

**MOVEMENT AND HABITAT-USE OF THE GREAT BASIN SPADEFOOT (*SPEA
INTERMONTANA*) AT ITS NORTHERN RANGE LIMIT**

by

JOCELYN LINDSAY GARNER

BSc (Honours), Queen's University, 2006

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

Master of Science

in

Environmental Science

Thompson Rivers University
Kamloops, British Columbia, Canada
April 2012

Thesis examining committee:

Karl Larsen (PhD), Professor and Thesis Supervisor, Natural Resource Sciences,
Thompson Rivers University

Purnima Govindarajulu (PhD), Adjunct Faculty Member, Natural Resource Sciences,
Thompson Rivers University

Brian Heise (PhD), Associate Professor, Natural Resource Sciences, Thompson
Rivers University

Roger Packham (RPBio), Senior Habitat Biologist (since retired), BC Ministry of
Natural Resource Operations

Alan Burger (PhD), Adjunct Associate Professor, Biology, University of Victoria
(External Examiner)

ACKNOWLEDGEMENTS

First, I would like to acknowledge my supervisor, Dr. Karl Larsen, for providing a supportive and challenging research experience. His expertise, patience, and state-of-the-art Graduate Student Work Ethic Indicator have been invaluable during my time at Thompson Rivers University. Special thanks to Roger Packham, without him this project would not have been possible. Roger helped secure funding for this research, provided continual support and guidance, and was a great help in the field during my first season. Thanks also to my committee members Dr. Purnima Govindarajulu and Dr. Brian Heise for their feedback and support.

To my fellow graduate students, Emily Lomas, Richard Klafki, Jessica Gosling, Nicole Schiller, Eric Stromgren, Steve Symes, Justine McCulloch, and Denise Clark, I would have gone crazy (crazier?) without your continual encouragement and support— thank you! Thanks also goes out to my field assistants, Jonquil Crosby, Alysa McCall and Melany Rosberg for chasing spadefoots with me in the middle of the night, to William Harrower for his statistical support, and to my family, who have been supportive throughout my academic endeavours. I am grateful to my partner, Jon Van Hamme, for his patience and moral support throughout the writing of this thesis. Finally, I must thank Dillon for always making me laugh.

My research was supported by the following organizations: the Natural Sciences and Engineering Research Council of Canada, the Grasslands Conservation Council of British Columbia, the British Columbia Ministry of Environment (Ministry of Natural Resource Operations), the Habitat Conservation Trust Fund, and the British Columbia Conservation Foundation. This work was conducted under British Columbia Ministry of Environment permit number VI09-54358, and was approved by the Thompson Rivers University Animal Care Committee, protocol no. 2009-05.

Thesis Supervisor: Karl W. Larsen (PhD)

ABSTRACT

The Great Basin Spadefoot (*Spea intermontana*) ranges from Arizona to British Columbia (BC) in western North America, being typically associated with arid environments. However, at the northern limit of the species (south-central BC), the ecosystem contains only small patches of grassland interspersed within a forested landscape, and the climate is cool and wet compared to the core of the spadefoot range. Due to the threatened status of spadefoots in BC, breeding ponds have been identified, but effective management requires data on habitat use away from these bodies of water. Using telemetry, I examined movement patterns and determined habitat associations of diurnal retreat sites (shallow self-made or pre-existing burrows) for these animals. I was able to track 19 spadefoots for varying lengths of time over two active seasons in 2009 and 2010. In general, telemetered spadefoots showed periodic, eruptive movements, where single (used one time only) or core (used multiple times) retreat sites were utilized for a period of time, prior to larger movements that took the animal to another area (with another set of retreat sites). Often retreat sites were used repeatedly; individuals would emerge to forage, travel to breeding ponds, and/or utilize other sites, sometimes retracing their movement patterns over large distances. The majority of terrestrial habitat used was within 112 m from breeding ponds and 136 m was the average maximum displacement, although telemetered spadefoots ventured up to 370 m from aquatic habitat. Grassland and forest path habitat-types were selected by spadefoots at a higher proportion than in random locations. At a smaller scale within these macro-habitats, spadefoots selected for retreat sites containing higher proportions of bare ground and rock compared to random locations. This study provides much-needed background information on the behaviour and terrestrial habitat preferences of Great Basin spadefoots, and can be used to inform management strategies for this species at the northern extent of their geographic range.

keywords: Great Basin spadefoot, *Spea intermontana*, Anura, resource selection, northern periphery, habitat, British Columbia, radio-telemetry.

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CHAPTER 1 • INTRODUCTION

The geographic distributions of species' represent the space that provides their ecological requirements. These distributions reflect large scale resource use patterns that are ultimately defined by the habitat choices of individuals (Morrison et al. 2006). An individual's habitat (where it lives) is determined by a complex interaction of various resources and environmental conditions at many spatial scales (Grinnell 1917, Hutchinson 1957, Thompson 2004, Morrison et al. 2006). Selection among these factors occurs when animals choose resources disproportionate to their availability, presumably favouring those that are more effective in fulfilling their physiological needs (Manly et al. 2002). Resource selection studies are employed to tease apart the competing factors and determine which are important, in terms of probability of use, to that particular species or individual (Boyce and McDonald 1999, Manly et al. 2002, Brunjes et al. 2006, Aarts et al. 2008). The results of such studies are often used in a management context, and may be extrapolated to an area outside of the study site (Boyce and McDonald 1999, Morrison et al. 2006). This approach assumes that individuals throughout the species' range behave similarly in terms of their resource utilization; however, this may not be the case for individuals in populations at the edge of the species' geographic range.

Individuals within peripheral populations are often exposed to environmental conditions or habitats that differ from those at the centre of their range. In general, conditions increase in variability and stress as you move from the core of a range out towards the periphery, where a 'boundary' (often climatic) is met beyond which individuals cannot survive and/or reproduce (Brown 1984, Parsons 1991, Lesica and Allendorf 1995). With this in mind, caution must be taken when applying habitat-use knowledge from one location to another for wide-ranging species, as the environmental variability within their range may be mirrored in terms of resource utilization. For example, northern peripheral populations of flammulated owls (*Otus flammeolus*) are known to utilize an atypical forest type at the northern periphery of their geographic range (Van Woudenberg and Kirk 1999), and butterflies *Maculinea arion* and their *Myrmica* ant hosts at their northern range edge utilize a different habitat in terms of aspect and vegetation structure than in the central portion (Thomas et al. 1998). These

examples indicate unique behavioural traits (in terms of habitat use) within peripheral populations.

The intricacies of habitat use and selection are further complicated when one considers species, such as amphibians, that require different habitat types at various life history stages. Some amphibians are exclusively aquatic and some are solely terrestrial, although, the majority exhibit a biphasic life cycle that requires both aquatic and terrestrial habitat (Dodd and Smith 2003). Breeding and larval development take place in aquatic habitat, while foraging, aestivation, migration, dispersal and over-wintering may occur on land (Semlitsch 1998). Amphibians congregate at breeding sites and then migrate to surrounding terrestrial habitat, also known as uplands, where they are more solitary and dispersed.

