

TRACKING HABITAT USE BY BOREAL TOADS IN DISTURBED FOREST
ON THE BOREAL PLAIN IN ALBERTA

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A THESIS SUBMITTED IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE IN FORESTRY

FACULTY OF NATURAL RESOURCES MANAGEMENT

LAKEHEAD UNIVERSITY

24 JUNE 2014

ACKNOWLEDGEMENTS

As with every large endeavour, there are many people to acknowledge for their assistance and support. I would first like to thank my supervisor, Dr. Ellie E. Prepas, and Dr. Michael J. Lannoo for their guidance throughout my graduate processes. I would also like to thank my committee members, Dr. Brian McLaren and Dr. Stephen J. Hecnar, for their constructive feedback and assistance, my external reviewer Dr. Ronald W. Russell, and Tim McCready for representing Millar Western Forest Products Ltd. on my committee.

I owe a great deal of thanks to Janice Burke for editing countless drafts of my thesis. Her experience and willingness to help were instrumental to improving my writing ability, and for that I will be forever in her debt. I would also like to thank Mark Serediak for sharing his field savvy and exercising incredible patience as he supported me through my fieldwork. Mark's blend of troubleshooting, humour and common sense had a great impact on me, and I am very grateful to have met him. I also thank Virginia Antoniak for helping coordinate various aspects of my graduate studies. Her involvement made quick work of the administrative processes associated with my fieldwork. I would not have been able to conduct my fieldwork without my wonderful field assistants: Kelly Boyle and Patrick Gilhooly. I could not have asked for better partners in the field, if for no other reason than for putting up with me as well as they did. I would also like to thank (in no particular order) Rebecca MacDonald, Nancy Serediak, Stephen Nadworny, Nicole Frasier, Tanya Rushcall, and the great many FORWARD Project field personnel over the years for their assistance and friendship.

I would also like to acknowledge my parents, Robert and Lorraine Long, for their incredible support throughout my graduate studies. I don't know if I would have managed half as well as I have without their motivation, understanding and compassion through the long years.

The FORWARD II Project, of which I participated in as a graduate student, was funded by the Natural Sciences and Engineering Research Council of Canada Collaborative Research and Development Program, with additional funding from: Millar Western Forest Products Ltd., Alberta Newsprint Company (ANC Timber) Ltd., AbitibiBowater, Blue Ridge Lumber Inc. (a division of West Fraser Timber Company Ltd.), Buchanan Forest Products Ltd., Buchanan Lumber (a division of Gordon Buchanan Enterprises Ltd.), Petrobakken Energy Ltd. (formerly TriStar Oil & Gas Ltd.), Talisman Energy Inc., Vanderwell Contractors (1971) Ltd., Vaquero Energy Inc., Alberta Innovates BioSolutions, the Canada Foundation for Innovation, FedNor, the Forest Resource Improvement Association of Alberta, the Living Legacy Research Program and the Ontario Innovation Trust. My personal funding was provided through a NSERC Industrial Postgraduate Scholarship, with Millar Western Forest Products Ltd as my sponsoring industrial partner.

On a personal note, I would like to dedicate my thesis to the late Dr. J. Stan Rowe. Stan was a friend of the family, but I only knew him when I was young. However, I now see how profoundly my worldview and appreciation of nature were informed by Stan's

personal philosophy, largely through his influence on my father. Although this thesis represents a very small contribution to natural science, Stan was a big part of what inspired me to pursue my passion for ecology. Stan, we had far too little time together, and I wish I had known you twice as well. But I will cherish the memories I have forever. Thank you.

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ABSTRACT

Radio-telemetry is an effective way of collecting detailed information on the behaviour of a great many species. However, the presence of the radio-transmitter may influence the behaviour of the subject, an effect for which one cannot necessarily control. I examined the relative impact of two common radio-transmitter attachment techniques (waistband harness and surgical implantation) on Wood Frogs and Boreal Toads to determine their efficacy for these species. The acute stress of surgical implantation appeared to have less impact than the chronic stress of the waistband harnesses, but logistic constraints limited their usefulness for monitoring Boreal Toad movements. Radio-telemetry provided the means of identifying Boreal Toad refuge microsites, which likely represent a critical resource for the persistence of the species. Refugia provided favourable microclimates with elevated relative humidity compared to the surrounding habitat. Boreal Toads tended to forage at night within 15 m from refugia. This distance was used to calculate activity centres across toad summer home ranges. This approach can be used to pinpoint critical habitat at the landscape scale, which may be of particular importance for conserving populations currently in decline.

CHAPTER 1

THE BOREAL ANURAN COMMUNITY IN CENTRAL ALBERTA

Most North American amphibian studies are conducted within the contiguous United States. Boreal systems are largely unstudied in comparison, resulting in many gaps in our understanding of these systems. Although information from other regions can be useful, regional variation may limit the degree to which inferences can be drawn (Constible et al. 2010). Present day Boreal systems are relatively young and dynamic, having only formed since the Pleistocene glaciation. The Boreal zone covers roughly 5.5 million km² of Canada, with approximately 3.2 million km² forested (Brandt 2009). The Boreal Plain ecozone comprises 650,000 km² (~20%) of the Canadian Boreal zone, with nearly half occurring within the province of Alberta (Fig. 1-1; Ecological Framework of Canada 2014). Despite the somewhat misleading name, the Boreal Plain is composed primarily of mixedwood forest, but ranges from aspen parkland in the south to mature pine forests in the north. The Boreal Plain represents approximately 75% of the forested lands in Alberta, covering nearly 288,000 km² (Anielski and Wilson 2001).

During the retreat of the last ice sheet, the land was likely first re-colonized by species resilient enough to persist in glacial refugia (Goebel et al. 2009, Holman 1992, 1998, Lee-Yaw et al. 2008, 2009). With the short disturbance cycle and young age of these systems, Boreal communities are largely composed of wide-ranging, disturbance-tolerant, generalist species (Krohne 2001). Nevertheless, declines have also been reported for 17 of Canada's 45 amphibian species (three occurring within the Boreal

Plain of Alberta; CARCNET 2012), with habitat loss reported as the primary cause (Findlay and Houlihan 1997, Houlihan and Findlay 2003, Lehtinen et al. 1999, Semlitsch 2000).

The Anurans of Central Alberta

The anuran community in the Boreal Plain of central Alberta—henceforth referred to as the ‘Boreal Anuran Community’ (BAC)—is relatively simple, consisting of three of the most widely distributed species in the province: Wood Frogs (*Lithobates sylvaticus*), Boreal Toads (*Anaxyrus boreas boreas*; the northern subspecies of Western Toad), and Boreal Chorus Frogs (*Pseudacris maculata*). Historically, Northern Leopard Frogs (*L. pipiens*) were distributed throughout the southern half of Alberta, including the focal region. However, Northern Leopard Frogs were extirpated from most of western Canada during a major decline first detected in the 1970s (COSEWIC 2009). Canadian Toads (*A. hemiophrys*) may also be present, but the focal region represents the western limit of their geographic range where they likely occur in very low densities, and as such were omitted.

The BAC species inhabit a wide range of habitats across their geographic ranges (Table 1-1). Wood Frogs are widely distributed, occurring from northern Alaska and south-central British Columbia in the west, and east to the Appalachians, coastal states and Maritime provinces (Fig. 1-1; Russell and Bauer 2000). Boreal Chorus Frogs are broadly distributed in central North America, occurring from west-central Northwest Territories east to southern James Bay, and south to the upper mid-west and Great Plains states as far as Northern New Mexico and Arizona (Fig. 1-1; Russell and Bauer 2000). Western Toads are restricted to western North America, ranging from southern Yukon

and coastal Alaska south to northern Baja California, and as far east as western Wyoming, with a few isolated populations in central Wyoming, Colorado, and New Mexico (Fig. 1-1; Russell and Bauer 2000).

Wood Frogs and Boreal Chorus Frogs are listed as species of ‘least concern’ and stable, but Western Toads are considered globally ‘near threatened’ due to declines documented through much of their range (Hammerson 2004, 2008, Hammerson et al. 2004). Within Canada, Boreal Toad populations have been split into two distinct conservation units based on the presence of advertisement vocalization and vocal sacs (COSEWIC 2012). Vocal populations are essentially limited to Alberta (Fig. 1-1; Pauly 2008), making them of particular conservation interest.

Locomotion, Orientation, and Phenology

Amphibians exhibit a range of physiological adaptations driving their energetics and locomotion. Wood Frogs are leapers or jumpers (i.e. saltatory locomotion) with long, powerful hind limbs that are capable of propelling them over relatively large distances in just a few leaps. Wood Frogs derive the energy required for locomotion through anaerobic metabolism, which cannot be sustained for long before lactic acid builds up and the animal fatigues (Duellman and Trueb 1986). Like many Hylidae, Boreal Chorus Frogs likely share a similar metabolism to Wood Frogs (Duellman and Trueb 1986), but their hind limbs are shorter relative to their body size, which limits the distance they can travel per leap. Boreal Toads hop or scramble on very short limbs. Energy for their locomotion is derived from aerobic metabolism that does not produce large amounts of lactic acid, allowing for continuous activity over extended periods of time (Duellman

and Trueb 1986). As such, Boreal Toads are likely better able to traverse the Boreal Plain landscape and hostile terrain than Wood Frogs and Boreal Chorus Frogs.

