOPY+MOIST+MICRO*ANTHRO	5	7	191.35	3.82	0.04	-88.23	0.23
~CANOPY*MOIST+MICRO+ANTHRO+WATER	12	8	192.31	4.78	0.03	-87.58	0.23
~CANOPY*MOIST+MICRO+ANTHRO+ROAD	11	8	192.31	4.79	0.03	-87.58	0.23
~CANOPY*MICRO+MOIST+ANTHRO+ROAD	19	8	193.25	5.72	0.02	-88.05	0.23
~CANOPY*MICRO+MOIST+ANTHRO+WATER	20	8	193.33	5.80	0.02	-88.09	0.23
~CANOPY+MOIST+MICRO+ANTHRO+ROAD+WATER	1	8	193.41	5.88	0.02	-88.13	0.23
~CANOPY*MOIST+MICRO+ANTHRO+ROAD+WATER	10	9	194.58	7.05	0.01	-87.56	0.23
~CANOPY+MOIST	8	4	195.13	7.61	0.01	-93.41	0.18
~CANOPY*MOIST	16	5	195.46	7.94	0.01	-92.50	0.19
~CANOPY*MICRO+MOIST+ANTHRO+ROAD+WATER	18	9	195.51	7.98	0.01	-88.03	0.23
~CANOPY+MOIST+MICRO	7	5	195.75	8.23	0.00	-92.64	0.19
~CANOPY+MOIST+MICRO+WATER	6	6	196.13	8.60	0.00	-91.74	0.20
~CANOPY*MOIST+MICRO	15	6	196.30	8.77	0.00	-91.82	0.20
~CANOPY*MOIST+MICRO+WATER	14	7	197.06	9.53	0.00	-91.09	0.20

Table 3.4: Individual parameter values from QAIC results of models predicting skink observations for 2013 and 2014 including coefficient estimates from model averaging and individual parameter model results for both 2013 and 2014. Bolded values indicate that the 95% CI excludes zero. McFadden's R^2 is included.

Year	Predictor	Model Averaging of parameters				Individual model scores			
		Coeff Avg	Std err	95% CI		QAIC weight	Evidence ratio	R^2	P
2013	CANOPY	-0.0277	0.0072	-0.0417	-0.0137	3.85E-04	17.62	0.15	<0.001
2013	MOIST	-0.0405	0.0141	-0.0682	-0.0128	2.19E-05	230042.68	0.12	<0.001
2013	WATER	0.0011	0.0031	-0.0049	0.0071	9.50E-11	2.55	0.02	<0.01
2013	ROAD	-0.003	0.0075	-0.0177	0.0117	3.73E-11	1.81	0.01	0.03
2013	ANTHRO	-0.0121	0.0054	-0.0226	-0.0016	2.06E-11	1.36	0.00	0.21
2013	MICRO	-0.016	0.0218	-0.0587	0.0267	1.52E-11	least likely	0.00	0.74
2014	Max.2	0.0624	0.0198	0.0237	0.1012	1.29E-06	428.73	0.21	<0.001
2014	CANOPY	-0.0262	0.0071	-0.04	-0.0123	3.01E-09	1607.81	0.17	<0.001
2014	Max.1	-0.0218	0.0262	-0.0731	0.0295	1.87E-12	289.93	0.11	<0.001
2014	WATER	-0.0085	0.0033	-0.0149	-0.0021	6.47E-15	2773.11	0.07	<0.001
2014	ROAD	0.0118	0.0077	-0.0033	0.0269	2.33E-18	2.00	0.01	<0.01
2014	MICRO	-0.0322	0.0173	-0.0662	0.0018	1.16E-18	1.60	0.00	0.04
2014	ANTHRO	-0.0231	0.0098	-0.0423	-0.0039	7.27E-19	least likely	0.00	0.37

3.3.2. 2014 Results

Skink use was positively correlated with Max.2, Max.1, ROAD and ANTHRO ($r=0.43 - 0.03$) and negatively correlated with CANOPY, MOIST, WATER and MICRO ($r= 0.38 - 0.07$; Table 3.2) as revealed in initial Pearson Correlation analyses.

Pearson Correlation largely agreed with the findings of QAIC and the subsequent model exploration. Skink use was best predicted by the model that included all habitat parameters with an interaction between CANOPY and Max.1 (model 10; Table 3.5). QAIC provided three models with substantial evidence for first place ($\Delta_i < 2$; Table 3.5). All three models were highly significant ($P < 0.001$) and had comparable fit with a high level of association ($R^2 = 0.36-0.34$). Two of the best models included an interaction of CANOPY and Max.1 (models 10 and 12), with one of these excluding ROAD and the third model without any interactions included all variables except Max.1 (model 7). All parameters of the top three models were highly significant ($P < 0.01$; see Appendix- Table 6.2 for full model list).

The 95% CI of the QAIC model averaged estimates indicated that skink observations were positively correlated with Max.2 (0.0237, 0.1012) and negatively correlated with CANOPY (-0.04, -0.0123) and ANTHRO (-0.0423, -0.004; Table 3.4). Model averaging indicated that skink use was best predicted by Max.2 (-0.0624) followed by CANOPY (-0.0262) and then ANTHRO (-0.0231). Individual parameter models obtained from QAIC as well as model fit identified Max.2 ($R^2 = 0.21$; $P < 0.001$) as the best single parameter model with the evidence ratio indicating that it was 429 times more likely than CANOPY ($R^2 = 0.17$, $P < 0.001$) which was 1607 times

more likely than Max.1. McFadden R^2 values were consistent with rankings obtained from the evidence ratios for all 2014 parameters.

Table 3.5: Predictive models and QAIC results of skink observations for the 2014 nesting period. Models are listed in decreasing order of likelihood as calculated by QAIC. All models identified as very unlikely ($\Delta_i > 10$) are excluded. McFadden's R^2 is included.

Model description	Model #	K	QAICc	Delta QAICc	QAICc Wt	Quasi.LL	R^2
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+ROAD+WATER	10	10	193.04	0.00	0.27	-85.63	0.36
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+WATER	12	9	193.84	0.80	0.18	-87.19	0.35
~CANOPY+Max.2+MICRO+ANTHRO+ROAD+WATER	7	8	194.25	1.21	0.15	-88.55	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+ROAD+WATER	1	9	195.61	2.57	0.07	-88.08	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+WATER	3	8	195.77	2.73	0.07	-89.31	0.33
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+WATER	19	9	196.39	3.35	0.05	-88.47	0.34
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+ROAD+WATER	41	10	196.49	3.45	0.05	-87.35	0.35
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+ROAD+WATER	17	10	196.49	3.46	0.05	-87.35	0.35
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+WATER	43	9	196.51	3.47	0.05	-88.53	0.34
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+ROAD	11	9	197.22	4.18	0.03	-88.89	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+ROAD	2	8	199.41	6.37	0.01	-91.13	0.32
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+ROAD	42	9	200.21	7.17	0.01	-90.38	0.33
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+ROAD	18	9	200.59	7.55	0.01	-90.57	0.32
~CANOPY*Max.1+Max.2+MICRO+ROAD+WATER	13	9	201.59	8.55	0.00	-91.07	0.32
~CANOPY+Max.1+Max.2+MICRO+ROAD+WATER	4	8	202.48	9.44	0.00	-92.66	0.31
~CANOPY*MICRO+Max.1+Max.2+ROAD+WATER	44	9	202.71	9.67	0.00	-91.63	0.32

Discussion

Habitat use by *P. fasciatus* at RPP was best explained by the microclimate and canopy cover of a site. Skinks used sites with higher ambient temperatures, lower soil moisture and less canopy cover. Spatial variables measuring the distance of sites to anthropogenic structure, nearest cover object, road and shoreline were relatively less predictive of skink observations. Overall my study highlights the importance of microclimate, particularly temperature, in determining *P. fasciatus* microhabitat selection. Further, these findings emphasize the challenges faced by *P. fasciatus* near the northern extent of its range, where cold climate presents a challenging environment to ectotherms.