In light of widespread amphibian declines there is a critical need to identify and understand amphibian habitat used during the entire life cycle (Marsh and Trenham 2001, Stuart et al. 2004). Terrestrial activities and habitat requirements of amphibians are poorly understood compared to our understanding of aquatic-based activities (Semlitsch 1998, Marsh and Trenham 2001, Regosin et al. 2003). “Core terrestrial habitat” has been used to describe the upland habitat used by pond-breeding amphibians. This area is measured in terms of distance from the aquatic breeding site and includes the area in which all terrestrial activities occur (foraging, annual migration, etc.; Semlitsch and Bodie 2003). Core terrestrial habitat may be interpreted as a buffer zone surrounding aquatic breeding sites. While buffer zones are usually areas set aside to protect the wetland from terrestrial activities, the use of buffer zones is a simple way to incorporate ecological information into management and conservation plans for amphibians. Buffer zones of 30 to 60 m surrounding aquatic areas are considered adequate protection for wetlands to protect against impacts from surrounding land-uses (Semlitsch and Jensen 2001). A review of amphibian habitat studies suggests that core terrestrial habitat extends 117 – 218 m from aquatic habitat for salamanders and 205 – 368 m for anurans (Semlitsch and Bodie 2003). In addition, data compiled from 13 habitat studies show that, outside of breeding season, most species of post-metamorphic amphibians are found to spend very little time in the area immediately adjacent (< 30 m) to wetlands (Rittenhouse and Semlitsch 2007). These studies suggest that typical buffer zones offer

inadequate protection of amphibian terrestrial habitat, which further highlights the need for habitat use studies.

Core terrestrial habitat provides a simple method for defining habitat use, although in reality it may disregard inherent heterogeneity in the uplands surrounding a breeding site. The reasons behind terrestrial location choices must be considered for a comprehensive understanding of suitable habitat for amphibians (Trenham and Shaffer 2005). Therefore, identifying the particular habitat factors that influence an individual's locations is just as important as knowing the location itself; these factors can be explored using resource selection studies. Resource selection by amphibians has been demonstrated in the literature (Eggert 2002, Faccio 2003, Baldwin et al. 2006, Bull 2006). Jefferson and spotted salamanders (*Ambystoma jeffersonianum* and *A. maculatum*) were found to prefer sites with high proportions of deciduous leaf litter and shrub cover (Faccio 2003), wood frogs (*Lithobates sylvaticus*) preferred microhabitats with high moisture levels, high proportions of canopy cover and of sphagnum ground cover (Baldwin et al. 2006), and western toads (*Anaxyrus boreas*) selected for locations with a more open forest canopy, ground cover with more rocks, water and forbs and fewer logs and less bare ground (Bull 2006). These studies suggest that an amphibian's choice of location may be influenced by the ability to maintain body moisture and avoid body temperature fluctuations in that location (Prest and Pough 1989).

STUDY SPECIES

Great Basin spadefoots (Family Scaphiopodidae: *Spea intermontana*) are small, toad-like amphibians (Figure 1.1). They can be found throughout the inter-montane region between the Rocky Mountains and the Coastal Ranges of western North America, with the northern portion of their distribution extending into the southern interior of British Columbia (BC), Canada (Figure 1.2; Matsuda et al. 2006). In the core of their range, this species is associated with arid environments, including its namesake, the Great Basin Desert. In BC, spadefoots are typically associated with semi-arid habitats, including bunchgrass grasslands, sagebrush steppe and open pine and Douglas-fir forests (Cannings 1999, Sarell 2004, Matsuda et al. 2006). In these habitats breeding occurs in a wide variety of ephemeral or permanent aquatic

sites anytime from April to June, depending on environmental conditions (Figure 1.3) (COSEWIC 2007, British Columbia Southern Interior Reptile and Amphibian Recovery Team 2008). Southern BC populations, such as those in the Okanagan region,



Figure 1.1 From top: Side and front view of two adult male Great Basin spadefoots. Photos by J. Garner.

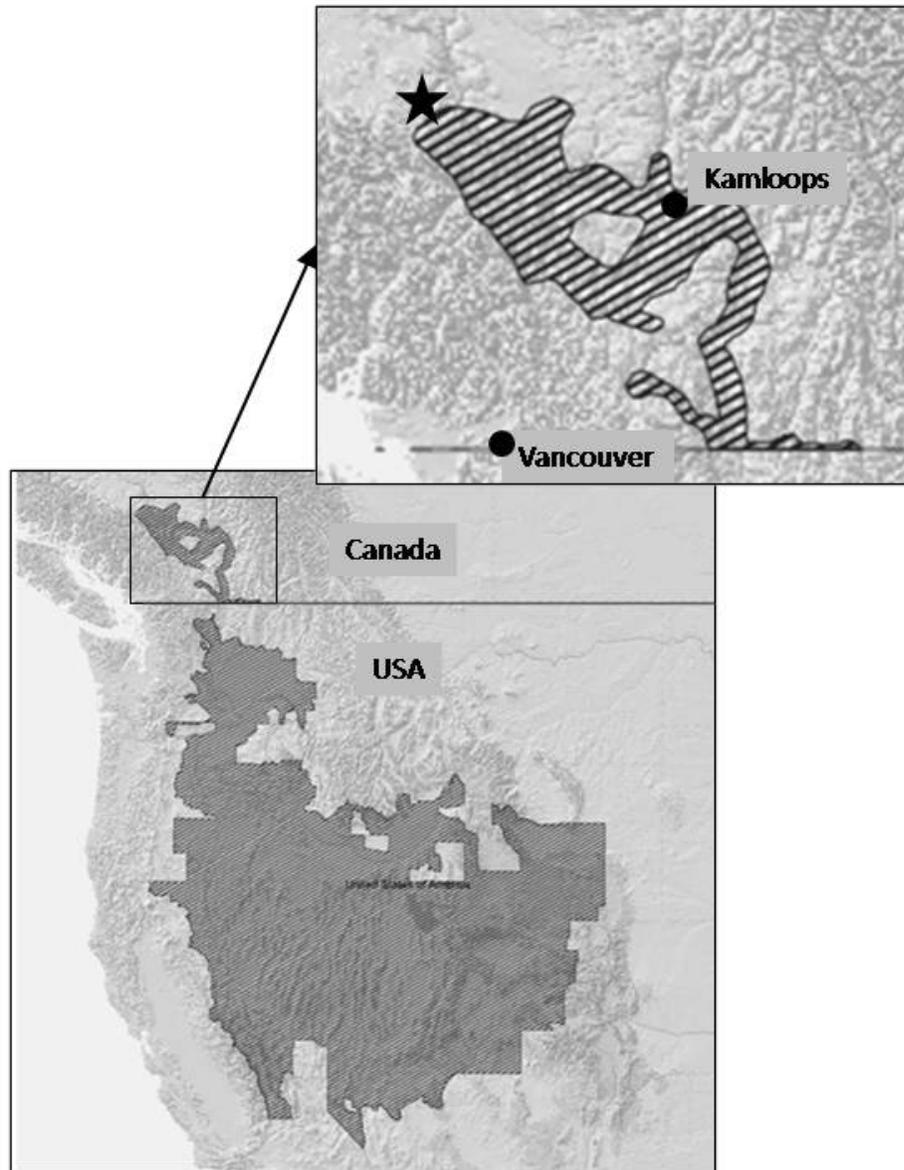


Figure 1.2. Geographic range map of Great Basin spadefoots. Inset map shows Canadian distribution of Great Basin spadefoots. The study site for this project is indicated by the star. Map modified from Hammerson 2004.



Figure 1.3. Great Basin spadefoot breeding sites in the south Cariboo region, BC. Photos by J. Garner.

likely will breed during April and May, while reproduction in populations at the northern range extent (south Cariboo region) can occur well into June (Kline and Packham 2009).

Great Basin spadefoots are fossorial anurans. It is thought that the majority of a spadefoot's time during the active season (April - September in BC) is spent in self-made underground burrows (created using keratinized spades on their hind feet) and to a lesser extent, small mammal burrows (Sarell 2004). Spadefoots use these burrows during the day and emerge at night; however, they may remain in the burrow for extended periods of time when environmental conditions are unsuitable (Matsuda et al. 2006).