Amphibians can orient themselves to breeding sites using a variety of mechanisms including: olfactory cues (Tracy and Dole 1969*a*), acoustic cues (Salthe and Mecham 1974), landmarks (Dole 1965, Wells 1977), humidity gradients (Lázár and Brändle 1994), topography (Adler 1980), celestial bodies (Tracy 1971, Tracy and Dole 1969*b*) and magnetic fields (Sinsch 1987). The relative importance of each mechanism varies both among species and with landscape familiarity (e.g., landmarks and topography vs. humidity gradient and acoustic cues; Ferguson 1971, Oldham 1966, 1967, Sinsch 2006). These orientation mechanisms are sufficiently numerous and diverse that should one or more be compromised (e.g., the loss of a landmark), another orientation mechanism may compensate, though perhaps not as efficiently.

There are three major seasonal movement events that all three BAC species share: migration to breeding sites, post-breeding emigration, and juvenile dispersal. The exact timing of these events varies among species depending on their life history traits. Wood Frogs and Boreal Chorus Frogs possess freeze tolerance (Costranzo and Lee 1994, Storey 1984, Storey and Storey 1987), allowing them to overwinter at the surface and enabling them to migrate to breeding sites as soon as the surface thaws. There is evidence that the duration and intensity of the freeze, as well as the concentration of cryoprotectant glucose in the bloodstream influences the likelihood of survival (Layne et al. 1998). Boreal Toads possess no freeze tolerance and must overwinter in hibernacula below the frost line, requiring that the ground be completely thawed for them to immerse (Muths and Nanjappa 2005). Adult toads also overwinter farther from breeding sites, so they are the last to arrive at breeding sites in spring.

Adult Wood Frogs tend not to travel very far from breeding sites after breeding, and have relatively small home ranges (< 0.05 ha; Bellis 1965). Bellis (1965) reported a mean distance travelled of 13 m, but subsequent studies reported distances in excess of 300 m (Vasconcelos and Calhoun 2004). Juveniles have been observed dispersing to non-natal breeding sites over distances exceeding 1200 m (Berven and Grudzien 1990). Males appear to overwinter closer to breeding ponds (Regosin et al. 2003, 2005) and have greater site fidelity (98%) than do females (88%; Vasconcelos and Calhoun 2004). It has been estimated that at least 40% of Wood Frogs within a population overwinter > 100 m from breeding sites south of the Boreal (Massachusetts; Regosin et al. 2005).

Adult Chorus Frogs have been located ~ 200 m from breeding sites, but the majority are found within 100 m (Kramer 1973). Kramer (1974) estimated Western Chorus Frog home ranges between 641–6024 m² (mean 2117 m²), and are likely smaller than the Wood Frog home ranges. Maximum juvenile dispersal appears to be around 690 m, but most individuals move less than 300 m (Spencer 1964).

Western Toads are considerably more mobile than Wood Frogs or chorus frogs, capable of making daily movements up to 439 m (Bartelt 2000). The toads are larger and more robust than both of the frog species, and possess adaptations that help them resist desiccation (e.g., pelvic patch), effectively enabling them to make larger-distance movements under warmer or drier conditions. Female toads tend to travel farther from breeding sites than males, although there is considerable variation among studies (Table 1-2). Similarly, home range sizes of 5.8 to 7.1 ha have been reported for males and 17 to 25 ha for females (Jones 2000, Muths 2003).

Western Toads may travel up to 900 m from summer foraging grounds to hibernacula (Campbell 1970), and between years may exploit alternate breeding sites that are spaced

up to 4 km apart (Muths and Nanjappa 2005). Males tend to return to the same breeding sites each year, but the proportion of males missing any given breeding season is quite variable (3 to 95%; Muths et al. 2006). Larger, older toads—presumably more familiar with their landscape—in Boreal Plain forests may maximize their fitness (condition, survival, and reproductive success) by retreating to suitable hibernacula as late in the season as possible (Browne and Paszkowski 2010).

Challenges of the Boreal Plain

Conditions within the Boreal Plain are not especially conducive to high amphibian diversity. Mean daily temperature can range from -17.5 to -22.5°C in January, and 12.5 to 17.5°C in July (Parks Canada 2003). There are roughly 114 frost-free days per year in the eastern extent of the ecozone (Smith et al. 1999). Annual lake evaporation (300 to 700 mm) often equals or exceeds mean annual precipitation (ranging from 300 to 500 mm; Ecological Framework of Canada 2014, Ministry of Supply and Services Canada 1978). This climate makes for a relatively short, cool, and dry activity period for amphibians.

Boreal systems are driven by natural disturbances, most notably wildfire, which is intrinsically linked to landscape-level ecological function. The wildfire interval ranges from 39–96 years depending on forest stand type; aspen and pine forests have considerably shorter fire cycles than do spruce forests (Larsen 1997). However, the effects of fire on amphibian populations are poorly understood. Although all three BAC species will actively use burned habitat (Constible et al. 2001), increased soil temperature and reduced litter following wildfire may be detrimental to species that

prefer cool, moist and stable environments (e.g., Wood Frog and Boreal Chorus Frog; Hossack et al. 2009). Boreal Toad abundance may increase following a severe fire (Guscio et al. 2008), where previously unused breeding habitat is quickly colonized (Hossack and Corn 2007). The toads further exhibit improved thermoregulation, growth, fertility, and disease resistance following fire (Hossack et al. 2009). Following fire, Boreal Toad abundance may decline over time as the site regenerates (Hossack and Corn 2007).

Another, more localized natural disturbance common to the Boreal Plain is the landscape modification (deciduous tree removal and reservoir creation) created by beaver (*Castor canadensis*) activity, which results in the formation of amphibian breeding habitat (Rosell et al. 2005, Stevens et al. 2007). As beavers move into an area, they increase the number and diversity of amphibian breeding habitats in a mosaic of active and abandoned beaver wetlands that are capable of supporting rich amphibian assemblages (Cunningham et al. 2007). Wood Frogs experience increased egg and larva development rates, as well as increased juvenile recruitment (Skelly and Freidenburg 2000, Stevens et al. 2006). However, amphibians may preferentially select for the abandoned reservoirs in a wetland complex (Cunningham et al. 2007).

The Boreal Plain is currently undergoing extensive industrial development. Human land uses, although diverse in function, affect amphibian populations through a few shared natural mechanisms. Land uses primarily affect amphibians, and indeed all wildlife, through the removal of natural vegetation. Intense land uses like urban development often result in the total loss of natural vegetation and water bodies, leading to lower amphibian diversity and abundance (Gagné and Fahrig 2007, Rubbo and Kiesecker 2005). Clearing vegetation reduces microhabitat elements important for the

persistence of amphibians (e.g., canopy closure, plant cover, and complex ground cover like litter and coarse woody debris), leading to increased temperatures and reduced moisture (Chan-McLeod and Moy 2007, deMaynadier and Hunter 1998, 1999, Maguire et al. 2004). Clearings can fragment the landscape, reducing amphibian abundance and genetic diversity, and restricting their movements (Crosby et al. 2009, deMaynadier and Hunter 1999), although clearings are unlikely complete barriers to amphibians (Rittenhouse and Semlitsch 2009).

A number of land uses result in the formation of linear features, such as roads, seismic lines, pipelines, and transmission line easements. Roads can act as strong barriers and filters for many species (Forman and Alexander 1998, Murphy et al. 2010, Trombulak and Frissell 2000) resulting not only from harsher conditions within the clearing, but also direct mortality from vehicle encounters (Ashley and Robinson 1996, Hels and Buchwald 2001) and toxicity effects from run-off (Collins and Russell 2009, Sanzo and Hecnar 2006). Whereas road surfaces are usually changed permanently, seismic lines are left to regenerate, making them shorter-lived disturbances. Nevertheless, seismic exploration is a substantial disturbance rivalling forestry in terms of the area affected annually (ACBS 2001). Although the fragmentation resulting from linear disturbances is generally detrimental to amphibians, linear clearings may also act as corridors facilitating landscape movement for the species more tolerant of disturbance (Deguise and Richardson 2009, Z. Long, personal observation).

The edges created by removing vegetation may be less permeable than contiguous habitats (Gibbs 1998), and detrimental effects may extend well into adjacent undisturbed habitat (i.e., 'edge effects'; deMaynadier and Hunter 1998). However, the effects of fragmentation are species-specific. Whereas Wood Frog movement may be restricted

(Gibbs 1998), boundaries on many forest clearings are highly permeable to the larger, more robust Western Toads (Deguise and Richardson 2009).

Many changes resulting from land use are permanent and do not involve a return to a forest succession that may be typical after a natural disturbance. Most ecologists also separate many human effects on the landscape as not part of a natural ecosystem function. Terrestrial disturbance can certainly influence the aquatic amphibian life-stages, but the greater risk is the disruption of metapopulation—a group of interconnected populations at the landscape scale (Hanski 2004, Levins 1969)—dynamics through the phenomenon “habitat split” (Becker et al. 2007). Although all pond-breeding amphibians may not exhibit true metapopulations (Smith and Green 2005), the potential for “habitat split”—wherein the scale and severity of disturbance is such that it creates a disconnection between the aquatic and terrestrial systems necessary for life-cycle completion—is very real. Understanding a species’ post-reproductive movements, and their interaction with disturbed habitat is therefore paramount to informing management strategies and conservation initiatives.