Skink habitat use responded most strongly to ambient temperatures suggesting that of those variables measured, temperature is likely the predominant environmental constraint placed on *P. fasciatus* at RPP. This is not surprising for an ectotherm near the northern extent of its range. The importance of ambient temperatures for skinks may indicate that selection of microhabitat is based upon ideal basking sites or the immediate line of travel. The ability of cover objects to buffer temperature extremes found in the ambient environment may reduce the importance of under-board temperatures in selecting thermally ideal sites. The importance of temperature for this species conforms to what is expected of ectotherm ecology as temperature can influence a lizard's energy budget, physiological processes and subsequently activity level (Congdon 1989). This also supports the findings of Watson and Gough (2012) who found that sympatry between *P. fasciatus* and two other skinks, the Southeastern Five-Lined Skink (*P. inexpectatus*) and the Broadheaded Skink (*P. laticeps*), was likely attributable to variability in thermal niches.

The negative response skinks exhibited to canopy cover also supports previous evidence of more northerly populations of skinks occurring in relatively more open habitats (Fitch 1954, Hecnar 1991, Watson and Gough 2012). These results also concur with my findings in Chapter II, in which forest habitat was used far less than expected for all age classes and for all activity periods. Quirt et al. (2006) identified cover rock size and canopy cover as the best predictors of *P. fasciatus* in a Great Lakes-St. Lawrence population and that individuals of *P. fasciatus* preferred cover rocks in open rock outcrop habitats over those in closed habitats.

The negative response of skinks to increased soil moisture supports the findings of Chapter II where dune habitat, the most xeric of those sampled, was identified as the preferred habitat of RPP. *P. fasciatus* is confined to mesic regions (Fitch 1954) and is unlikely to be found in truly arid environments (Bogert and Cowles 1947 cited in Fitch 1954). The preference of skinks for relatively drier sites may be related to nest site preferences. Female skinks are likely better able to raise rather than reduce the moisture of a nest site. Female *P. fasciatus* can control moisture of the nest through covering eggs with dilute urine produced from drinking morning dew (Fitch 1954, Hecnar 1994), moving the nest vertically in the substrate (deeper when dry and higher when wet) and altering brooding position (high contact or low contact) to control moisture levels (Hecnar 1994). The absence of skinks from low dune areas after a heavy rainfall event (Chapter II) also supports the idea that wet soil conditions limit skink distribution in eastern Canada (Ussher and Cook 1979).

Skink habitat use was overall less affected by spatial variables. Further, results of the spatial variables were overall less consistent between analyses and years. Of the distance variables,

distance to shoreline was identified as the most likely spatial variable (Pearson and R^2). Skink observations in 2014 decreased with increased distance to shoreline. This is contradictory to previous observations at PPNP (see Hecnar and Hecnar 2012b) and RPP (Brazeau pers. obs. 2013-2015) which identified storm surges, flooding and erosion as damaging and reducing shoreline dune habitat. Interpretation of this variable should be made with caution due to variation of results between analyses as well as sampling years. Further, although multicollinearity was not identified, it is possible that the landscape structure of RPP prevents detection of this issue. Specifically, dune habitat at RPP occurs between the storm surge line and forest edge.

Skink observations were weakly predicted by the distance of sites to the nearest cover object, with both positive and negative correlations between years. The quality and size of cover objects has been previously identified as an important factor for occupancy (Hecnar 1991, Seburn 1993, Quirt et al. 2006) and nest site selection (Hecnar 1994). Further, the availability of cover objects was identified as an important component of population persistence of the PPNP population (Hecnar and M'Closkey 1998) with some of the highest densities of skinks having been observed in woodpiles (Fitch 1954). The use of cover boards for my sampling design is dependent upon the history of these observations and the use of standardized cover objects in an area with relatively little natural debris likely impacted the measure of this parameter. The results found in RPP may not be representative of other areas within *P. fasciatus* range in which debris is widely available.

Skink observations were not strongly influenced by the distance of sites to the nearest anthropogenic infrastructure. Observations from my macrohabitat selection study (see Chapter II) found that use was higher than expected in anthropogenic sites only during the beginning and end of the active season when age and sex class data was pooled. The interaction between anthropogenic environments and animals is inherently complicated with anthropogenic structure providing various advantages and disadvantages compared to what may be considered the 'natural' habitat of species (Germaine and Wakeling 2001). Skinks can thrive in agricultural or rural areas near human infrastructure where open habitat is maintained and cover is provided. Some of the highest skink densities have been recorded in wood, debris or compost piles (Fitch 1954, Hecnar and Hecnar 2011a). Proximity to cottages greatly increases the loss of potential refuge sites through firewood collection and ornamental beach wood (Hecnar and M'Closkey 1998, pers.obs), but human structures including building foundations, walls, decks, patios, firewood piles, and discarded building materials can provide habitat where it is otherwise not available (see Chapter I for further discussion of anthropogenic effects).

Skink observations were not consistently predicted by the distance of sites to the nearest road, with both positive and negative effect of this variable detected by analyses. Farmer and Brooks (2012) studied road mortality at RPP and PPNP and found that skinks and turtles were observed less frequently than other herpetofauna, mammals or birds. This is largely consistent with my personal observations throughout 2013 and 2014, when I rarely observed skinks on roads at RPP. Road ecology is a complicated interaction of anthropogenic and ecological interactions (i.e. traffic volumes, speed limits, driver awareness, characteristics of the surrounding habitat, noise and chemical pollution; Forman et al. 2003, Fahrig and Rytwinski 2009, Farmer 2012).

Roadways within RPP and PPNP are not as wide and have lower speed limits relative to other areas within the Carolinian range and findings may not be representative of more heavily trafficked areas. Rutherford and Gregory (2003) suggested that low dispersal distances between activity periods likely limit the effect of roads on *P. skiltonianus* and dispersal ability may be a factor to consider for *P. fasciatus* as well. Indeed, although my previous results (see Chapter II) may indicate migrations among habitats, low overall dispersal distances previously recorded for this species (Fitch 1954, Seburn 1993, Fitch and von Achen 1977) may account for the relatively poor predictive power of all distance variables measured. Further, the main road of RPP is located at the division of dune and forest habitat. Because canopy was identified as a strong predictor of habitat use there is relatively little incentive for individuals to cross the road toward less favourable habitat (also see Chapter II). An increased understanding of *P. fasciatus* movement patterns and maximum distances travelled at the study location may help to elucidate some of these findings.

Soil type has been suggested as a determining factor in distribution of *P. fasciatus* (Fitch 1954, Seburn 1993) and may have been a useful addition to this study. Because RPP and PPNP are sand spit formations, soil type is likely to be relatively homogeneous across the entirety of the study site, with sites varied only in organics. Further, the use of woodland habitat (organic surface soils) in the southern portion of its range (Fitch 1954, Watson and Gough 2012) suggest surface soil type is unlikely to provide considerable insight into microhabitat use. Furthermore, my study focused exclusively on habitat factors and the density of available food resources was not explored. The Five-lined Skink is a generalist arthropod predator (Fitch 1954, Hecnar et al. 2002, Brazeau et al. 2015) and arthropods tend to be quite abundant in coastal dune zone

(McLachlan 1991). Previous research at PPNP suggests that *P. fasciatus* abundance was not likely limited by density dependent effects (Hecnar 1991) and it is therefore unlikely that food resources would greatly influence habitat selection in the RPP study population. However, I made no attempt to test for density dependent effects in this study and therefore such effects cannot be ruled out as a potential factor in the observed habitat use.