Great Basin spadefoots in BC have typically been associated with open grassland, shrub steppe and open forest habitats. No previous observational studies of Great Basin spadefoot terrestrial habitat use have been conducted in BC or elsewhere; therefore, these habitat associations are likely based on location of known breeding ponds. A study of the closely related common European spadefoot (*Pelobates fuscus*) showed those animals to be more likely to use areas with bare soil or short vegetation than shrub-covered areas (Eggert 2002). Similarly, Johnson (2003) found a preference for open areas with friable soils of sandy loam, loamy sand or sand among eastern spadefoots (*Scaphiopus holbrookii*). To my knowledge, these are the only studies that have explicitly looked at the upland habitat associations of spadefoots, and there is a scarcity of information of this type for the Great Basin spadefoot.

It is not known how Great Basin spadefoots at their northern periphery are responding in that somewhat atypical environment during the terrestrial portion of their lifecycle. Great Basin spadefoots in that location are exposed to climatic conditions that are much cooler and wetter in comparison to the conditions typical in more central and southern portion of their range (Figure 1.4). They may be strictly associated with the pockets of open grassland that most closely resemble their 'typical' habitat, never venturing far from breeding sites and avoiding densely forested areas. On the other hand, spadefoots may be displaying atypical resource use, allowing them to utilize this 'novel' environment.

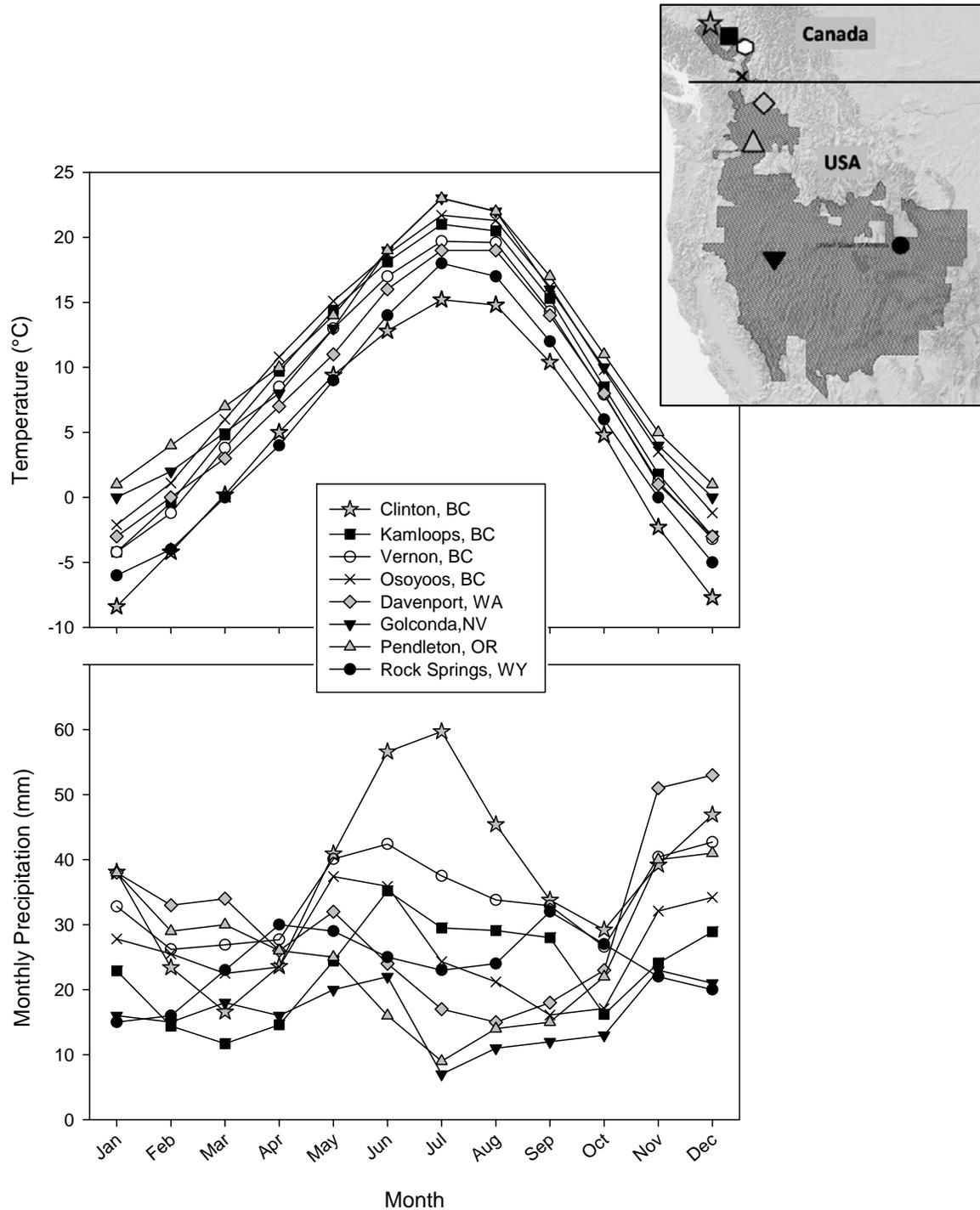


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Given the paucity of ecological information on Great Basin spadefoots, the overarching goal of my research was to gain a basic understanding of how spadefoots at the northern edge of their range use upland habitats during the active season. Radio-telemetry allowed me to follow individual spadefoots and obtain detailed records of movement paths and habitat features encountered along the way. Chapter 2 focuses on this work. Specifically, my objectives in that chapter are to document how far individuals travel from breeding ponds, identify any patterns seen in movement over the course of the active season, and examine the relationship between weather and movement. In Chapter 3, I hone in on the habitat choices made by individuals. In that chapter I explore the fine-scale habitat characteristics of diurnal retreat sites and provide some observational data on the selection of hibernation sites by these animals. I begin Chapter 4 by summarizing the most significant results obtained in this thesis and follow with my advice for future research priorities and management considerations regarding Great Basin spadefoots.

STUDY AREA

My study was conducted approximately 120 kilometres northwest of Kamloops, BC in the Cariboo Forest Region (Figure 1.5). In this part of BC's central interior, elevation ranges from 750 to 1200 m above sea level (Meidinger and Pojar 1991, Steen and Coupé 1997). The climate in this region is affected by three air masses: Pacific air (warm, moist), Arctic air (cold, dry), and Great Basin air (warm, dry) (Steen and Coupé 1997). In the summer hot, dry air from the Great Basin can reach the Fraser River Valley in the southern portion of the Cariboo and result in relatively high daytime temperatures and clear skies. Conversely, arctic air inflow leads to very cold temperatures during the winter months (Steen and Coupé 1997). Temperature and precipitation levels occurring during the years of my study are shown in Figure 1.6.