The BAC species possess certain attributes that facilitate their persistence in a disturbed landscape. Foremost, the BAC species are not obligate forest dwellers. They occur across a wide range of habitats, including prairie. Many studies involving the BAC species report declines in diversity and abundance, as well as restricted movement following disturbance. However, the overwhelming majority of these studies were conducted outside of the Boreal. Species within the Boreal Plain cope with harsh temperature and weather regimes from day-to-day and in annual cycles, and frequent natural disturbance from year-to-year. The evolutionary history of the BAC species relating to their persistence in glacial refugia, and re-colonization of northern latitudes

following the retreat of the continental ice sheet also likely contributed to their resilience and adaptability. These adaptations facilitate their persistence in the face of increasing industrial development (e.g., Wood Frogs and Boreal Chorus Frogs use similar microhabitats following fire and clear-cutting; Constible et al. 2001). Of the few studies within the Boreal, a number have reported the BAC species displaying a preference for open habitat (e.g., Browne et al. 2009, Stevens et al. 2007), likely reflecting community-level adaptation to the region's natural disturbance regime.

Intent of Thesis

The intent of my thesis is to expand our knowledge about foraging by anurans in a disturbed forest of the Boreal Plain. To do so, I ask two main questions. First, what is the best technique for studying anuran movement on the Boreal Plain? Secondly, how can information of amphibian fine-scale habitat use enhance our perception of landscape-level habitat use?

In Chapter 2, I examine the effects of two radio-transmitter attachment techniques on adult Wood Frogs and Boreal Toads. Radio-transmitters, by virtue of their presence, are liable to influence the behaviour of the focal individuals. In this chapter I compare the movements and change in bodyweight between animals fitted with external (waistband harness), and internal (surgically implanted) radio-transmitters to identify the technique best suited for studying these species.

In Chapter 3, I describe Boreal Toad refuge microsite characteristics, and the toads' interactions with these critical microhabitats in a disturbed landscape. Individuals select habitat at a variety of scales (e.g., placement of a home range on the landscape, and placement of the individual within the home range; Indermaur et al. 2009). However,

their day-to-day activities are confined to a smaller scale. In this chapter I use local-scale foraging behaviour associated with refuge microsite use to refine home range estimates for a species of particular conservation concern.

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Table 1-1. BAC species occurrence by terrestrial ecoregion*.

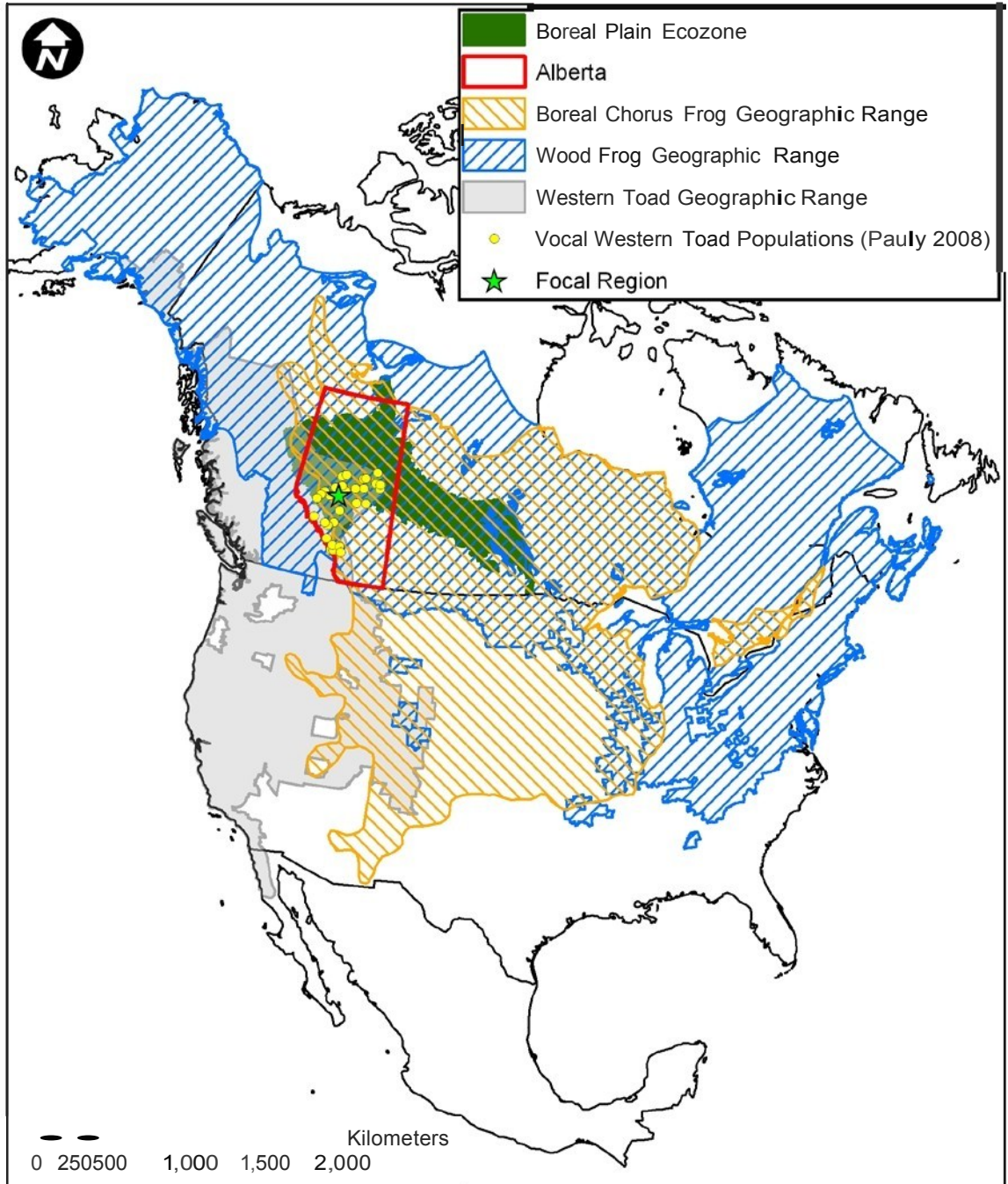
ECOLOGICAL REGION	WESTERN TOAD	WOOD FROG	BOREAL CHORUS FROG
Alaska Tundra		X	
Brooks Range Tundra		X	
Southern Arctic		X	X
Alaska Boreal Interior		X	
Taiga Cordillera		X	X
Taiga Plain	X	X	X
Taiga Shield		X	X
Hudson Plain		X	X
Softwood Shield		X	X
Mixedwood Shield		X	X
Atlantic Highland		X	X
Boreal Plain	X	X	X
Boreal Cordillera	X	X	X
Western Cordillera	X	X	X
Marine West Coast Forest	X	X	
Mixedwood Plain		X	X
Central USA Plain		X	X
Southeastern USA Plain		X	X
Ozark/Ouachita-Appalachian Forests		X	X
Mississippi Alluvial and Southeast USA Coastal Plain		X	X
Temperate Prairie	X	X	X
West-Central Semiarid Prairie	X	X	X
South Central Semiarid Prairie	X	X	X
Cold Desert	X	X	X
Warm Desert	X		X
Mediterranean California	X		
Western Sierra Madre Piedmont			X
Upper Gila Mountains			X

* Species occurrence data by ecological region was derived by overlapping range map shapefiles acquired from the IUCN Redlist website (iucnredlist.org) and ecological classification maps acquired from the Commission for Environmental Commission (CEC 2006; cec.org).

Table 1-2. Western Toad travel distances by sex. SE = standard error.

STUDIES	Male	Female
	Mean \pm SE (m)	Mean \pm SE (m)
Muths (2003)	218 \pm 142	721 \pm 167
Bartelt et al. (2004)	581 \pm 98	1105 \pm 272
Bull (2006)	997 \pm 151	2543 \pm 268

Figure 1-1. Geographic distribution of the BAC species relative to the Boreal Plain ecozone and the focal region.



CHAPTER 2

ASSESSMENT OF INTRACOELOMIC IMPLANTATION AND WAISTBAND HARNESS RADIOTRANSMITTER ATTACHMENT ON WOOD FROGS (*LITHOBATES SYLVATICUS*) AND BOREAL TOADS (*ANAXYRUS BOREAS BOREAS*)¹

Introduction

Radio-telemetry has proven to be a valuable tool for determining amphibian activity, dispersal and migration patterns because amphibians are often secretive, nocturnal and sometimes move long distances in short periods of time (Madison et al. 2010, Richards et al. 1994). Despite this success, transmitter attachment is often problematic for amphibians, especially anurans. Two techniques for transmitter attachment are available: “harness attachment” (also called belt or backpack) where radios are secured externally via a waist belt, and “implantation” where radios are inserted intracoelomically (sometimes subcutaneously) via surgery through the abdominal wall.