This chapter identified forest canopy cover and its associated microclimate variables temperature, and moisture as better predictors of *P. fasciatus* occupancy than spatial variables near the northern extent of its range. The importance of microclimate for physiological functioning and biochemistry of temperature dependent lizards is well known (Heatwole 1977, Huey 1991) and the results of this study emphasize their importance for the microhabitat selection of *P. fasciatus* at my study location. My study is the first to quantify microhabitat selection of the Carolinian population of *P. fasciatus* at this scale, as well as the first to quantify microhabitat selection of *P. fasciatus* while controlling for cover object characteristics. My findings complement what we know about determinant factors of skink and possibly other reptile distributions in Ontario, and will aid in the search for surviving populations as well as the recovery of previously extirpated populations.

Chapter 4: Common Five-lined Skink (*Plestiodon fasciatus*) habitat use as a function of forest canopy cover and microclimate

4.1. Introduction

Forest canopy cover is a predominant factor in creating microclimate regimes and adds important structural complexity (Chen et al. 1999, Pringle et al. 2003, Huang et al. 2014). Reducing forest canopy cover with management practices such as prescribed fire and selective timber harvesting can promote restoration of reptile communities (Langford et al. 2007, Todd and Andrews 2008, Pike et al. 2011). Sun-exposed habitats support a wide range of endemic and rare species that are often absent from nearby forested areas, and these specialists contribute substantially to local biodiversity (Hunter 1999).

Ectotherms, such as reptiles, may be relatively more sensitive than endotherms to changes in structural microhabitat, with changes potentially important for behavioural thermoregulation (Heatwole 1977) and over-wintering, especially at higher latitudes (Seburn and Bishop 2007, Lesbarrères et al. 2014). Preferred body temperatures often coincide with optimal performance temperatures for physiological requirements (Huey and Bennett 1987) and overall fitness (Huey and Kingsolver 1989). Climatic extremes, such as those found near a species' northern range limits, make thermoregulation particularly important for reptiles because temperatures are often far from a species optimum (Blouin-Demers and Weatherhead 2001, Powell and Russell 2007).

Moving beyond the simple directional response of species to habitat characteristics, the identification of ecological thresholds is of particular interest for conservation efforts (Cunningham and Johnson 2012). Determining when and how severely populations will respond

to changes in the environment is fundamental for successful management. Ecological thresholds can be characterized as abrupt changes in a response variable as a consequence of continuous change in an independent variable (Muradian 2001), or similarly a zone(s) at which relatively rapid change occurs from one ecological condition to another (Bennett and Radford 2003). Habitat selection beyond critical levels (thresholds) is important for understanding gradual population declines in relation to habitat loss and fragmentations (Cunningham and Johnson 2012). However, threshold relationships in nature are often difficult to identify and studies often produce spurious results that are not effectively duplicated (Mönkkönen and Reunanen 1999, Hugget 2005).

The study of ecological thresholds, at both species and community levels, has much to offer both theoreticians and conservationists. Threshold relationships in nature are thought to be very dynamic and often change through time because of organism phenology (Huggett 2005). These issues, among others, have led to an ongoing debate among researchers on the incidence and utility of ecological thresholds for use by conservation based land management (Mönkkönen and Reunanen 1999, Lindenmayer and Luck 2005, Groffman et al. 2006, Rhodes et al. 2008). For ecological thresholds to function as effective tools in conservation and resource management future research should seek to identify variability among species, geography and landscapes (Guenette and Villard 2004). Much the current literature on ecological thresholds has focused on larger scale spatial threshold relationships with a particular emphasis on the effects of habitat fragmentation, distance to forest edge and minimum patch size (see Andren 1994, Drinnan 2005, Guenette and Villard 2005, Radford et al. 2005, Denoel and Ficetola 2007, Rhodes et al. 2008). Studies investigating threshold relationships at local scales with processes acting on available

microhabitat are currently rare (see however van der Ree et al. 2004). Further, herpetofauna are greatly underrepresented in many areas of ecological inquiry (Hecnar 2009). Thus detailed threshold studies of ectotherms are likely to yield valuable information for understanding the northern range limits of reptiles. The importance of microclimate for lizard functionality makes these animals suggests these animals will be ideal for understanding critical changes in habitat use.

Watson and Gough (2012) suggested that in the northern parts of its range, *P. fasciatus* is found in increasingly open habitats. In a Great Lakes – St. Lawrence *P. fasciatus*, population Quirt et al. (2006) found that the relative openness of a site will affect how exposed the cover rock surface is to solar radiation. Seburn (1993) suggested the degree of shading may be less significant in microhabitat selection of *P. fasciatus* at PPNP because canopy structure is not necessarily indicative of a specific type of substrate. Specifically, savannah habitats of RPP are relatively open but also have organic surface soils.

Watson and Gough (2012) explored the canopy and temperature relationship of *P. fasciatus* in the southern portion of its range (Louisiana, United States) where it lives sympatrically with two other Plestiodontid species the Southeastern Five-Lined Skink (*P. inexpectatus*) and the Broadheaded Skink (*P. laticeps*). Watson and Gough (2012) found that canopy cover, mean temperature, and daily maximum temperatures differed among the preferred habitats of these three species, and concluded that co-existence was likely attributable to variability in thermal niche. Analysis using multiple predictors of site occupancy (see Chapter III) indicated that forest canopy cover structure and associated variables (moisture, temperature) are strong indicators of

occupancy. In behavioural laboratory experiments, Fitch (1954) identified a preferred temperature range of 28-34 °C for *P. fasciatus*; however, the temperature profile of available forest canopy structures in *P. fasciatus* habitat has never been made. Near its northern range limits *P. fasciatus* is likely living near the limit of the thermal environments it can survive in. *P. fasciatus* is likely an ideal species to explore the interactive effects of forest canopy cover structure and temperature microclimates in creating abrupt or critical changes in ectotherm behaviour.

My objectives were to determine if the response of *P. fasciatus* to forest canopy cover is best described by a threshold response as well as to examine the thermal quality among of available habitats at RPP.

4.2. Methods:

4.2.1. Study Area

The study area, Rondeau Provincial Park (RPP; 42°17' N, -81° 52' W), is located adjacent to Lake Erie near Morpeth, Ontario, Canada (Figure 1.1). RPP is a rounded 35 km² cusped peninsula with flora of the Carolinian forest region (see Chapter 1 for details).

4.2.2. Data collection

Canopy and skink use data were collected using the same sampling design from Chapter III (Figure 3.1). To create a canopy temperature profile I used data loggers (Thermochron i-button, DS1921KI) to record temperatures of ten canopy categories/deciles ranging from 0 to 100%,

with four loggers for each decile. This was done so that a representative sample of all canopy categories could be accomplished using a limited number of loggers over a limited time frame.

The boards were randomly chosen from sites established in 2013, with sites ground-truthed for canopy class prior to logger placement. Ambient and under-board temperatures were sampled for each site. Refer to Chapter III methods for further details on placement. Temperatures were recorded for four consecutive days just prior to nesting season (June 20-June 23, 2014).

4.2.3. **Statistical methods**

Data were pooled across surveys in canopy deciles (0-100%), with observed use (skink observations) calculated as a proportion of sites/decile (see Homan et al 2004, Denoel and Ficetola 2007). Data pooled across the entire active season and for mating, nesting and post-hatching seasons were used for analysis (Table 4.1). To identify thresholds and identify cut-off points, piecewise regression was completed using the *R* software package segmented (Muggeo 2008). To approximate breakpoints for the piecewise regression, I used scatter plot smoothers (LOESS) to identify abrupt changes in slope (Toms and Lesperance 2003). There are many methods for determining thresholds in ecological data (see review by Guenette and Villard 2004), each with its own advantages depending on the nature of the data. Techniques such as Piecewise regression, used to detect abrupt thresholds, have the advantage of estimating position and probability of a threshold accurately, particularly when the change in slope is large (Denoel and Ficetola 2009). Further, utilizing all count data (as compared to binary) weighs the effect of multiple individuals or similarly the same individual maintaining a location across multiple

surveys. A linear regression was completed on minimum and maximum temperature readings as a function of canopy cover (%) for under-board and ambient logger locations.