Small pockets of grassland are found among lakes, wetlands and forested areas throughout the study area (Figure 1.7 and Figure 1.8). According to BC's biogeoclimatic ecosystem classification (BEC) scheme, the study area fell within the Interior Douglas-fir dry cool subzone, Fraser variant "IDFdk3" (Meidinger and Pojar 1991). The climax tree species for this zone is Douglas-fir (*Pseudotsuga menziesii*), although the seral tree species' of lodgepole

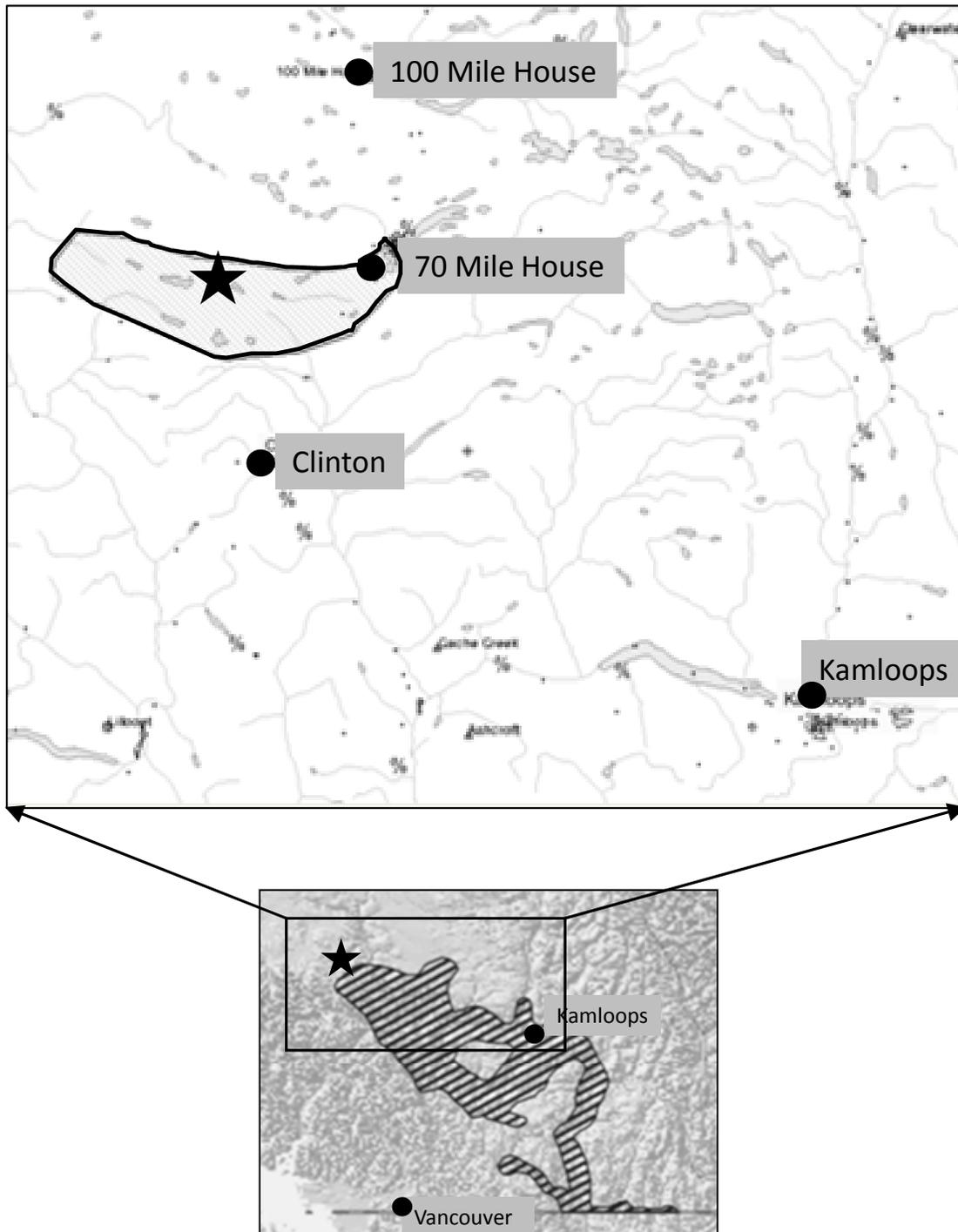


Figure 1.5. Map showing Great Basin spadefoot distribution in British Columbia (BC), Canada. Inset map shows the study site (star) within the known distribution of Great Basin spadefoots in the south Cariboo region (black polygon) (Maps adapted from Hammerson 2004, and Kline and Packham 2009).

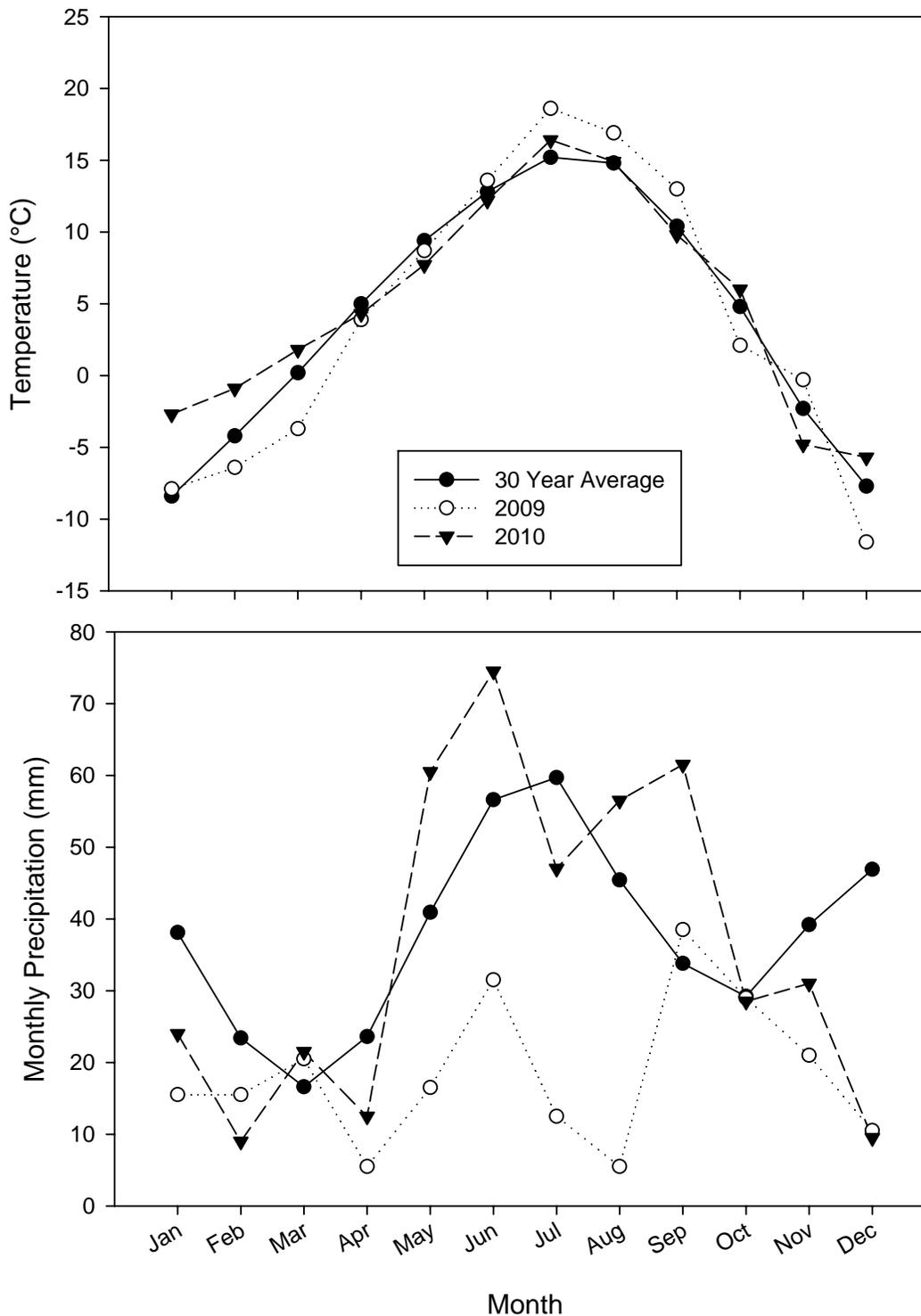


Figure 1.6. Mean monthly average temperature (°C) and mean monthly total precipitation (mm) experienced at the Clinton, BC weather station for the 2 years of the study, 2009 and 2010 (available at: http://www.climate.weatheroffice.gc.ca/climateData/canada_e.html), and for the 30 year period from 1971 to 2000 (available at: http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html).