Harness attachment is most commonly used for anurans, because fitting harnesses *in situ* is relatively quick (5–10 min) and external transmitters with whip-like antennae are detectable over great distances (> 200 m), reducing the likelihood of losing subjects. If harnesses break or are fitted too loosely animals can shed transmitters; if fitted too tightly harnesses can restrict animal mobility and cause blood pooling in extremities (Bartelt and Peterson 2000). Skin lesions are often associated with external harnesses as well (Goldberg et al. 2002, Weick et al. 2005), which can cut through muscle if left unchecked. Skin lesions can also produce infections. A wide variety of harness materials

¹ This chapter is a copy of the work previously published as Long, Prepas and Lannoo, 2010. Herpetological Review 41:315–318.

have been used in past studies in an attempt to maximize transmitter retention while minimizing harm to animals (Goldberg et al. 2002), but injuries are still common. Given these possibilities and associated behavioural changes, external transmitters can produce conclusions on activity patterns that are not representative of the species as a whole (Bartelt and Peterson 2000, Johnson 2006).

To avoid these issues, many researchers favour internal transmitters. The acute stress associated with surgical implantation of radio-transmitters may be less taxing on animals than the chronic stress associated with harnesses, particularly for prolonged studies (Johnson 2006). Intracoelomic and subcutaneous surgical implantation techniques have been used on a variety of amphibian taxa (Eggert 2002, Johnson 2006, Stouffer et al. 1983). Surgical incisions from transmitter implantation in both laboratory and field settings have healed well in previous studies (Goldberg et al. 2002, Johnson 2006, Weick et al. 2005). Disadvantages of internal transmitters include a smaller detection radius (20–50 m) of the helical coiled antennae, increasing the likelihood of losing subjects that move greater distances over short periods of times. There is also the potential for mortality either directly from surgical error or in response to anaesthesia. For example, the most problematic aspect of implantation surgery on the Barking Frog (*Eleutherodactylus augusti*) was determining the appropriate level of anaesthesia to use (Goldberg et al. 2002), which can vary with water temperature (ASIH et al. 1987). Infections are also possible.

Investigations into the relative impacts of radio-transmitter attachment techniques are necessary because of these variables. Generalizations might be made for species within the same genus or family, provided that the species in question share similar physiologies, habitat requirements, life-history traits and behaviour. However, species-

specific responses are known to exist (Rowley and Alford 2007) and rigorous assessments of data quality and methodology are scarce. Therefore, the objective of this study was to assess the suitability of waistband-harnessed and intracoelomic implantation radio-transmitter attachment techniques for use on Wood Frogs (*Lithobates sylvaticus*) and Boreal Toads (*Anaxyrus boreas boreas*). Adult Wood Frogs are relatively small (40–57 mm snout-vent length (SVL)) semi-aquatic anurans with thin, smooth skin. Boreal Toads are larger (63–78 mm SVL) terrestrial anurans with thick, rough skin.

Methods

Radio-telemetry was conducted from May through August in 2007 and 2008, on a total of 111 Wood Frogs (62 external and 49 internal transmitters) and 38 Boreal Toads (22 external and 16 internal transmitters) in four wetland areas on the Canadian Boreal Plain near Whitecourt, Alberta. Animals were collected by hand, using a D-frame aquatic net, or in pitfall traps maintained by an amphibian monitoring study (the Study of Forestry and Amphibians (SOFA) project) established at the same sites. All animals (regardless of intended radio-transmitter attachment method) were transported to a base camp where body weight and SVL were recorded and radio-transmitters were attached. For Wood Frogs, 0.7 g BD-2 (external) and 0.8 g BD-2H (internal) transmitters (3 week runtime) were used. For Boreal Toads, 1.4 g BD-2 and 1.5 g BD-2H transmitters (9 week runtime) were used in 2007, and 1.6 g BD-2 and 1.7 g BD-2H transmitters (11 week runtime) were used in 2008. Transmitters were obtained from Holohil Systems Ltd. (Carp, Ontario).

Transmitter attachment and radio-telemetry procedures were approved by the Lakehead University Animal Care Committee. External transmitters were attached via waistband harnesses constructed from stretch bead cord following Baldwin et al. (2006). The surgical procedure employed for radio-transmitter implantation was similar to that described in Goldberg et al. (2002). Subjects were anaesthetized in 0.01% solution of MS-222. Time to suitable anaesthesia was highly variable, but generally was 10–30 min. Boreal Toads required longer to anaesthetize. Lateral incisions (12–15 mm) were made first through the skin and then through the muscle layer (rectus abdominus) along the right side near the ventral midline. Transmitters were inserted within the coelomic cavity along the muscle wall. Muscle and cutaneous layers were sutured separately using absorbable suture material (4/0 chromic gut in 2007 and 4/0 polydioxanone suture in 2008). Three to five simple, interrupted sutures were used to close each tissue layer. Tissue glue (Dermabond© in 2007; Vetbond© in 2008) was applied to sutures and surrounding skin to seal the cutaneous incision. Each surgical procedure took an average of 20–30 min. Animals were revived in local stream water and held overnight for observation before being released at the site of their capture the following morning.

The 3-week runtime of the Wood Frog radio-transmitters required that transmitters approaching the end of their battery lives be exchanged for fresh ones. Individuals with external transmitters were refitted with new transmitters only if skin lesions were absent. Re-implantation of coelomic transmitters was performed in 2007 but not in 2008.

Animals were located once every 24–48 h by using R-1000 receivers (Communication Specialists Inc., Orange, California) with a 3-element yagi-style antennae. Each animal location was marked using GPS. Animals were examined for presence of injuries or infection associated directly with radio-transmitter attachment, or

notable weight loss. Animals were recaptured for transmitter removal on the final day of the average runtime of their respective transmitters. Final weights of recaptured animal were recorded after radio-transmitters were removed.

Home range is likely to be positively related to observation period for species that do not actively defend territorial home ranges; the longer an animal is followed, the farther it moves. Both species in this study were expected to exhibit this relationship. Three simple movement parameters were derived to assess the suitability of both attachment techniques for collecting geospatial data. Home range area (HR; m²) and linear distance travelled (LD; m) describe seasonal movement patterns. Mean patch spacing (MPS; m) describes movement behaviour over a shorter timeframe (24–48 hr).

Univariate analysis of variance was used to describe the relationships between transmitter attachment, tracking period (the length of time data were collected on an individual), animal condition (change in body weight and the presence of injuries) and movement parameters. Movement parameters were log₁₀-transformed for analysis. Species were considered separately. Tracking period was divided into 6 categories for Wood Frogs, and 7 categories for Boreal Toads (Table 2-1). Animals with single observations were omitted from analysis. A critical alpha value of 0.05 was employed.

Results

Tracking period and movement

Transmitter attachment method had no effect on Wood Frog tracking period or movement parameters ($p > 0.87$). Boreal Toad tracking period ($F_{1,36} = 4.08, p = 0.05$) and HR ($F_{1,36} = 4.25, p = 0.05$) were greater with external transmitters, but MPS and LD did not differ between transmitter types ($p > 0.47$; Table 2-2). Tracking period was

positively related with Wood Frog HR ($F_{1,104} = 18.32, p \ll 0.01$) and LD ($F_{1,104} = 2.51, p = 0.03$), as well as Boreal Toad HR ($F_{1,36} = 7.12, p \ll 0.01$). All other movement parameters were unaffected by tracking period ($p > 0.72$).

Mortality due to surgery

Six animals did not recover from anaesthesia (1 Wood Frog and 5 Boreal Toads, not included in the 149 animals used for our analyses). We do not know why these animals died; the general surgical methodology was consistent throughout, as was the concentration of MS-222 used.

Post-operatively, most sutures healed completely and suture material disappeared after 3 weeks. In 2008, there were four instances where Wood Frogs either developed lesions around sutures, or suture material did not fully dissolve by the time transmitters were removed. Nevertheless, these individuals were still active in the field. There were no confirmed cases of infection associated with surgical incisions or harness lesions. Multiple implantation surgeries had no observable impact on animals in 2007, with the exception of one Wood Frog that exhibited severe weight loss.

Weight loss

Transmitter attachment method was associated with changes in body weight in Wood Frogs ($F_{1,43} = 6.43, p = 0.02$). More animals gained weight with internal transmitters than with external transmitters, although individuals from both categories exhibited weight loss (Table 2-3). All Boreal Toads observed until the end of their transmitter runtimes exhibited weight gain regardless of transmitter attachment method (Table 2-3).

Injuries

Injuries were associated most commonly with external transmitters (Wood Frog: $F_{1,104} = 8.48, p < 0.01$; Boreal Toad: $F_{1,36} = 8.11, p < 0.01$; Table 2-2). The development of injuries was positively related with tracking period for Boreal Toads ($F_{1,36} = 13.51, p < 0.01$), but not Wood Frogs ($F_{1,104} = 3.14, p = 0.08$). The presence of injuries did not influence the movement parameters of either species (Wood Frog: $p > 0.39$; Boreal Toad: $p > 0.11$). Injuries were most common and developed earlier among Wood Frogs.

Susceptibility to predation

There were only two confirmed cases of predation (Table 2-2), both associated with external transmitters and attributed to avian predators.

Reproduction

The presence of external transmitters did not prevent amplexus. Grasping males would sometimes shed transmitters fitted to gravid females. Amplexus was not observed in animals fitted with internal transmitters, but there was no evidence suggesting implantation interfered with reproduction (but see Heemeyer et al. 2010).