4.3. Results

In 2013 I observed a total of 391 skinks over 16 surveys (24 skinks per survey). I observed a marked increase in 2014, with a total 1097 skinks over 32 surveys (34 skinks per survey; see Table 4.1).

4.3.1. 2013 Piecewise Regression

Skink observations declined rapidly with increasing canopy cover during the active season and a threshold response was identified for all activity periods with the strongest response identified for the nesting period (Figure 4.1). Piecewise regression models provided varied levels of fit, significance and breakpoint estimation across activity periods. All curves indicated sharp declines in occupancy with increased canopy cover, with identification of the inflection point nearly at zero observations (Figure 4.1). Breakpoint estimates ranged from 39 to 83 % and were identified predominately at or just above zero observations. Model fit was comparable or better than linear models for all periods (Figure 4.1; Table 4.2). With the exception of the nesting period all regressions were significant ($P < 0.05$). Although the nesting period was not significant ($P = 0.92$), analysis detected the highest level of fit ($R^2 = 0.93$), two breakpoints and the lowest standard error (39.32 ± 3.7 and 53.17 ± 3.4) of all 2013 sampling periods. When fitted with a single breakpoint the regression was significant ($P < 0.01$), but the regression coefficient was

diminished ($R^2 = 0.82$) and breakpoint location was increased, with increased standard error (70.2 ± 18.29).

Table 4.1: Total skink observations within canopy cover deciles with the total number of sites and results for all periods of activity which were used for piecewise regression.

Canopy Cover%	Total Sites	2013 Surveys				2014 Surveys			
		Total 2013	Mating (n=6)	Nesting (n=6)	Post-Hatching (n=4)	Total 2014	Mating (n=8)	Nesting (n=7)	Post-Hatching (n=19)
10	76	312	95	146	71	844	289	312	243
20	6	21	4	9	8	74	25	20	29
30	9	32	8	17	7	93	16	30	47
40	3	12	4	5	3	37	12	7	18
50	5	6	1	3	2	7	1	0	6
60	3	3	2	1	0	8	3	0	5
70	7	1	0	0	1	8	3	0	5
80	6	3	0	1	2	17	4	6	7
90	4	1	0	1	0	4	1	1	2
100	15	0	0	0	0	5	0	2	3

Table 4.2: Piecewise regression and linear regression results of 2013 and 2014 observations in response to canopy cover. Breakpoint (bp).

Year	Period	(n)	Piecewise regression				Linear regression	
			P-value	R ²	Estimated break point	SE	P-value	R ²
2013	Pooled all	16	0.003	0.82	71.02	21.66	<0.001	0.82
2013	Mating and Nesting	12	0.007	0.76	71.72	24.52	<0.001	0.78
2013	Mating	6	0.025	0.542	82.86	43.17	0.003	0.64
2013	Nesting	6	0.92	0.931	39.32 53.17	3.702 3.443	<0.001	0.79
2013	Nesting, 1 bp	6	0.002	0.821	70.2	18.29	<0.001	0.79
2013	Post-hatching	4	0.02	0.702	60.68	25.3	<0.001	0.72
2014	Pooled all	34	0.024	0.694	64.55	23.08	<0.001	0.71
2014	Mating and Nesting	15	0.0101	0.804	55.71	12.36	<0.001	0.69
2014	Mating	8	0.071	0.61	53.7	26.36	0.003	0.65
2014	Nesting	7	0.004	0.856	56.76	8.294	<0.001	0.68
2014	Post-hatching	19	0.421	0.618	22.77	8.401	0.007	0.57

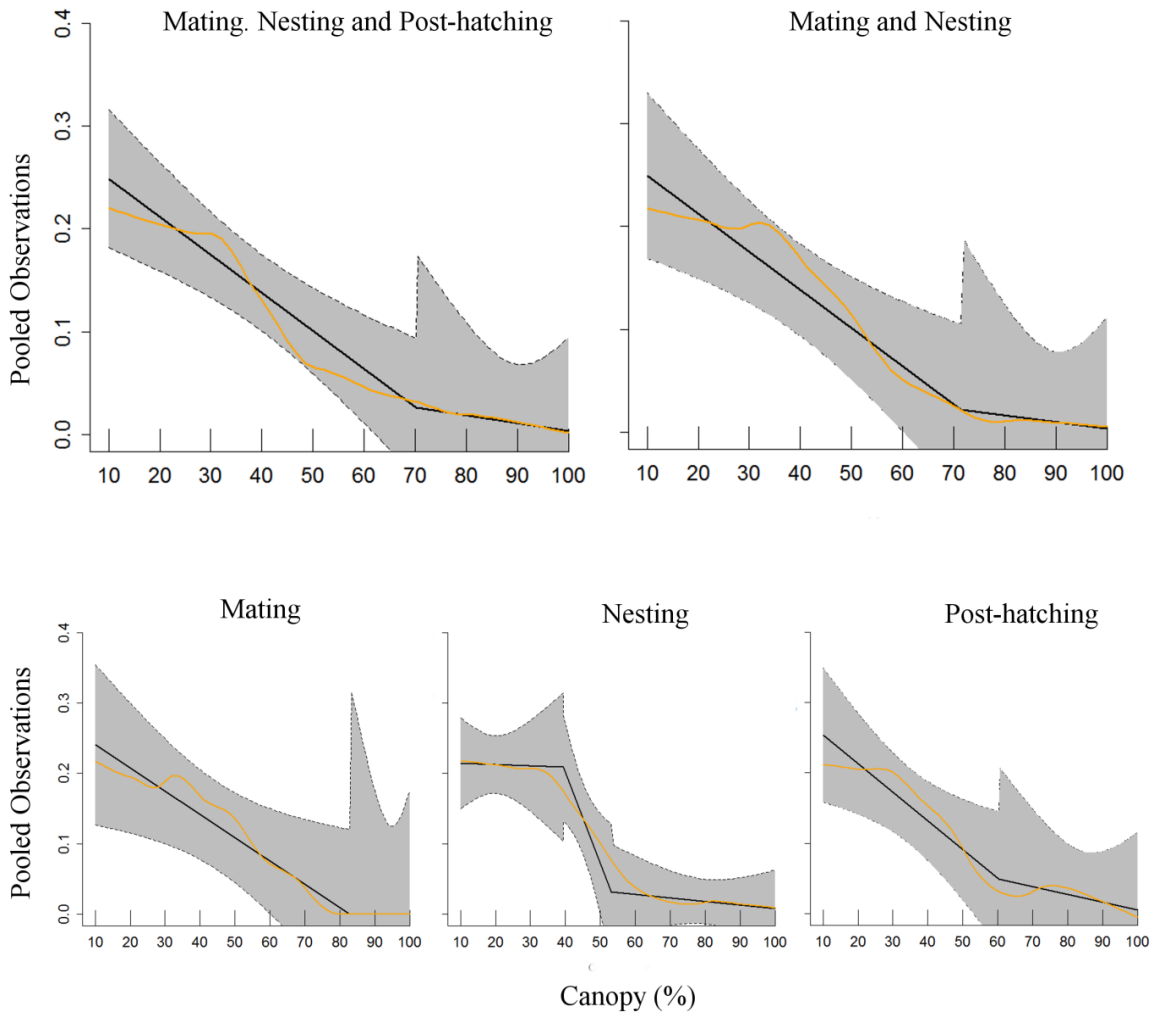


Figure 4.1: Piecewise regression of 2013 observations in response to canopy cover. The black solid lines are predicted results based on piecewise regression analysis and grey is 95% CI. The LOESS curve is in orange.