Figure 1.7. Photograph of typical landscape in study area (location: 51°21'31" N; 121°39'31" W). Photo by J. Garner.



Figure 1.8. Photo of ephemeral ponds in grassland surrounded by forest, 70 Mile House, BC.
Photo by J. Garner.

pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) were most predominant in study (Steen and Coupé 1997).

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CHAPTER 2 • SPATIAL ECOLOGY OF GREAT BASIN SPADEFOOTS (*SPEA INTERMONTANA*) AT THEIR NORTHERN LIMIT IN BRITISH COLUMBIA, CANADA

INTRODUCTION

Peripheral populations of vertebrate species provide an interesting backdrop for investigating changes in life-history traits and habitat requirements, along with their implications for conservation. These populations often exist under marginal conditions that, in many cases, test the physiological limits of individuals and present higher selection pressures than conditions in the range core (Brown 1984, Lesica and Allendorf 1995). In response, individuals within peripheral populations may exhibit unique traits, be it genetic, morphological or behavioural (Kawecki 2008). As the geographical ranges of many species (in the northern hemisphere) are predicted to move poleward in response to climate change, unique traits of northern peripheral populations may facilitate range shifts into ‘new’ frontier habitat (Lesica and Allendorf 1995, Thomas et al. 2001, Kawecki 2008).

Amphibians near the northern periphery of their range may be particularly susceptible to the effects of climate change, yet surprisingly little research has been done on northern populations of these animals. Studies on northern peripheral populations of other herpetofauna, particularly snakes and turtles, have revealed unique behavioural traits in terms of their movement patterns and habitat associations when compared to core/central populations (eg. Larsen 1987, Weatherhead and Prior 1992, Smith 2000, Arvisais et al. 2002, Kapfer et al. 2008). Of particular interest here are elongated movements and/or larger home ranges at northern range edges, such as those seen in the wood turtle (*Clemmys insculpta*; Smith 2000, Arvisais et al. 2002), bull snake (*Pituophis catenifer sayi*; Kapfer et al. 2008), garter snake (*Thamnophis sirtalis*; Larsen 1987) and eastern massasauga rattlesnake (*Sistrurus c. catenatus*; Weatherhead and Prior 1992). As these animals are ectothermic, one may predict an opposite pattern, where movements at the northern extent are constrained due to colder temperatures. An alternative hypothesis for this observed pattern is that animals may have to travel greater distances to meet their energetic requirements in less productive northern landscapes (Harestad and Bunnell 1979, Arvisais et al. 2002), or that peripheral

individuals have more specific habitat requirements that necessitate greater travel between required resources (Thomas et al. 1998, Oliver et al. 2009).

Pond-breeding amphibians often travel significant distances overland to reach summer habitat after breeding season (Semlitsch 1998, Smith and Green 2005). Movements of amphibians and core terrestrial habitat, the area in which foraging, aestivation, migration, dispersal and over-wintering occur (Semlitsch and Bodie 2003), may be markedly different in northern peripheral populations. Physiological requirements of amphibians are satisfied largely through behavioural responses to the environment (Preest and Pough 1989, Seebacher and Alford 2002), and thus activity and habitat choices are often correlated with weather (Sexton et al. 1990, Sinsch 1990, Seebacher and Alford 2002, Greenberg and Tanner 2005). These factors may determine an individual's tolerance limits at the northern extreme of their range.

One especially wide-ranging amphibian is the Great Basin spadefoot (*Spea intermontana*), found throughout the intermontane region of western North America. The distribution of this species ranges from desert-type environments near the southern extreme, to cold, semi-arid grasslands along the northern periphery. In British Columbia, Canada, the northernmost extent of the species' range spans a transitional ecotone. Here the landscape is primarily forested with small pockets of wetland and grassland throughout. The climate is much cooler and receives more precipitation than the core of the species' range (see Chapter 1), suggesting a more stressful environment for this population.

The terrestrial habits of Great Basin spadefoots are virtually unstudied; any information available generally is inferred from observations of closely related species (Hovingh et al. 1985, Buseck et al. 2005, COSEWIC 2007). For example, the extent to which these animals travel between breeding sites and summer grounds is unknown, as is their sensitivity to the components of weather (eg. temperature, precipitation). The research presented in this chapter was part of a larger study that sought to broadly describe, for the first time, the ecology of Great Basin spadefoots at their northern periphery. In this chapter, I focus on the terrestrial core habitat and movement patterns of Great Basin spadefoots within their northernmost population. My specific objectives herein are to (1) determine core terrestrial

habitat, (2) examine movement patterns between diurnal retreat sites and over the course of the active season, and (3) identify correlation between weather factors and movement. Understanding the ecology of Great Basin spadefoots in this atypical environment, and revealing to what extent (if any) the life history and behaviour of the animal has responded, will ultimately contribute to our overall understanding of this species as well as highlight the significance of this northern peripheral population.

METHODS

Study Area

I conducted this research during the Great Basin spadefoot active seasons of 2009 and 2010, in the area immediately west of the town of 70 Mile House in south-central British Columbia, Canada (51°18'11" N, 121°23'51"W). Just over half of the total annual precipitation in this region falls during the four months in which Great Basin spadefoots are typically active (May - August). Average monthly temperature during this period ranges from 9.4°C in May to 15.2°C in July, with average lows from 2.0°C in May to 7.4°C in July (see Figure 1.5). The landscape here is a mixture of grasslands, wetlands and upland forests, comprised mainly of lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Open range cattle-grazing is the most prevalent land-use followed by timber harvesting in selected pockets of forest. Aside from these activities, there are minimal anthropogenic disturbances in this area. Prior to my study, Great Basin spadefoots in this region were known to breed in a variety of water bodies including shallow/ephemeral ponds, edges of lakes and cattle watering dugouts (Kline and Packham 2009).

Radio-telemetry

Great Basin spadefoots were captured by hand at ponds during the breeding season, or were found opportunistically on roads and open areas surrounding breeding sites. Captured individuals were weighed to the nearest 0.1 g (using a digital scale in the field) to determine suitability for transmitter attachment. Depending on the weight of the animal, the telemetry package consisted of either a 0.70 g (16 day life) or an 0.85 g (21 day life) BD-2 external radio-transmitter (Holohil, Carp, ON) attached to a Flexi-fix™ harness. The transmitter-belt

package did not exceed 6 % of body weight and most were < 5 % (Bartelt and Peterson 2000). Thereafter, each animal was briefly re-captured 2-3 days before the transmitter battery was set to expire and was refitted with a new transmitter, provided that no injuries from carrying the transmitter and harness package were evident. Further explanation of the transmitter attachment process is found in Appendix A.

Telemetered individuals were tracked for varying durations (4 – 90 days) from 10-Jun until 7-Sept 2009 and 17-May until 26-Aug 2010. Individuals were located every 1 to 3 days (average = 1.5 days). To avoid unnecessary disturbance to the animal, the majority of relocations took place during daylight hours when spadefoots were in retreats. Each location was marked and Universal Transverse Mercator (UTM) coordinates were recorded with a Garmin 76CX handheld GPS unit.