Discussion

Transmitter attachment method had mixed effects between Wood Frogs and Boreal Toads. Both transmitter types were able to capture Wood Frog movements to the same degree. However, Boreal Toad home ranges were larger with the use of external transmitters. The toads were capable of pulse movements that far exceeded the detection radius of internal transmitters, and were easily lost during these periods. This also

accounts for the shorter tracking periods reported for Boreal Toads fitted with internal transmitters. HR values for both species and Wood Frog LD expressed a positive relationship with tracking period, as expected for species without fixed, defended territorial home ranges. MPS was not affected by tracking period, which reflects the relative scales of the three movement parameters. Home range and LD reflect areas exploited and distance traveled over the entire tracking period, whereas MPS reflects the distance an animal can travel in a single tracking interval (24–48 h).

Internal transmitters appear to be most appropriate for longer studies, since the chance of developing lesions as the result of chronic harness exposure increases with time. More Wood Frogs gained weight when fitted with internal transmitters than those with external transmitters. Although amphibian weights are known to be extremely variable and are often linked to dehydration (Stebbins and Cohen 1995), the weight changes observed corroborate our data on abrasion injuries which demonstrates that transmitter implantation is in fact less harmful to anurans. While there are health risks associated with either radio-transmitter attachment technique (Goldberg et al. 2002; Weick et al. 2005), the chronic distress associated with belt abrasion appears to be greater than the short-term and admittedly intense strain imposed by radio-transmitter implantation.

Boreal Toads appear to be better than Wood Frogs at withstanding the perturbations associated with transmitters. In the case of harness attachments, this could be attributed to skin structure (thickness and irregularity) and body size, but might also reflect the relative transmitter-to-animal weight ratio. The transmitter percent of body weight in Wood Frogs (approaching 10%) was greater than that for Boreal Toads (under 5%). Our

findings support the recently recommended maximum ratio of 5% (Goldberg et al. 2002).

Our data also support the notion of species-specific transmitter effects (Rowley and Alford 2007), although generalizations can be made. Internal transmitters are recommended for smaller bodied anuran species with semi-aquatic life-history traits, like Wood Frogs and many other species belonging to the genera *Rana* and *Lithobates*. Larger species, and those sharing more terrestrial or semi-arid life-history traits (e.g., *Bufo* and *Anaxyrus*) are likely better able to withstand waistband harnesses. It is also necessary to consider a species' behaviour. Internal transmitters were capable of capturing the movements of Wood Frogs as accurately as external transmitters. However, external transmitters were better able to capture the longer-distance pulse movements of Boreal Toads. We generally recommend internal transmitters whenever appropriate.

Acknowledgements. — We would like to thank Millar Western Forest Products Ltd. for their involvement, support and assistance throughout this study, and the private landowners who allowed us to work on their land. We also thank Kelly Boyle and Patrick Gilhooly, and the Study of Forest Amphibians (SOFA) Project for their field assistance, Janice Burke for reviewing earlier drafts of the manuscript, and John Crawford for his consultation. Funding for Z. Long was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarship, with Millar Western Forest Products Ltd. as the industry partner. This study is part of the NSERC funded CRD project FORWARD and their partners (<http://forward.lakeheadu.ca/>). The authors have complied with Lakehead University

Animal Utilization Protocol A03 06-07 and obtained the following permits: 2007 — Alberta Sustainable Resource Development, General Research Permit #30069 and Fish Research License #07-3008FR; 2008 — Alberta Sustainable Resource Development, Collection License #30049 and General Research Permit #30070 and Fish Research License #08-3001FR.

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Table 2-1. Summary of tracking periods for 38 Boreal Toads and 108 Wood Frogs.

Tracking Period (Days)	Boreal Toad (N)	Wood Frog (N)
1-9	4	10
10-19	9	57
20-29	3	22
30-39	6	9
40-49	8	7
*	5	3
70-89	3	

* 50-69 for Boreal Toads; 50-75 for Wood Frog

Table 2-2. Summary of animal fates (pooled 2007 and 2008): HR=home range, MPS=mean patch spacing, LD=linear distance, SE=standard error.

Species	Transmitter	Animals (N)	Injuries (N)	Deaths (N)	Lost (N)	Tracking Period Mean (min-max) (Days)	HR Mean \pm SE (m ²)	MPS Mean \pm SE (m)	LD Mean \pm SE (m)
Wood Frog	External	62	24	*7	19	20 (1-74)	175 \pm 13	15 \pm 2	51 \pm 5
	Internal	49	9	11	7	21 (3-55)	192 \pm 17	16 \pm 2	54 \pm 6
Boreal Toad	External	22	9	*5	7	41 (6-79)	5839 \pm 623	58 \pm 9	302 \pm 61
	Internal	16	0	5	9	28 (1-88)	3908 \pm 675	73 \pm 15	223 \pm 41

The difference between the total number of animals and those that died or were lost represents animals that were successfully released

* 1 confirmed case of predation

Table 2-3. Summary of animal weight change observed during 2008 for 43 Wood Frogs and 6 Boreal Toads.

Species	Transmitter Type	Weight Loss (N)	Weight Gain (N)	Proportion of Animals Exhibiting Weight Loss (%)	Tracking Period [Days] Mean (min-max)
Wood Frog	External	18	3	86	19 (7–40)
	Internal	12	10	55	18 (13–22)
Boreal Toad	External	0	3	0	54 (34–79)
	Internal	0	3	0	68 (53–87)

CHAPTER 3

SCALE AND LANDSCAPE PERCEPTION: THE CASE OF BOREAL TOAD (*ANAXYRUS BOREAS BOREAS*) REFUGE USE²

Introduction

The use of refuge microsites (i.e., refugia) has been well documented in many amphibian species, and individuals often display a high degree of fidelity towards them. This suggests that these microsites likely represent a critical resource necessary for survival. Refugia are often structurally diverse, with multiple refuge types being exploited within a population (Bull 2006, Schwarzkopf and Alford 1996, Seebacher and Alford 1999). These microsites are particularly important to poikilotherms because, in addition to shelter, they provide favourable microclimates necessary for thermo- and hydroregulation (Duellman and Trueb 1994). Moisture may be more important than temperature for amphibians (e.g., Bartelt et al. 2004), since their physiology makes them particularly susceptible to desiccation. However, what constitutes suitable refugia is unclear (Shoo et al. 2011), and likely to vary among species.

Radio-telemetry studies have documented that refugia are generally occupied during the day (Bull 2006, Cohen and Alford 1996), with the assumption that the occupants leave to forage the surrounding habitat at night when predator, temperature and desiccation stresses are low (Forester et al. 2006). In this respect, these species behave as central-patch foragers, likely exploiting several patches over the course of the summer.

² This chapter is a copy of the work previously published as Long and Prepas, 2012. Canadian Journal of Zoology 90:1015–1022.

Intrinsic to this behaviour are homing abilities used to orient towards breeding sites, foraging grounds and shelter (displayed by many amphibians; e.g., Rittenhouse and Semlitsch 2009, and Sinsch 1987), which imply that individuals possess some measure of spatial memory. Information collected at the local scale is theoretically comprehensive because animals are able to sample an entire area (Indermaur et al. 2009, Orians and Wittenberger 1991), with knowledge decreasing outward from the centre, or refuge in this case (Fauchald 1999, Roshier et al. 2008). It is likely that foraging takes place within this familiar space, and that maximum foraging distances from refugia represent 'activity centre' patch boundaries.

Activity centres represent the habitat most frequently exploited, and likely to be critical to the persistence of a species. Forester et al. (2006) suggested that American Toad (*Anaxyrus americanus* Holbrook, 1836) home ranges might be better represented by a series of activity centres and narrow movement corridors connecting them, based on their overall movement behaviour. This approach has merit, but their activity centre boundaries were arbitrarily selected, and not based upon local-scale movement behaviour. Although these areas would still be captured by more conventional home range estimations, the relative proportion of the different habitat types would most probably vary between techniques. If individuals were preferentially selecting scarce habitat types for their activity centres, these habitats might be overlooked within larger home range estimates.

The goals of our study were to describe Boreal Toad (*Anaxyrus boreas boreas* Baird & Girard, 1852) habitat selection and local-scale movement behaviour associated with refuge use, and to assess how our perception of landscape-level habitat use might change by incorporating local-scale movement information. The Western Toad (*A. boreas*) is a

species of conservation interest in North America due to several documented declines throughout its global range (Hammerson et al. 2004). However, Boreal Toad populations in Canada appear to be stable or expanding, particularly in the Boreal forest (Wind and Dupuis 2002). Refugia likely represent a critical resource necessary for the persistence of Boreal Toad populations. However, the features that distinguish refugia from their surroundings are unclear, as is the degree to which the area surrounding refugia is exploited (Smith et al. 2003).

Our study tested whether Boreal Toad refugia were selected for physical structure, specific ground layer vegetation or microclimate, and whether refugia were distinct from their surroundings. We conducted a pilot study in 2008, from which we predicted that refugia would be selected primarily for physical structure in the form of coarse woody debris (CWD); we expected CWD abundance and volume to decline with distance from refugia. The pilot study further suggested that the toads were not selecting refugia for specific ground layer communities. Refugia were also expected to provide favourable microclimates, with moisture likely being more important than temperature. In addition to refuge features, we investigated how local-scale movement behaviour associated with refugia might be used to provide a novel perspective of landscape-level habitat selection. We expected that activity centres would prioritize different habitats when compared to more conventional home range estimations.