4.3.2. 2014 Piecewise Regression

Skink observations declined rapidly with increasing canopy cover during the active season and a threshold response was identified for all activity periods with the strongest response identified for the nesting period (Figure 4.1). Results are largely consistent with findings of 2013 with breakpoints of >50-60 % identified for all periods except post-hatching. Model fit was comparable or better than linear models for all periods. (Figure 4.2, Table 4.2). Piecewise regression models were significant ($P < 0.05$) for pooled data as well as the nesting period but not for mating or post-hatching period. Analyses identified a single breakpoint with comparable breakpoints between 50 and 60% for mating (53.7 ± 26.36) and nesting (56.76 ± 8.29). Curves for mating and nesting indicate a decline with increased canopy cover, with a breakpoint that was close to zero. Skink response to canopy was markedly different for the post-hatching period, with a piecewise regression that indicated a rise in observations from 0 to ~25% where a break point was identified (22.77 ± 8.4), followed by decline to zero occupancy at 100% canopy cover.

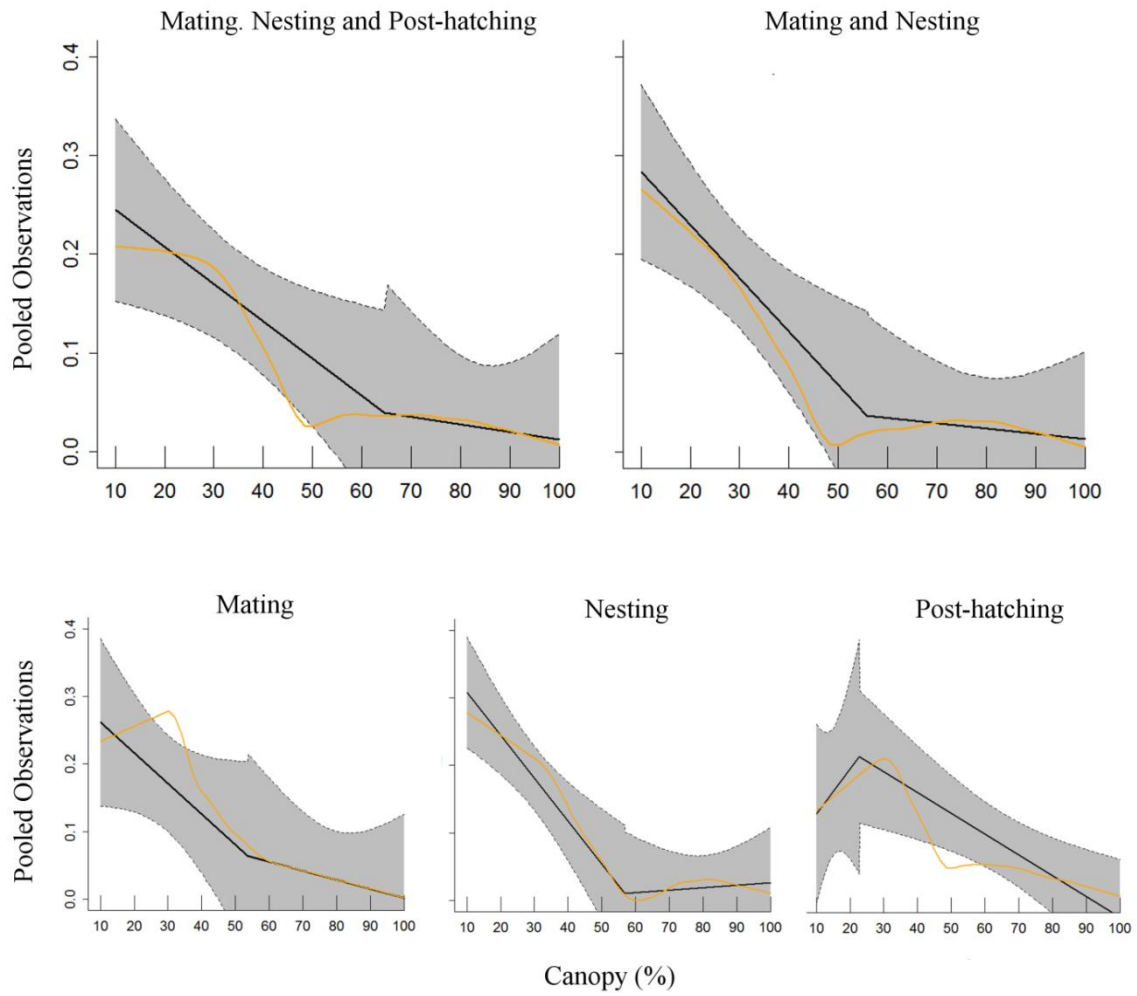


Figure 4.2: Piecewise regression of 2014 observations in response to canopy cover. The black solid lines are predicted results based on piecewise regression analysis and grey is 95% CI. The LOESS curve is in orange.

4.3.3. Temperature profile

As canopy cover increased the maximum ambient ($R^2= 0.85, F_{1,8}= 50.02, P<0.001$), maximum under-board ($R^2= 0.86, F_{1,8}= 50.63, P<0.001$) and minimum under-board ($R^2= 0.86, F_{1,8}= 56.35, P<0.001$) temperatures decreased (Figure 4.3). Minimum ambient temperatures increased with increasing canopy cover ($R^2= 0.52, F_{1,8}= 11.11, P<0.001$).

Maximum ambient temperatures (Table 4.3) ranged from 52.75 °C (0-10% cover) to 25.13 °C (90-100% cover), maximum under-board temperatures ranged from 33.38 °C (0-10% cover) to 19.59 °C (90-100% cover). Minimum ambient temperatures ranged from 12.88 °C (0-10% cover) to 15.65 °C (80-90% cover), minimum under-board temperatures ranged from 18.69 °C (0-10% cover) to 16.5 °C (90-100% cover). Maximum under-board temperatures of the 40-50 % measurements were on average 28.5 °C, at the lower end of the ideal range (28-34 °C).

Maximum under-board temperatures from 60-70 % canopy cover were on average 25.13 °C.

Table 4.3: Temperature profile data collected using I-button data loggers in 2014. Four boards were measured for each decile of canopy cover (0-100%).

Canopy Cover%	Ambient °C		Under-board °C	
	Max	Min	Max	Min
0-10	52.75	12.88	33.38	18.69
10-20	49	14	29.19	18.53
20-30	51.17	14.22	29.72	18.25
30-40	49.75	14.97	29.78	18.25
40-50	50.81	14.78	28.84	18.31
50-60	43.31	13.75	28.47	17.09
60-70	38.84	15.63	25.13	17.31
70-80	32.22	14.72	21.34	16.53
80-90	34.22	15.66	23.81	16.97
90-100	25.13	15.28	19.59	16.5