Core Habitat

I measured the straight-line distance to the nearest edge of an aquatic breeding site for each Great Basin spadefoot location I observed. If this distance was < 20 m, the precise distance was taken using a measuring tape; otherwise, I plotted the location on Google Earth and measured straight-line distance using the ruler function. This approach was tested for accuracy using a paired t-test. There was no significant difference in movement distances measured both with a measuring tape and in Google Earth (paired $t = 1.31$, $df = 10$, $P = 0.22$). In all cases, I considered the high water line to be the edge of the pond.

To determine core terrestrial habitat used by telemetered individuals over the active season, I calculated a 95% confidence interval for distance of retreat sites from breeding sites using all observed locations. This provides a range of distance from aquatic habitat in which the majority of the study population spends their active season (Semlitsch 1998, Semlitsch and Bodie 2003). A 95% confidence interval was also calculated for maximum distance from aquatic breeding sites. In cases where I calculated an average, I also reported standard deviation.

Movement in Relation to Weather

My study animals generally showed nocturnal activity patterns: activity started late in the evening of one day ('Day 1') continuing through until early the following morning ('Day 2'). To calculate weather metrics for each such 'active period', I used data from a weather station located 30 km south of the study site in Clinton, BC (Environment Canada 2011). Daily mean temperature over a 24 hr period was calculated as the average of readings recorded on the hour from 0500 hrs (Day 1) through to 0400 hrs (Day 2). Similarly, average nighttime temperature was calculated from hourly readings taken from 2100 hrs (Day 1) through to 0400 hrs (Day 2). Humidity metrics were calculated in an analogous fashion. As precipitation data were only available for each calendar date, I used the total precipitation datum recorded for Day 2 of each active period.

For movement data to be included in my analysis, I used only 'single-night movement' observations (where data were collected for an animal in Day 1 and on Day 2). Preliminary analysis did not reveal linear relationships between my measurements of movement distances and the weather metrics, so I used binary logistic regression (movement : no movement) for further analysis. Model selection followed an information-theoretic approach using Akaike's Second-Order Information Criterion (AIC_c) for small samples and Akaike weights (w_i) as outlined in Burnham and Anderson (2000).

RESULTS

Radio-telemetry

All told, I captured 55 Great Basin spadefoots by hand, both opportunistically (on paths or in open areas surrounding breeding sites) or during pond edge searches. Radio-transmitter harnesses were attached to 19 adults. Eight individuals were caught at ponds during the breeding season, while 11 were caught away from the water bodies. This sample of animals provided a total of 946 tracking days, or an average of 49.8 ± 28.2 days per individual (min = 4, max = 90). I obtained 707 fixes in total and the average per individual was 37.2 ± 20.3 (min = 4, max = 59). See Table 2.1 for an overview of tracking success.

Table 2.1. Summary information for 19 Great Basin spadefoots radio-tracked during the course of this study. Tracking start date, end date, duration (days), number of times the individual was relocated, number of single night observations, and maximum distance recorded between animal and its associated breeding site are included in this table.

Spadefoot ID	Dates monitored	Duration	No. of relocations	No. single night movements	Maximum dist. to pond
SM101	16 Jun-25 Jun 09	11	14	9	-
SM102	16 Jun-25 Jul 09	41	49	33	80.3
SM103	16 Jun-19 Jul 09	35	31	24	106.7
SM104	3 Jul-7 Sep 09	67	73	40	219.5
SF101	16 Jun-19 Jun 09	4	4	2	-
SF102	22 Jun-28 Jul 09	37	41	29	85.5
SF103	17 Jul-1 Sep 09	47	51	31	25.3
SM201	17 May-14 Jul 10	58	42	24	371.0
SM202	17 May-5 Jul 10	49	36	22	-
SM203	18 May-30 Jul 10	73	49	28	123.0
SM204	27 May-26 Aug 10	90	59	34	243.0
SM205	2 Jun-24 Aug 10	83	54	29	47.0
SM206	2 Jun-12 Aug 10	71	31	14	71.0
SM207	2 Jun- 23 Aug 10	82	50	30	105.0
SM208	17 Jun-27 Jun 10	10	6	2	-
SF201	18 May-24 Jul 10	67	45	25	153.0
SF202	26 May-13 Jun 10	18	9	2	-
SF203	27 May-14 Jun 10	18	8	4	-
SF204	31 May-24 Aug 10	85	55	28	-
Average		49.5	37.2	21.6	135.9
SD		28.2	20.3	12.2	98.2

Movement Pattern

All Great Basin spadefoot activity occurred at night (breeding, movement, foraging) and daytime was spent resting in retreats. These diurnal retreats were mainly shallow, self excavated burrows into the soil, although use of small mammal tunnels under rocks was observed for 3 retreat locations (see Chapter 3 for more information on retreat types). Only once did I observe an individual outside of a retreat during daylight hours (~ 0830 hrs); however, that individual had entered a retreat by the time he was located 30 minutes later. Overnight, individuals were observed to do any of the following: emerge and return to the same retreat site, move to another retreat site, move to the breeding pond, or remain in the retreat site.

Of 946 tracking days, I compiled 400 single night observations (42.3 %) from 15 individuals. The mean number of observations per animal was 26.4 ± 7.5 (max = 39, min = 9). No detectable movement occurred 58.5 % (n = 234) of the time, and 166 movements (41.5 %) with confirmed start and end points were observed. The majority of movements (60.8 %, n = 101) were less than 20 m (displacement). Only 4.2 % (n = 7) of observed single night movements were over 100 m (Figure 2.1). Figures 2.2 to 2.4 show movement paths taken by 9 individuals.

Distance between consecutively-used retreat sites was highly variable, both within and among individuals. Retreats were detected as close together as 0.4 m and as far apart as 223.0 m (Table 2.2). Some retreat sites, hereafter termed 'core sites', were used repeatedly, with interruption by emergence to forage, to use other retreat sites or to move to breeding sites. Of all observed retreat sites, 23.5 % (40/170) were classified as core sites. The use of core sites was so predictable that I was able to find 3 spadefoots whose transmitters had died, based solely on previous knowledge of their preferred retreats. Two individuals were observed re-tracing their steps when leaving the breeding pond (i.e. utilizing the same retreats they used on the way there). Neighbouring retreats often made up distinct 'activity centers', that consisted of two or more retreats in close proximity to each other (~ < 30 m), at least one of which was a core site (Figure 2.5).