Materials and methods

Study area

Four wetlands were selected within 50 km of Whitecourt, Alberta (54° 08' 34.1" N, 115° 41' 06.9" W; NAD 83). Each wetland was within a spatially discrete forest stand, two dominated by lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm), and two dominated by balsam poplar (*Populus balsamifera* L.) and trembling aspen (*P. tremuloides* Michx.). White and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill.) BSP, respectively) also occur throughout the region. The study area falls within the western Boreal Plain ecozone of Canada, where mean daily temperatures range from -17.5 to -22.5°C in January, and 12.5 to 17.5°C in July (Parks Canada 2009). Mean annual precipitation (300 to 500 mm) is often equal to or exceeded by annual surface evaporation (300 to 700 mm; Fisheries and Environment Canada 1978), making this landscape relatively dry.

Patterns of refuge use

Radio-telemetry data were collected from 35 toads (16 males and 19 females) from April through September 2009 and 2010. Individuals were located during the day, on average once every 24–48 hours for periods ranging from 2–126 days. This sampling interval was selected due to logistic constraints (number of animals and distance between sites). Radio-transmitters (1.6 g BD-2; Holohil Systems Ltd., Carp, Ontario) were attached via external waistband harnesses fashioned from stretch bead cord (Baldwin et al. 2006). See Long et al. (2010) for a detailed description of this attachment technique. Transmitters weighed < 5% animal body mass in all cases.

Radio-telemetry provides point data useful for determining seasonal movement patterns, and is indispensable for finding occupied refugia. However, telemetry does not provide useful information on the local-scale movement behaviour within the described sampling interval. Fluorescent powder/UV-light night tracking was used to determine patterns of refuge use and local-scale movement behaviour for 7 refugia in 2009. Refugia were selected for night-tracking opportunistically, and timing depended on weather conditions (i.e., several days without precipitation), and the individual behaviour of the animal (i.e., animals that had already occupied a refuge for a long period were less likely to abandon their refugia following pigment application). Orange fluorescent pigment powder was deposited at refuge openings or directly on animals when they were either partially or fully exposed. Powder on the animals transferred to vegetation and debris they contacted during their nocturnal movements, which then luminesced under UV light. Distances travelled and corridor use was recorded for 1–3 nights following powder deposit. Fluorescent powder remained visible on the animal and environment after this period, but it became relatively inert and would not readily transfer.

Refuge characteristics

A refuge was defined as a microsite often no larger than the individual, providing shelter in most cases, and occupied for a period ≥ 5 days. Once refugia were identified, a series of ten 1-m² plots were established: 1-m² plots were sufficient to describe refugia in the context of their immediate surroundings. Plots were separated into three categories based on distance from refugia. A plot was established directly over the refuge ('Refuge'), four plots were established immediately adjacent to the refuge plot and

oriented to the cardinal directions ('Near-refuge'; NR), and five additional plots were randomly distributed within a 20 m radius from the refuge centre ('Random'; RAN). This radius was selected to reflect the local-scale movement behaviour described with night tracking.

A total of 26 refugia (260 plots) distributed among 20 animals were sampled (Table 3-1). These animals were collected either at breeding wetlands early in spring ($n = 11$), or in the surrounding uplands as the summer progressed ($n = 9$). GPS coordinates were collected at each refuge location, which were then used to determine the distance from breeding site (when known; D_B : m), and all surface-water features, including confirmed breeding sites, streams, and all other wetlands (D_W : m). Several datasets were collected from the plots.

Community data—per cent cover of vegetation by species and growth form (i.e., groups that would likely serve the same function for toads). The nine vegetation growth forms were: 1) mosses, club mosses and liverworts; 2) ferns and horsetails; 3) graminoids; 4) short forbs (< 40 cm); 5) tall forbs (≥ 40 cm); 6) creeping shrubs; 7) short shrubs (< 1 m); 8) tall shrubs (≥ 1 m); and 9) mushrooms/lichens.

Environmental data—per cent cover of exposed soil, water, stone, litter (including dead grass) and CWD, and crown closure (%); and CWD volume (CWDv: m^3/ha). Crown closure was estimated using a convex spherical densitometer; four measurements (oriented to the cardinal directions) were taken at each plot, and averaged together. Canopy measurements with densitometers are often biased (Nuttle 1997), however fine differences in canopy cover were not explicitly important in our study (as in Bartelt et al. 2004). CWDv was estimated from length and width measurements taken from all CWD with a diameter ≥ 5 cm.

Soil data—temperature (°C), moisture (% volume) and compaction (kg/cm²). Soil characteristics were averaged from three randomly selected points in each plot. Temperature and moisture were measured with a Delta-T WET Sensor (at a depth of ~10 cm). Soil compaction was measured with a pocket penetrometer (Forest Suppliers Inc.).

Microclimate data—temperature (T: °C) and relative humidity (RH: %) were collected from a total of ten refugia (four in 2009, and six in 2010). As with night tracking, refugia were selected opportunistically. Microclimate data were restricted by cost (the number of weather stations/data loggers available) and animal behaviour (data were only desired while refugia were occupied). Kestrel 4000 pocket weather stations were used in 2009; three weather stations (one in each plot category) were established per refuge. DS1923-F5 Hygrochron Temperature & Humidity iButtons were used in 2010; five iButtons (one in the refuge plot, two NR plots, and two RAN plots) were established per refuge.

Data analysis

Refugia were split into four ‘refuge types’ based on dominant physical structure: ‘CWD_R’ (coarse woody debris), ‘BRW’ (burrows, in litter or soil), ‘VEG’ (vegetation), and ‘EXP’ (exposed, no cover). Non-metric multidimensional scaling (NMS: a form of ordination used for data visualization) was conducted to visualize and explore ground layer community data. We used Sorensen’s distance measure (due to the non-linear nature of the data), and ran the ordination using the “slow and thorough” autopilot option in PC-ORD (McCune and Mefford 2005). NMS simply presents the strongest trend, but does not summarize data like Principle Component Analysis would, so we ran the test five times to ensure our results were consistent. We then ran a multi-response

permutation procedure (MRPP: a non-metric analogue of discriminant functions analysis) to test for potential plot category grouping effects on ground layer community structure. Tests were run by both species and growth form.

Environmental, soil, and microclimate data (i.e., refuge characteristics) were analysed separately from vegetation communities. A simple microclimate index was constructed by taking the difference between a given refuge (assigned a value of 0) and corresponding NR and RAN plot T and RH values. Scaling the microclimate data relative to refugia helped control for temporal variation, since all refugia were not sampled concurrently because data collection depended entirely on each animal's unique behaviour.

Kruskal-Wallis analysis was used to investigate refuge characteristics (i.e., environmental, soil, and microclimate data) among plot categories. Non-parametric tests were appropriate because the dataset was non-normal, and could not be suitably transformed for normality or homogeneity of variance. Distance data (i.e., D_B and D_W) were square root transformed for normality and analysed by sex and time (month) with analysis of variance. Refugia were considered discrete units, even in instances where multiple refugia were sampled from the same animal, or when a refuge was shared by several animals. We acknowledge the issue of statistical independence in this analytical approach, but refugia were the sampling unit of interest in this study, not the individual.

Providing that the toads forage at night, the distance travelled to and from refugia likely represents the radius for areas with the most intensive resource exploitation. We calculated activity centre areas for all 35 toads using fixed kernel density home range estimation that was adjusted to reflect the night-tracking distances. We also calculated 50 % fixed kernel home range estimates for each animal. Both home range estimates

were constructed using the Home Range Tools (HRT: Rodgers et al. 2007) extension for ArcMap (ESRI®). We then compared the proportions of different habitat types between the 15-m activity centre and 50% core home range estimates using a G-test. Habitat was defined by dominant vegetation at two scales: stand-type (wetland, grass/shrub, deciduous, coniferous); and canopy (open and closed). Habitat categories were derived from the forest inventory; closed canopy habitat consisted of all tree-dominated areas, open canopy habitat consisted of grass, shrub and wetland dominated areas. Anthropogenic (cutblocks, roads and seismic lines) and natural clearings were grouped together. G-test compares the similarity of two distributions, and is typically performed on count data. Our dataset, however, was best expressed by averaging across multiple individuals, resulting in each habitat type being presented as a mean and associated standard error (SE). G-tests do not accommodate this internal variation, and operate entirely on the mean values. We acknowledge the limitations of this analysis, but we believe this technique is suitable for illustrating underlying trends in our data.

Results

Patterns of refuge use

Boreal Toads used an average of 1.3 refugia over the course of this study (12 individuals each used a single refuge, and 8 used two), which were occupied for an average of 22 ± 3 d (range 7–50 d; Table 3-1). We were unable to follow individuals throughout their post-breeding activity, so it is likely that toads exploited additional refugia over the summer. Refugia were established increasingly farther from breeding sites as the summer progressed ($D_B: F_{2,14} = 5.63, p = 0.02$); females tended to establish their refugia farther from breeding sites than males early in the summer, but males

eventually caught up (Fig. 3-1). Males and females established their refugia at similar distances from all surface water features (D_W : 125 ± 51 m and 131 ± 35 m, respectively; range 1–571 m).