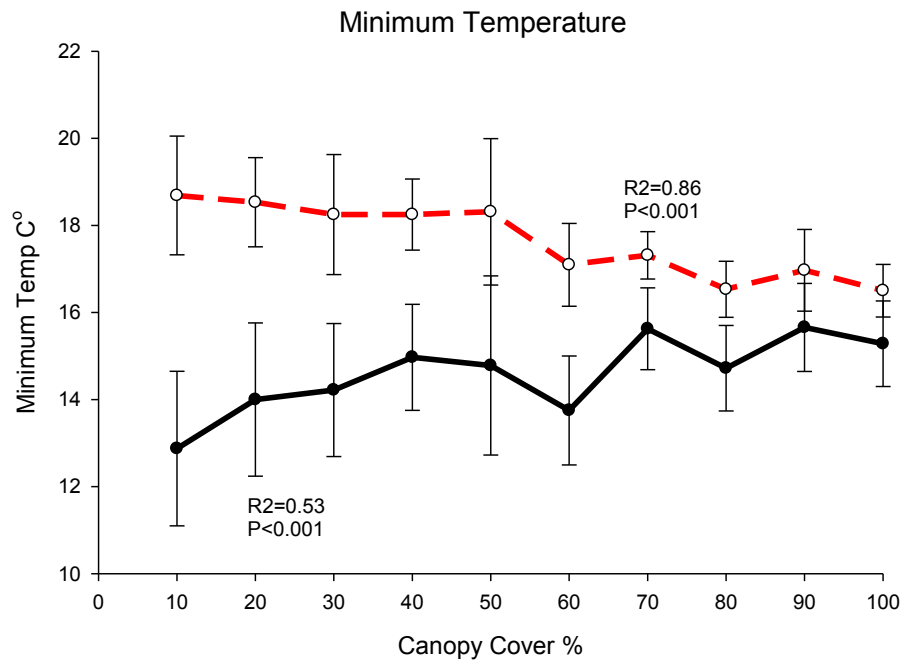
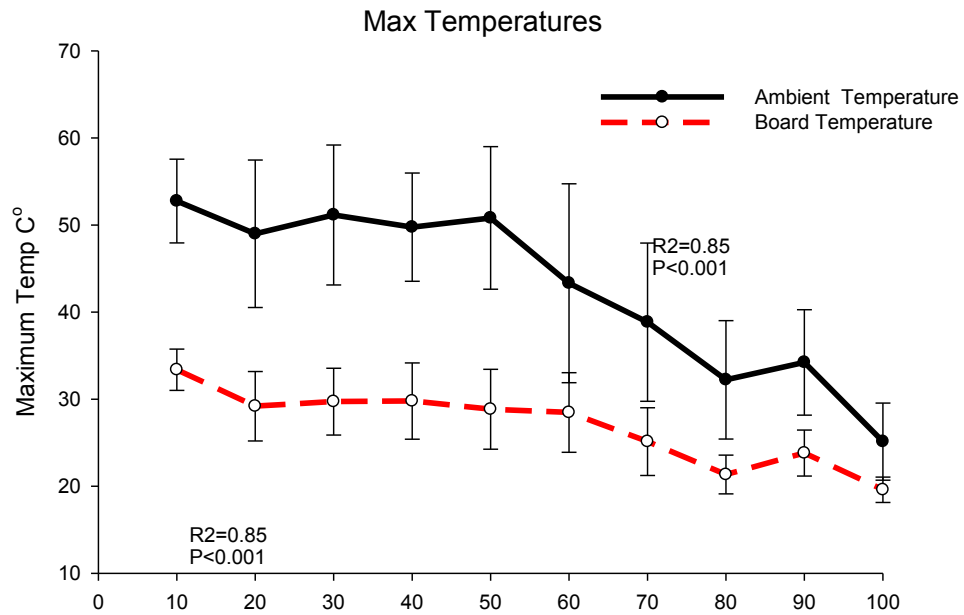


Figure 4.3: The maximum and minimum ambient and under board temperature relationship with canopy cover. Linear regression results provided.

4.4. Discussion:

Microhabitat use by *P. fasciatus* exhibits a threshold response to canopy for much of the active season at Rondeau Provincial Park, with the effect most pronounced during the nesting period. Further, skink use declined from zero canopy cover until it reached a threshold response, which was above 50% canopy cover for most of the active season. Furthermore, the response of skinks to canopy cover is likely driven by thermoregulatory behaviour. The temperature profile strongly agreed with the threshold response of skinks to canopy cover, with cover object temperatures above 60% canopy cover below the ideal temperature range of *P. fasciatus*. Considering the directions and extents of temperature variation, cover boards provided a suitable thermal environment for skink refuge and nesting at or near thermal optima by buffering ambient extremes.

Most of the thresholds identified were located at or near zero occupancy which is particularly significant as analyses was completed on multiple surveys within activity periods in a study site known to have relatively large abundance of *P. fasciatus* (Hecnar and Brazeau 2014, 2015). This shows that the thresholds identified are in fact locations of critical change after which the probability of encountering any individuals is unlikely. Estimating a precise breakpoint is difficult given the complex nature of seasonal observations and overall variability within the available data set. However, consistently higher skinks observations at sites with canopy cover ranging from 0-50 % indicates that habitat within this range is most likely to be successfully utilized compared to sites outside of this range. The nesting period was the peak of activity at RPP for both 2013 and 2014 survey years (Hecnar and Brazeau 2014, 2015). Furthermore, although the extent of the threshold differed somewhat from 2013 to 2014, the increased sample

size and time from initial board set up appears to only have strengthened the measured threshold relationship. Skink use declined with increasing canopy until reaching a threshold response for all activity periods, with the exception of the post hatching period. During the post-hatching period skinks responded positively to from zero to 20% canopy cover, at which point observations rapidly declined. A reduced preference for the most open habitats parallels findings of Chapter II, in which I found that skinks observation in savannah habitat increased during the post-hatching period but remained low in forest habitat. A change in the response of skinks to canopy cover near the end of the active season may represent a shift in habitat preferences associated with hibernation, but this trend cannot be verified without mark recapture data.

The temperature profile strongly agreed with the canopy occupancy thresholds, with temperatures above 60% canopy cover below the ideal temperature range of 28-34 °C for *P. fasciatus* as identified by Fitch (1954). These results strongly corroborate findings of Watson and Gough (2012), who suggested that *P. fasciatus* occurs in open habitats in the northern parts of its range to maximize thermal efficiency. These findings are also consistent with a study completed on the Great Lakes-St. Lawrence population where cover rocks in closed canopy forest failed to reach the range of temperatures preferred by *P. fasciatus* (Quirt et al. 2006). Skinks in the Great Lakes – St. Lawrence are strongly associated with rock outcrops as habitat. These results highlight the importance of *P. fasciatus* thermoregulatory behaviour near the northern extent of its range. Inversely, the temperature and canopy profiles indicated that maximum ambient temperatures below 50% canopy cover reach critically high levels (>50°C). With the absence of cover objects these habitats would effectively prevent individuals from being active during the hottest time of the year. A possible advantage of having suitable debris in hot open habitat is

that it would allow skinks to bask on or near cover and reach optimal temperatures quickly for their short foraging forays.

My observations largely correspond to what is expected for ectotherm behaviour, with skinks using habitat that will maximize thermal efficiency (Heatwole 1977, Huey 1991). In many cases lizards are capable of passive thermoregulation (Smith and Ballinger 2001), but the range of temperatures that *P. fasciatus* experiences at RPP, just over 350 km from its northern maximum (Conant and Collins 1998), would require relatively high levels of thermoregulatory behaviour to maximize the benefits of a shorter active season. As such, in addition to microhabitat availability (Hecnar and M'Closkey 1998), canopy and subsequently temperature are likely also factors limiting *P. fasciatus* and distribution in the Carolinian region of Ontario.

Along with microhabitat availability (Hecnar and M'Closkey 1998) the availability of open habitats, which provide an ideal thermal environment, is likely a limiting factor for *P. fasciatus* near the northern extent of its range. These results agree with findings for other reptile species. Huang et al. (2014), found that increasing forest cover created increasingly cooler microclimates that were outside of the preferred temperatures of the Taiwanese grass lizard *Takydromus hsuehshanensis*. Pringle et al. (2003) suggested that availability of thermally suitable retreat sites may be a limiting factor for population persistence of the Australian broad-headed snake (*Hoplocephalus bungaroides*), based on the canopy structure and thermal properties of retreat site characteristics.