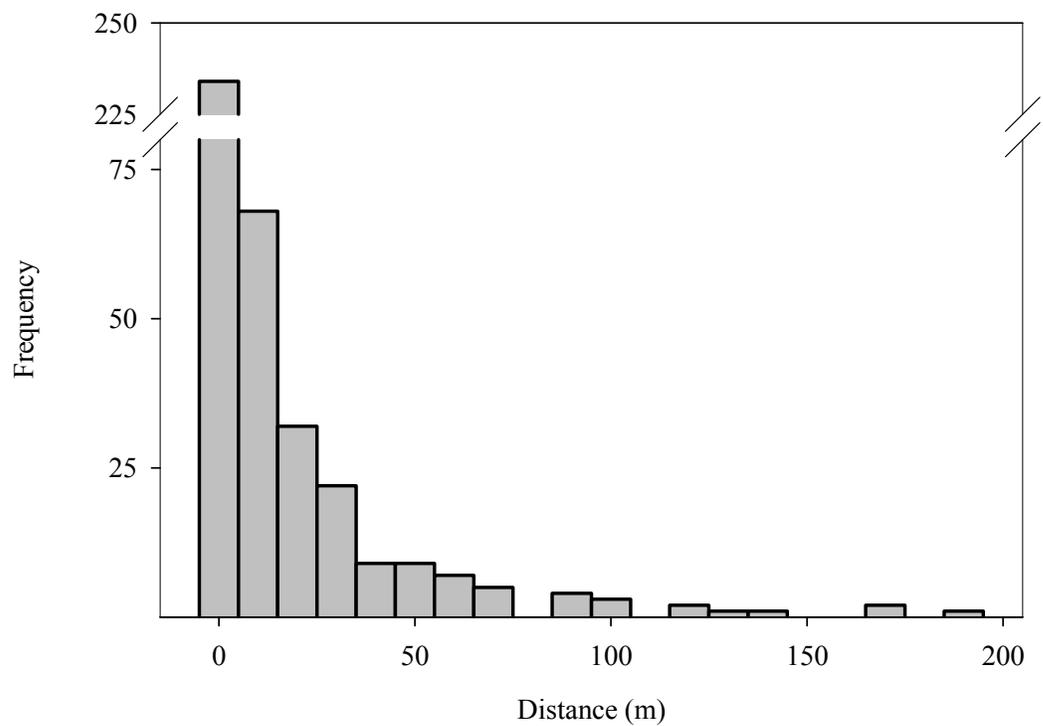


Figure 2.1. Frequency of displacement distance observed over a single nighttime activity period recorded for radio-tagged Great Basin spadefoots in this study ($n=19$). The first bar represents nights where no movement occurred.



Figure 2.2. Movement paths of 7 telemetered spadefoots during 2009 and 2010 tracking seasons. Circle icons represent sites of capture and square icons show the final location of each animal at end of telemetry (image obtained from GoogleEarth, 10/22/11).



Figure 2.4. Movement path of a telemetered male spadefoot (grey line) from 27 May to 26 Aug 2010. The circle icon represents the site of capture and the square icon shows his hibernation site. Two activity centers, labeled a and b, are outlined by white dashed lines (image obtained from GoogleEarth, 10/22/11).

Table 2.2. Terrestrial retreat data for telemetered spadefoots (n = 19). Retreat column shows total number of diurnal terrestrial sites used by each spadefoot, core retreats are those that were used multiple times, and mean, minimum and maximum summarize the distance between consecutively used retreat sites.

Spadefoot ID	Retreats	Core retreats	Distance between retreat sites (m)		
			Mean	Minimum	Maximum
SM101	2	1	42.1	2.6	95.7
SM102	5	1	22.9	1.4	93.0
SM103	6	2	54.8	2.4	131.0
SM104	15	5	14.9	0.4	81.1
SF101	1	0	23.1	16.0	35.6
SF102	7	0	7.4	0.6	27.3
SF103	4	1	4.6	0.4	18.0
SM201	27	0	39.1	1.2	124.0
SM202	6	4	8.7	2.1	21.1
SM203	12	4	28.8	3.2	122.0
SM204	20	3	31.8	6.0	132.0
SM205	17	7	11.6	1.4	43.0
SM206	9	5	21.5	0.7	58.0
SM207	12	3	10.6	1.9	68.0
SM208	3	-	-	-	-
SF201	19	3	42.8	2.2	223.0
SF202	1	-	-	-	-
SF203	2	-	-	-	-
SF204	25	1	64.5	3.2	206.0
Average	10.2	2.5	28.8	2.9	92.4
SD	8.2	2.1	17.8	3.8	61.8

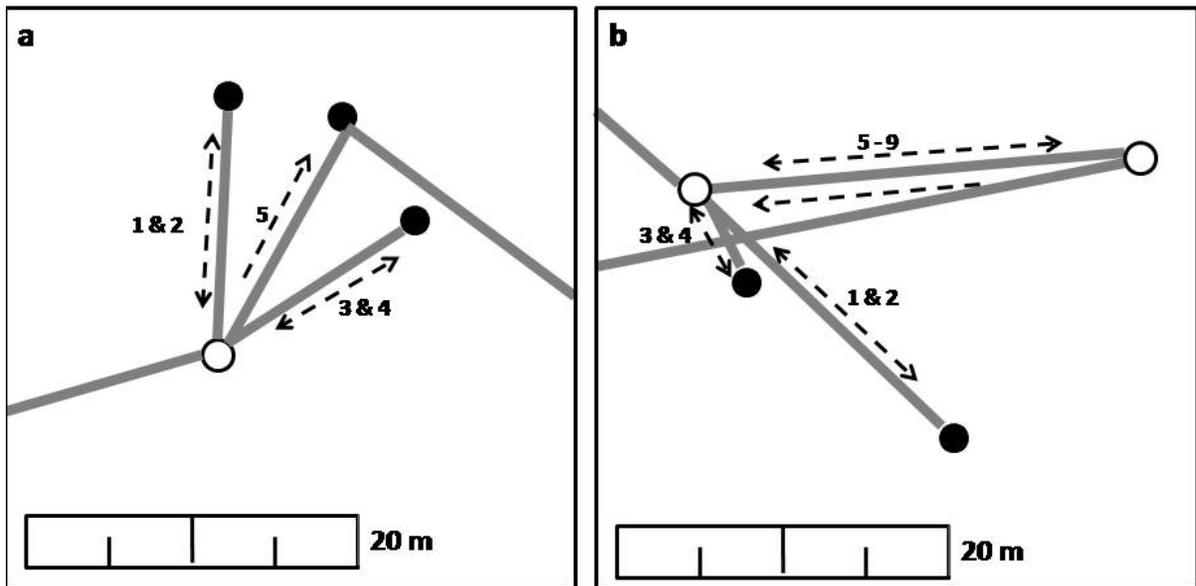


Figure 2.5. Two activity centers (as seen in Figure 2.4) of a telemetered spadefoot. The open circles represent core sites, and the filled circles are retreat sites used only once. Movements between the sites are labelled sequentially.

In addition to multiple-use of retreats, some individuals used activity centers more than once. I considered an activity center to be used more than once when an individual traveled some distance from the activity center (to breed or visit other retreat sites) and then returned to the activity center and continued to move within its closely-spaced retreats.

Core Habitat

Individual spadefoots that were tracked over 35 days and for whom breeding location could be assigned or deduced were used in the analysis of core habitat ($n = 12$, see Table 2.1). Out of a total of 12 such individuals, 10 were either captured at a breeding pond or were observed at a pond during breeding season. For the remaining two, breeding pond associations had to be deduced from their location data. For one of these individuals all the retreat sites were located in close proximity to a breeding pond (min = 7 m, max = 25 m), and so that individual was associated with that pond as the breeding location. Another individual was captured moving away from a breeding pond and he subsequently returned to hibernate 40 m from the edge of the same pond, therefore indicating that the pond may have been his breeding location (Figure 2.4). Note that breeding activity by other spadefoots had been documented in both of these assigned ponds.

The mean distance from aquatic habitat of all observed retreat sites was 100.1 ± 79.0 m, with a 95 % confidence interval of 85.3 – 111.7 m. The furthest distance traveled by spadefoots from their respective breeding pond was highly variable (Figure 2.6). The average maximum observed distance from breeding ponds was 135.9 ± 98.2 m, with a 95 % confidence interval of 73.5 – 198.2 m. The maximum observed distance was 371.0 m and minimum was 25.0 m. Pearson's product-moment correlation did not show a significant relationship between tracking duration and the maximum distance from breeding sites ($r = 0.21$, $df = 10$, $p = 0.52$).