The dominant refuge type was CWD_R (10 refugia (38%); Table 3-1). Including EXP refugia that were established on top of woody debris, 13 refugia (50%) used CWD in some form. Of the remaining refugia, 6 (23%) were BRW, 5 (19%) VEG, and 5 (19%) were EXP (or 2 (8%) excluding those located atop CWD). Six refugia were closely associated with basking sites and surface water; five of these refugia were VEG or EXP. The refugia occupied longest in 2010 (two females for 41 and 46 d, and a male for 50 d) were immediately adjacent (< 0.5 m) to small pools of water or shallow (~ 2 cm) standing water, and three more were located at the edges of wetlands. Multiple refuge strategies were associated with animals using CWD_R and BRW refuge types. Individuals that occupied multiple refugia did not appear to preferentially select microsites with similar characteristics (Table 3-1). In 2010, two refugia were each occupied by two toads (one male, one female) simultaneously: one refuge was in a CWD cavity, and the other was under shrubs (*Salix* spp.) at the bottom of a depression with exposed soil at the edge of a beaver pond (water < 1 m). In the same year, two female toads in succession occupied a refuge characterized by moss substrate under shrubs (*Salix* spp.) near surface water < 0.5 m deep.

The mean straight-line distance travelled before returning to refugia in a single night was ~ 15 m (median 15 m, range 8–18 m). Most individuals travelled in linear paths, leaving and returning using the same routes over multiple nights. One male and two females travelled in straight lines between closely associated refugia. Most travel routes occurred on the surface in areas with short to no vegetation, but some individuals made

use of tunnels (e.g., root systems, hollow logs, and squirrel middens) or travelled along the tops of downed logs. Some individuals made extensive use of the structure provided by CWD. For example, a female toad in the pilot study (not included in these analyses) used a cavity at the top of a stump ~1.5 m high, and two females from 2009 used suspended logs. Our observations suggested that certain toads used landmarks to navigate. There were two female toads that left their refugia in straight lines, hooked around a tree before continuing, and hooked back around the same side of the tree when returning. A single female was observed engaging in circular search patterns in opposing directions, resulting in a figure-8 pattern over two nights; she ventured only 8 m from the refuge.

Refuge characteristics

Clearings up to 325 m, and forest edges were not barriers to Boreal Toad movement. Most (54%) refugia were established in clearings, and were located 19 ± 5 m from the nearest forest patch or edge. The remaining refugia were established in forested areas and were 40 ± 6 m from edges. This strip of habitat along forest edges accounted for ~25% of the total landscape over which the toads ranged. NMS produced a three-dimensional model that accounted for 65% of the variation expressed in the ground layer community by species, but no grouping among categories was identified by MRPP ($p = 0.49$). The NMS model for growth forms was more robust, accounting for 79% of the variation. Again, however, MRPP did not identify grouping among categories within the data ($p = 0.15$). Further, environmental parameters did not differ among categories ($p \geq 0.19$ in all cases). Although CWD volume and per cent cover appeared to decrease with distance from refugia (i.e., rank order), this relationship was not significant ($p = 0.32$ and

0.19, respectively). Likewise, temperatures were similar among refuge, NR and RAN areas ($\chi^2 = 1.40$, $df = 2$, $p = 0.50$). Relative humidity was greatest in Refuge plots ($\chi^2 = 7.49$, $df = 2$, $p = 0.03$), and decreased with distance from refugia (Fig. 3-2).

Home range estimation

From night-tracking distances, we determined that 15 m represents a realistic patch radius whose area is accessible (and likely to be exploited) by an individual at any given time. Total activity centre areas were 0.57 ± 0.06 ha for males and 0.55 ± 0.07 ha for females. There were no differences in the habitat proportions between activity centre and core home range areas at the stand-type level when pooling all individuals ($G = 5.07$, $p = 0.17$); however, open habitat was under-represented in the 50% core home ranges ($G = 4.24$, $p = 0.04$; Fig 3-3a). Male habitat proportions were similar between estimation techniques (stand-type: $G = 4.44$, $p = 0.22$; canopy: $G = 1.08$, $p = 0.30$). For females, wetlands made up a larger proportion of activity centre habitat when compared to the 50% core home ranges ($G = 19.92$, $p < 0.01$), which was also reflected in the differences between open and closed habitat ($G = 8.37$, $p < 0.01$; Fig 3-3b).

Discussion

Refuge characteristics

Boreal Toad refugia were different from their surroundings. Toads selected their refugia for favourable microclimates with local-scale increases in RH (Fig. 3-2). Several other studies have noted the importance of moist refugia for a variety of anurans, including Crowned Bullfrogs (*Hoplobatrachus occipitalis* Gunther, 1858; Spieler and

Linsenmair 1998), Wood Frogs (*Lithobates sylvaticus* LeConte, 1825; Baldwin et al. 2006), Natterjack Toads (*Epidalea calamita* Laurenti, 1768; Oromi et al. 2010) and Cane Toads (*Rhinella marina* L., 1758; Seebacher and Alford 2002). Our results prioritized RH over substrate moisture, contrary to the findings of Seebacher and Alford (1999) for Cane Toads. This difference may be the result of interspecific variation, but might also reflect the relative scales at which moisture measurements were taken; our study measured local-scale (within 20 m) RH variation over relatively short periods (22 ± 3 d), whereas Seebacher and Alford (1999) used mean monthly trends, presumably describing larger areas.

Our data suggest that Boreal Toads did not select their refugia for specific ground layer vegetation communities or characteristics. They used a variety of habitat features as refugia (Table 3-1), and CWD was a substantial component of many. Although there were no differences in CWD among plot categories, CWD did appear to decline with distance from refugia, at least superficially (i.e., rank order). Nevertheless, our initial prediction of CWD being an important structural component of Boreal Toad refugia was not supported.

Boreal Toads displayed a number of strategies within the CWD_R and BRW refuge types. This observation, and the variety of structurally diverse refugia, suggests that Boreal Toads are habitat generalists at fine scales. Other anurans, like the Green and Golden Bell Frog (*Litoria aurea* Lesson, 1827) have also been identified as microhabitat generalists (Hamer et al. 2003). The microsites we examined offered more than simply shelter and relatively moist conditions. Basking sites and the presence of surface water likely represent crucial complementary microhabitats. For instance, Northern Cricket Frogs (*Acris crepitans* Baird, 1854) preferred moist substrates within proximity to

shelter and surface water (Smith et al. 2003). These complementary microhabitats may be as important for behavioural thermo- and hydoregulation as the refugia themselves.

From the six refugia associated with surface water, five were classified as VEG or EXP (Table 3-1). These refuge types provide abundant escape routes from predators (Spieler and Linsenmair 1998), but the least resistance to desiccation (Seebacher and Alford 2002), despite evidence that shrub-based refugia may provide greater protection from dehydration for Western Toads (Bartelt et al. 2004). The presence of adjacent surface water may be important in offsetting the greater desiccation rates expected for these refuge types.

Movement behaviour

At the landscape scale, females established refugia farther from breeding sites than males, particularly early in the summer (Fig. 3-1), supporting the general patterns from several Western Toad studies (Bartelt et al. 2004, Bull 2006, Muths 2003). Females may quickly disperse following egg deposition to escape male harassment at breeding sites, also giving them the first opportunity to exploit relatively untouched foraging grounds. In contrast, males may tend to remain at breeding sites to increase their chances of encountering late-arriving females, and migrate into upland foraging grounds later on.

We were unable to determine a proximate mechanism that could have triggered individuals to abandon established refugia in favour of new habitat. Localized resource depletion and travel distance between patches (both of which increase with patch residence time) were likely influences (Barrette et al. 2010, Townsend-Mehler et al. 2011). Competition for refugia might also have played a role, but we documented a few individuals that displayed a willingness to share refugia with other toads.

The 15 m nocturnal foraging distance represents the local-scale radius to patches of habitat that are actively exploited (i.e., activity centres) where individual knowledge of the landscape would likely be maximal. Individuals most certainly, could venture farther than these boundaries in a single night, as suggested by their landscape movement behaviour.

Boreal Toads tended to use linear corridors within a 15 m radius during nocturnal foraging. This suggests that they may not actively seek prey over large areas, but rather they consume prey they encounter while moving, and reposition themselves to ambush prey at alternate locations during the night. The use of downed logs and tunnels as local-scale corridors, and the use of suspended or elevated CWD as refugia also suggests that Boreal Toads make greater use of the three-dimensional habitat structure than previously assumed.

Habitat use

We were able to illustrate how perception of the landscape can change between fine (local-scale) activity centre and larger home range estimates, supporting our hypothesis. Our data suggest that open habitat (Fig. 3-3a), primarily in the form of wetlands for female toads (Fig. 3-3b), may be more important at the local scale than previously thought. Boreal Toads are not an obligate forest species, and have been reported to prefer open habitat in several other studies (Guscio et al. 2008). When considering landscape disturbance, our data suggest that Boreal Toads should be easy to conserve on the Boreal Plain. This species appears to be a habitat generalist. They occurred within every landscape habitat type in our study, and used structurally diverse refugia, exhibited a willingness to cross forest edges as previously described in other studies at a

similar latitude (i.e., Deguise and Richardson 2009), and established refugia in clearings (including recent clearcuts). However, nocturnal foraging distances are likely to vary within the Western Toad global range (e.g., as a function of resource distribution, competition, or climate). Our approach could be valuable for pinpointing critical habitat at the landscape scale, which could be a valuable conservation tool, particularly for populations currently experiencing decline.