The maximum under-board temperatures observed below 50% canopy cover would allow *P. fasciatus* to reach optimal temperatures at the hottest part of the day without leaving the protection of cover. Results of my study indicate that *P. fasciatus* predominately utilizes habitat that exhibits the highest available temperatures with the greatest daily variability.

Thermoregulation is thought to only be adaptive when costs resulting from associated losses of time and energy are low (Huey 1974, Huey and Slatkin 1976). However, based on findings of an Ontario population of Black Rat Snakes (*Elaphe obsoleta*) Blouin-Demers and Weatherhead (2001) suggested this traditional model of thermoregulation may not adequately describe species near their northern range extent. Temperature is likely a limiting factor for reptiles at northern latitudes which subsequently increases the importance of effective thermoregulation.

Increasingly open habitats create several potential risks for lizards including: 1) visibility to predators, 2) vulnerability to stochastic effects such as heavy rainfall (refer to Chapter II discussion), 3) critically high temperatures that are likely to prevent dispersal during the hottest periods of the day, and 4) greater variability in overall temperature. My results suggest that the thermoregulatory advantages of open habitats supersede any of these associated risks further emphasizing the importance of thermally optimal sites for *P. fasciatus* near its northern range limit. Assessing the associated cost of risks accrued by *P. fasciatus* when using open habitats is however unattainable with my current data. Body temperature data directly testing thermoregulatory cost-benefit predictions would aid in determining if *P. fasciatus* conforms to the traditional model of thermoregulation near its northern range limits.

Quirt et al. (2006) suggested comparing thermal properties of occupied sites in the Great Lakes-St. Lawrence Population of *P. fasciatus* with sites north of current range limits in an attempt to

identify whether temperature of cover objects is a limiting factor for northern range expansion of this species. From my findings at RPP I make comparable suggestions: that both ambient and cover object temperatures (in both open and closed habitats) be recorded at and just north of the current range limit to determine if temperature extremes outside of the suggested optimum exist. Further, experimental manipulation of canopy cover in multiple habitats is likely to provide a better response curve with reduced potential of confounding factors.

Because the rate of natural succession is a concern for the conservation of Carolinian populations of the skink (COSEWIC 2007), and elsewhere in its range (Fitch 2006 a, b), this information regarding canopy cover may allow for more efficient management and restoration of *P. fasciatus* habitat. Specifically, this data will assist decision making regarding frequency of fire management and thinning to ensure persistence of populations in specific target habitats. Where habitat management seeks to improve skink habitat in the Carolinian region, thinning of forest should be considered when tree canopy cover exceeds 50%. Tree canopy cover provides structural complexity within an ecosystem (Chen et al. 1999, Hunter 1999, Pike et al. 2011) and where possible maintaining a mosaic is likely to confer the greatest overall advantage. Long term field research in Kansas (Fitch 2006b) revealed that forest encroachment reduced *P. fasciatus* abundance relatively quickly when compared to native snakes of the area. Further, the historical range of *P. fasciatus* highly overlaps with historic tall grass prairie extent in Ontario (Hecnar et al. in progress) suggesting that an availability of open habitats allowed this species to expand its range to where it is today.

The results of this study support the efficacy of thresholds for management of *P. fasciatus* within the Carolinian portion of its range in southwestern Ontario. Further, this study identifies thresholds of occupancy in response to habitat structure at the microhabitat scale. Because thresholds are a contested issue in conservation and management research, hopefully this study will promote further discussion and research on this currently insufficiently studied topic in herpetology and conservation biology. Further, this study is the first to create thermal profile of canopy structure for *P. fasciatus* habitat, and this will aid in the assessment and identification of ideal *P. fasciatus* habitat for future management and conservation efforts.

Chapter 5: Conclusion

My findings emphasize the importance of thermally optimal microclimates and the availability of open habitats near this species' northern range limits. Further, findings indicate that *P. fasciatus* occupancy responds to increasing forest canopy cover, and results strongly suggest this is related to ideal thermoregulatory behaviour. A critical/abrupt response to canopy cover during the peak of the active season suggests that availability of open habitats may limit population persistence. All aspects of this study indicate that management efforts should focus on protecting and if possible enhancing dune habitats in northern extant populations of the Five-lined Skink. Dune habitat was preferred among the main terrestrial habitats, and is the most open available habitat of the study location.

The negative response that *P. fasciatus* exhibited to canopy cover supports previous evidence of more northerly populations of skinks occurring in relatively more open habitats (Fitch 1954, Hecnar 1991, Watson and Gough 2012). This also supports the findings of Watson and Gough (2012) who found that the sympatry between *P. fasciatus* and two other skinks, the Southeastern Five-Lined Skink (*P. inexpectatus*) and the Broadheaded Skink (*P. laticeps*), was likely attributable to variability in thermal niches. Although competitive release cannot be tested at RPP this may be a factor of the *P. fasciatus*' increased use of open habitats in the northern extent of its range. Alternatively, *P. fasciatus* may be better able to survive in colder environments when compared to *P. laticeps* and *P. inexpectatus* allowing it to successfully invade more northern environments where it is limited to using open habitats in order to reach a thermal optima.

My observations are likely to be of general value for management of reptiles at the northern limit of their range. The increase in canopy cover acts to decrease the availability of sites with temperatures that a reptile can expect to find at more southerly locations. Because temperature is ultimately the most likely factor in limiting northern range extensions of ectotherms the link between canopy cover and microclimate explored in this thesis is also likely to provide valuable insight in the context of reptile distributions at northern latitudes.

Despite a paucity of debris, the RPP the population appears healthy and thriving, while in other areas in the region it has become extirpated or exists at relatively low densities. This is likely because of the overall heterogeneity of available habitat at RPP and I suggest that the current mosaic of canopy cover available at RPP be maintained. Because of the overall success of *P.fasciatus* at RPP, it is likely that RPP can act as a suitable model for remediating sites where *P.fasciatus* has become extirpated.

Future investigations of this species should seek to identify seasonal dispersal patterns that identify the presence or absence of migratory behaviour and the location of preferred hibernacula. Perhaps more important and urgent is a need for experimental exploration of the interaction of forest cover and persistence of skink and other reptile populations at northern latitudes.

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Appendix

Table 6.1: 2013 AIC results for the nesting period with all models included. McFadden's R^2 is included as additional reference. Models are listed in decreasing order of likelihood as calculated by QAIC.