Acknowledgements. — We would like to thank Millar Western Forest Products Ltd. for their involvement, support and assistance throughout this study, and the private landowners who allowed us to work on their land. We also thank Patrick Gilhooly and the Study of Forestry and Amphibians (SOFA) Project for their field assistance, Rebecca MacDonald for advice on methodology and analysis, and Janice Burke for reviewing earlier drafts of the manuscript. Funding for Z. Long was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Postgraduate Scholarship, with Millar Western Forest Products Ltd. as the industry partner. This study is part of the NSERC funded CRD project FORWARD and their partners (<http://forward.lakeheadu.ca/>). The authors have complied with Lakehead University Animal Utilization Protocol A03 06-07, and obtained from Alberta Sustainable Resource Development Collection Licenses #30052 and #30058, General Research Permits #30073 and #30074, and Fish Research Licenses #09-3006FR and #10-3004FR.

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Table 3-1. Summary of refuge structure and use by individual male (M) and female (F) Boreal Toads.

Male						Female					
Unique Refuge	Animal	Year	Micro-habitat*	Strategy	Residence (days)	Unique Refuge	Animal	Year	Micro-habitat*	Strategy	Residence (days)
1	M1	2009	CWD	C3	10	6	F1	2009	CWD	C3	13
2		2009	EXP	C4	37	7	F2	2009	CWD	C1	38
3	M2	2009	BRW	B1	19	8		2009	CWD	C2	7
4	M3	2009	EXP	C4	19	9	F3	2009	EXP	C4	46
5	M4	2009	BRW	B2	10	10	F4	2009	BRW	B1	14
						11		2009	BRW	B2	28
						12	F5	2009	CWD	C2	10
13	M5	2010	CWD	C1	7	20	F6	2010	VEG		46
14		2010	VEG		50	21	F7	2010	VEG		41
15	M6	2010	BRW	B1	10	22	F8	2010	BRW	B2	11
16		2010	EXP		27	23		2010	CWD	C1	27
17	M7	2010	CWD	C1	12	24	F9	2010	CWD	C1	7
18	M8	2010	VEG		25	17	F10	2010	CWD	C3	33
19	M9	2010	VEG		18	25		2010	EXP		22
						26	F11	2010	CWD	C2	10
						19		2010	VEG		16

* Microhabitat – CWD: coarse woody debris; BRW: burrow; VEG: vegetation; EXP: exposed. Refugia using coarse woody debris or burrows were split into sub-strategies – C1: cavity within CWD; C2: sheltered by CWD with no physical contact; C3: CWD/ground interface; C4: exposed, but resting atop CWD; B1: shallow burrow in substrate; B2: deep burrow in soil.

Figure 3-1. Mean \pm SE distances from breeding sites by month for 7 male and 10 female Boreal Toad refugia.

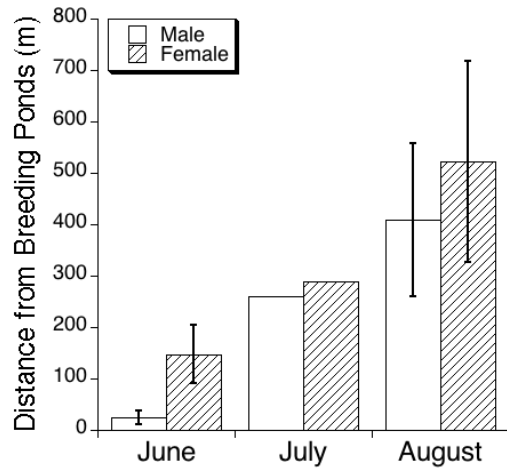


Figure 3-2. Relative humidity by plot category for 10 Boreal Toad refugia; a) Raw mean RH \pm SE, b) Mean \pm SE relative humidity by categories relative to refugia.

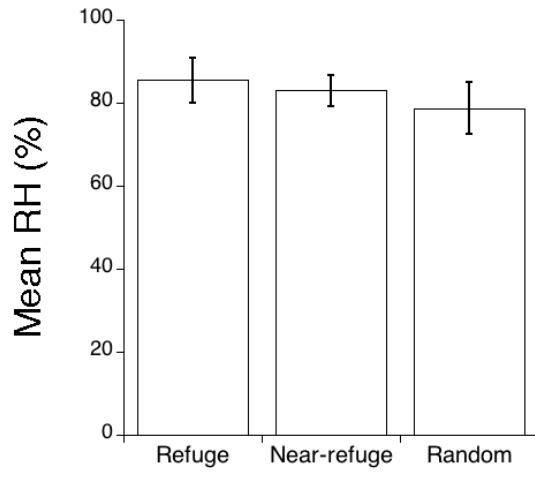
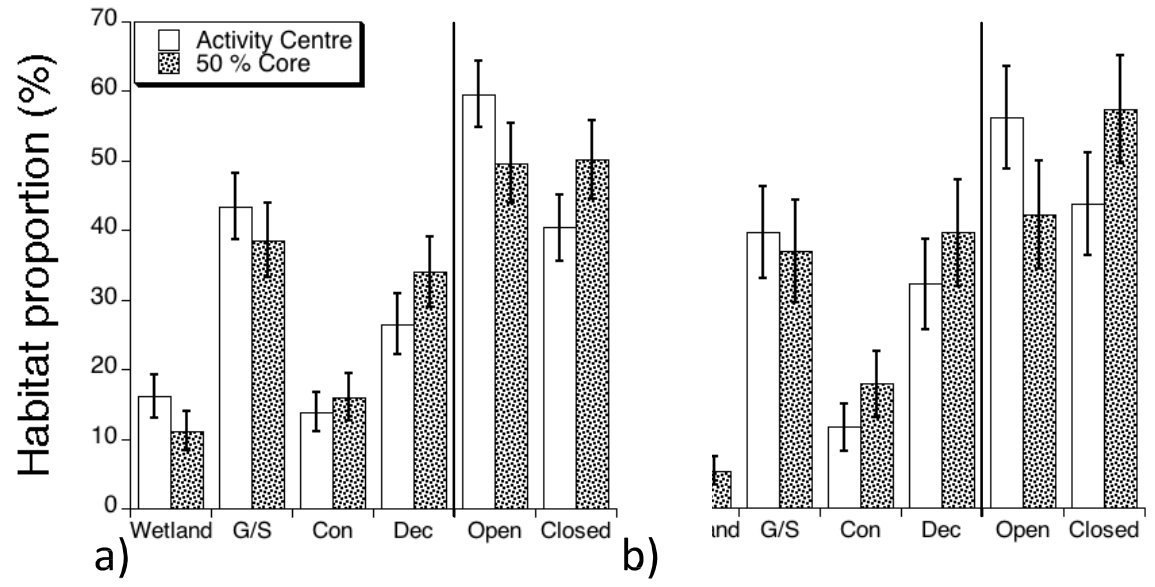


Figure 3-3. Habitat proportions compared between Boreal Toad activity centre and 50% core home range estimates, presented by stand type and canopy; a) all (35) individuals, b) only females (19).



CHAPTER 4

CONCLUSION

Habitat loss resulting from human land use is the leading cause of species population declines worldwide, and amphibians are particularly in jeopardy. Integral to conservation efforts and management strategies is detailed information on a species' resource requirements and movement behaviour. In this thesis I sought to: 1) refine how we study anuran movement by assessing the impacts of two radio-transmitter attachment methods, and 2) examine Boreal Toad refuge microsite use and characteristics, and use this information to refine home range estimate.

Radio-telemetry is best suited for providing information on an individual's landscape-level movement behaviour given the punctuated nature of the data (i.e., a series of locations at specific times). Although invasive in nature, the acute stress of surgical implantation had less of an impact than the chronic stress of the waistband harnesses on Wood Frogs and Boreal Toads, as reflected by changes in body weight ($p = 0.02$; Chapter 2). However, the limited detection range of the internal transmitters (~50 m) was logistically impractical for use on Boreal Toads that were able to travel several hundred meters in a single sampling interval. The most important finding from the investigation of transmitter attachment on anurans was the discovery of a relationship between observation period (i.e., the total time an animal was observed) to area and distance movement parameters in both species. Pond-breeding amphibians, like the study species, tend towards linear expansion over the course of their activity season, so this relationship is not surprising. However, home range values are all-too-often

presented without controlling for the time period over which animals were observed. Crude movement rates like home range expansion (area/time) can control for this phenomenon.

Radio-telemetry provided the means of identifying Boreal Toad refuge microsites, which represent a critical resource likely necessary for the persistence of this sensitive species (Chapter 3). Although structurally diverse, the refugia provided microclimates with greater moisture than their surroundings ($p = 0.03$). Examination of the local-scale movements associated with refugia suggested that Boreal Toads primarily forage at night within 15 m of refugia. Although Boreal Toads are wide ranging, often travelling several kilometers over their post-reproductive activity period, the area actively exploited for resources is likely smaller than initially thought from conventional home ranges estimation techniques.

The findings of this thesis represent mere building blocks to improving our understanding of amphibian movement behaviour and habitat use in the Boreal Plain. The logical next step is to apply this new information to a study directly examining the effects of land use on Boreal amphibians. The Boreal Toad warrants special consideration, given the unique nature of the vocal populations in Alberta. In-depth comparisons between vocal and non-vocal populations, and studies of mixed or intermediate populations will provide important information on Boreal Toad evolutionary history that may ultimately help explain why southern populations are declining while Boreal populations appear to be stable.