Models	Model #	K	QAICc	Delta QAICc	QAICc Wt	Quasi.LL	R^2
~CANOPY+MOIST+ANTHRO	9	5	187.53	0.00	0.29	-88.53	0.23
~CANOPY*MOIST+ANTHRO	17	6	188.37	0.84	0.19	-87.85	0.23
~CANOPY+MOIST+MICRO+ANTHRO	4	6	189.17	1.65	0.13	-88.26	0.23
~CANOPY*MOIST+MICRO+ANTHRO	13	7	190.12	2.59	0.08	-87.61	0.23
~CANOPY+MOIST+MICRO+ANTHRO+ROAD	2	7	191.19	3.67	0.05	-88.15	0.23
~CANOPY*MICRO+MOIST+ANTHRO	21	7	191.19	3.67	0.05	-88.15	0.23
~CANOPY+MOIST+MICRO+ANTHRO+WATER	3	7	191.27	3.75	0.04	-88.19	0.23
~CANOPY+MOIST+MICRO*ANTHRO	5	7	191.35	3.82	0.04	-88.23	0.23
~CANOPY*MOIST+MICRO+ANTHRO+WATER	12	8	192.31	4.78	0.03	-87.58	0.23
~CANOPY*MOIST+MICRO+ANTHRO+ROAD	11	8	192.31	4.79	0.03	-87.58	0.23
~CANOPY*MICRO+MOIST+ANTHRO+ROAD	19	8	193.25	5.72	0.02	-88.05	0.23
~CANOPY*MICRO+MOIST+ANTHRO+WATER	20	8	193.33	5.80	0.02	-88.09	0.23
~CANOPY+MOIST+MICRO+ANTHRO+ROAD+WATER	1	8	193.41	5.88	0.02	-88.13	0.23
~CANOPY*MOIST+MICRO+ANTHRO+ROAD+WATER	10	9	194.58	7.05	0.01	-87.56	0.23
~CANOPY+MOIST	8	4	195.13	7.61	0.01	-93.41	0.18
~CANOPY*MOIST	16	5	195.46	7.94	0.01	-92.50	0.19
~CANOPY*MICRO+MOIST+ANTHRO+ROAD+WATER	18	9	195.51	7.98	0.01	-88.03	0.23
~CANOPY+MOIST+MICRO	7	5	195.75	8.23	0.00	-92.64	0.19
~CANOPY+MOIST+MICRO+WATER	6	6	196.13	8.60	0.00	-91.74	0.20
~CANOPY*MOIST+MICRO	15	6	196.30	8.77	0.00	-91.82	0.20
~CANOPY*MOIST+MICRO+WATER	14	7	197.06	9.53	0.00	-91.09	0.20
~CANOPY*MICRO+MOIST	23	6	197.90	10.37	0.00	-92.62	0.19
~CANOPY*MICRO+MOIST+WATER	22	7	198.30	10.77	0.00	-91.70	0.20
~CANOPY	29	3	200.75	13.22	0.00	-97.28	0.15
~CANOPY*MICRO+ANTHRO	25	6	201.46	13.93	0.00	-94.40	0.17
~CANOPY+MICRO	28	4	201.68	14.15	0.00	-96.68	0.15
~CANOPY*MICRO	24	5	203.74	16.21	0.00	-96.64	0.15
~MOIST	30	3	206.49	18.96	0.00	-100.15	0.12
~ANTHRO*ROAD	27	5	224.09	36.56	0.00	-106.81	0.07
~WATER	34	3	231.18	43.65	0.00	-112.50	0.02
~ROAD	33	3	233.05	45.52	0.00	-113.43	0.01
~ANTHRO+ROAD	26	4	234.02	46.49	0.00	-112.85	0.01
~ANTHRO	32	3	234.24	46.71	0.00	-114.03	0.00
~MICRO	31	3	234.85	47.32	0.00	-114.33	0.00

Table 6.2: 2014 AIC results for the nesting period with all models included. McFadden's R^2 is included as additional reference. Models are listed in decreasing order of likelihood.

Models	Model #	K	QAICc	Delta QAICc	QAICc Wt	Quasi.LL	R^2
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+ROAD+WATER	10	10	193.04	0.00	0.27	-85.63	0.36
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+WATER	12	9	193.84	0.80	0.18	-87.19	0.35
~CANOPY+Max.2+MICRO+ANTHRO+ROAD+WATER	7	8	194.25	1.21	0.15	-88.55	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+ROAD+WATER	1	9	195.61	2.57	0.07	-88.08	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+WATER	3	8	195.77	2.73	0.07	-89.31	0.33
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+WATER	19	9	196.39	3.35	0.05	-88.47	0.34
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+ROAD+WATER	41	10	196.49	3.45	0.05	-87.35	0.35
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+ROAD+WATER	17	10	196.49	3.46	0.05	-87.35	0.35
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+WATER	43	9	196.51	3.47	0.05	-88.53	0.34
~CANOPY*Max.1+Max.2+MICRO+ANTHRO+ROAD	11	9	197.22	4.18	0.03	-88.89	0.34
~CANOPY+Max.1+Max.2+MICRO+ANTHRO+ROAD	2	8	199.41	6.37	0.01	-91.13	0.32
~CANOPY*MICRO+Max.1+Max.2+ANTHRO+ROAD	42	9	200.21	7.17	0.01	-90.38	0.33
~CANOPY*Max.2+Max.1+MICRO+ANTHRO+ROAD	18	9	200.59	7.55	0.01	-90.57	0.32
~CANOPY*Max.1+Max.2+MICRO+ROAD+WATER	13	9	201.59	8.55	0.00	-91.07	0.32
~CANOPY+Max.1+Max.2+MICRO+ROAD+WATER	4	8	202.48	9.44	0.00	-92.66	0.31
~CANOPY*MICRO+Max.1+Max.2+ROAD+WATER	44	9	202.71	9.67	0.00	-91.63	0.32
~CANOPY*Max.2+Max.1+MICRO+ROAD+WATER	20	9	203.47	10.43	0.00	-92.01	0.31
~CANOPY*MICRO+Max.2	47	6	204.45	11.41	0.00	-95.89	0.28
~CANOPY+MICRO+ANTHRO+ROAD+WATER	23	7	204.73	11.69	0.00	-94.92	0.29
~CANOPY*Max.1+Max.2+MICRO	14	7	205.85	12.82	0.00	-95.48	0.29
~CANOPY+Max.1+Max.2+MICRO	5	6	206.44	13.40	0.00	-96.89	0.28
~CANOPY*MICRO+Max.1+Max.2	45	7	206.63	13.59	0.00	-95.87	0.28
~CANOPY+Max.1+MICRO+ANTHRO+ROAD+WATER	8	8	206.96	13.92	0.00	-94.90	0.29
~CANOPY*Max.1+Max.2	15	6	207.20	14.17	0.00	-97.27	0.27
~CANOPY*Max.2	31	5	207.43	14.39	0.00	-98.48	0.26
~CANOPY*Max.2+Max.1+MICRO	21	7	207.94	14.90	0.00	-96.52	0.28
~CANOPY+Max.1+Max.2	6	5	208.12	15.09	0.00	-98.83	0.26
~Max.1*Max.2+MICRO+ANTHRO+ROAD+WATER	16	9	208.66	15.62	0.00	-94.60	0.29
~CANOPY*Max.1+CANOPY*Max.2	30	7	209.42	16.38	0.00	-97.27	0.27
~CANOPY*Max.2+Max.1	22	6	209.62	16.58	0.00	-98.48	0.27
~Max.1+Max.2+MICRO+ANTHRO+ROAD+WATER	9	8	212.16	19.13	0.00	-97.51	0.27
~Max.1*Max.2	36	5	213.15	20.11	0.00	-101.34	0.24
~CANOPY+MICRO+ANTHRO*ROAD	26	7	214.11	21.07	0.00	-99.61	0.26
~CANOPY+MICRO+ANTHRO+ROAD	24	6	214.15	21.11	0.00	-100.74	0.25
~Max.2	38	3	217.52	24.48	0.00	-105.67	0.21
~CANOPY+MICRO+ANTHRO	25	5	219.84	26.80	0.00	-104.69	0.22
~CANOPY*MICRO+Max.1	46	6	223.91	30.87	0.00	-105.62	0.21
~CANOPY*MICRO	48	5	224.86	31.82	0.00	-107.20	0.20
~CANOPY+MICRO	27	4	224.98	31.94	0.00	-108.33	0.19
~CANOPY*Max.1	32	5	225.12	32.08	0.00	-107.33	0.20
~CANOPY	39	3	229.64	36.60	0.00	-111.73	0.17
~Max.1	37	3	244.41	51.37	0.00	-119.11	0.11
~WATER	35	3	255.75	62.71	0.00	-124.78	0.07
~ANTHRO*ROAD	28	5	261.11	68.07	0.00	-125.32	0.06
~ANTHRO+ROAD	29	4	267.50	74.46	0.00	-129.59	0.03
~ROAD	34	3	271.60	78.56	0.00	-132.71	0.01
~MICRO	40	3	272.99	79.95	0.00	-133.40	0.00
~ANTHRO	33	3	273.93	80.89	0.00	-133.87	0.00