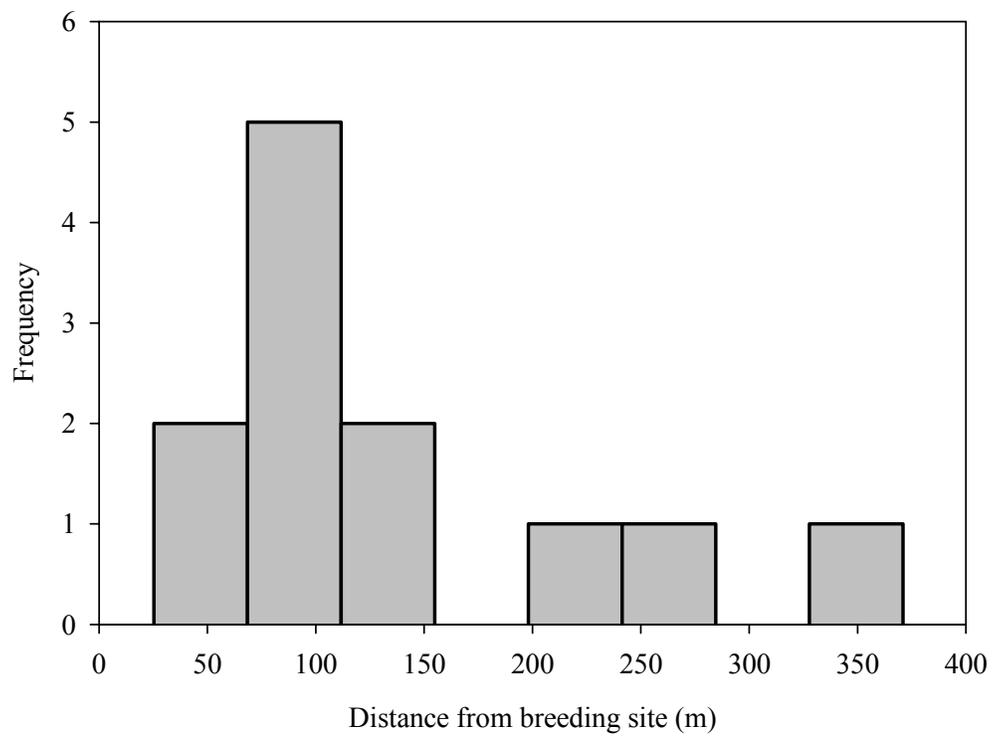


Figure 2.6. Frequency histogram of maximum distances recorded for 12 telemetered Great Basin spadefoots from their respective breeding sites, over the course of a single active season.

Movement in Relation to Weather

A slight positive correlation was seen between distance moved (single-night) and both daily precipitation ($r = 0.178$, $p < 0.001$), and average relative humidity ($r = 0.102$, $p < 0.050$). No correlation was seen for average temperature ($r = -0.018$, $p = 0.722$), night temperature ($r = 0.032$, $p = 0.522$), or night relative humidity ($r = 0.082$, $p = 0.100$). Univariate logistic regression models were created with each of these explanatory environmental variables, average temperature, nighttime temperature, average relative humidity, nighttime relative humidity and daily precipitation. The variables contained in the top two ranking models, nighttime relative humidity and average relative humidity, were the best predictors of movement on the basis of Akaike weight (w_i) and AIC_c (Table 2.3). Given the high correlation between these two variables ($r = 0.93$, $p < 0.0001$) and the fact that nighttime relative humidity intuitively best represents the conditions an active spadefoot encounters, I selected the model containing this variable as the most relevant and parsimonious predictor of movement. The effectiveness of this model as a predictor of movement was, however, biased. Using a confusion matrix to show the predicted classifications of the model versus the actual movements (Kohavi and Provost 1998), I found that only 23% (38/166) of the instances of movement were correctly predicted by the model, whereas 87 % (205/234) of the cases where movement was not observed were correctly predicted by the model.

I observed 3 individuals (captured prior to the start of breeding season in 2010) move to breeding ponds following large rainfalls on May 28 (16 mm), May 29 (11 mm), June 6 (12 mm) and June 10 (17.5 mm). Multiple breeding attempts were made by two individuals (one male and one female): each moved to the pond following rainfall, back to terrestrial habitat after finding the pond dry and ultimately returned to the pond after another rainfall, presumably for a second attempt at breeding.

Table 2.3. Univariate binary logistic regression models (movement : no movement) predicting movement using environmental data. ‘Null’ corresponds to an intercept only model.

Model Coefficient	Coefficient Value	AIC_c	ΔAIC_c	AIC_c w_i	Cumulative AIC_c w_i
night relative humidity	0.02	537.53	0	0.54	0.54
average relative humidity	0.02	538.07	0.54	0.41	0.95
daily precipitation	0.06	543.56	6.03	0.03	0.98
null	-	544.91	7.38	0.01	0.99
average temperature	-0.02	546.43	8.90	0.01	1.00
night temperature	0.00	546.91	9.38	0.00	1.00

DISCUSSION

To my knowledge, this study provides the first quantitative data on the upland movement of this species. Some aspects of activity patterns and movements of the animals were similar to those reported for other primarily terrestrial anurans, namely, site fidelity and pattern of movement distances. On the other hand, some observations were dissimilar, including relatively small core habitat and lack of strong correlation between movement and weather. Additionally, the data do not indicate elongated movements at the northern periphery, as has been observed in other herpetofauna.

Core Habitat & Movement Pattern

Spadefoots in my study demonstrate an apparent reduced core habitat range as compared to other primarily terrestrial anurans (Semlitsch and Bodie 2003). This may reflect a difference in movement patterns of spadefoots as compared to these other species. The average core habitat distance recorded in this study falls below the range of 205 – 368 m reported by a review of anuran studies covering 19 species (Semlitsch and Bodie 2003). It is also lower than the figures reported in studies of other terrestrial anurans (i.e. true toads): 275 m for Yosemite toads (*Anaxyrus canorus*; Liang 2010), 686 m for female American toads (*A. americanus*; Forester et al. 2006); 2543 m (female)/997 m (male) for western toads (*A. boreas*; Bull 2006), 1105 m (female)/581 m (male) for western toads (Bartelt et al. 2004); and 721.5 m (female)/218.2 m (male) for boreal toads (*A. boreas boreas*; Muths 2003). Highly directional movements are common for anurans tracked from the breeding site to summer grounds (e.g. Kusano et al. 1995, Bulger et al. 2003, Bull 2006, Forester et al. 2006, Constible et al. 2010). Bull (2006) and Constible et al. (2010) both found that the majority of telemetered western and Canadian toads (*A. hemiophrys*), respectively, moved in relatively linear, unidirectional patterns, and Forester et al. (2006) describe the post-breeding movements of female American toads as containing activity centers but overall showing a linear pattern. Only one such linear movement was observed in my study. The overarching pattern shown by spadefoots approached that seen at the ‘end’ of post-breeding migration by true toads: a tortuous path in which the individual moved within and between distinct activity

centers (Forester et al. 2006). This behavioural difference likely results in a smaller core terrestrial habitat in terms of straight-line distance from the aquatic site.

An abundance of short-distance movements and relatively few long-distance movements were completed by spadefoots in my study. Canadian toads (Forester et al. 2006) and female American toads (Constible et al. 2010) also showed a similar frequency pattern of movement distances, despite the absolute distances traveled being greater than those seen in my study. The short movements I observed (between retreat sites within activity centers) likely are indicative of foraging behaviour (Dingle and Drake 2007). Additionally, foraging may occur on nights where movement was undetected. Incidental observations during this study have shown that spadefoots often emerge to forage and return to the same burrow in a single night, giving the impression that no movement was made when locations are checked on consecutive days. This behaviour is also displayed by giant burrowing frogs (*Heleioporus australiacus*; Penman et al. 2008) and giant bullfrogs (*Pyxicephalus adspersus*) that forage mainly within 20 m from their burrow sites (Yetman and Ferguson 2011). Foraging in close proximity to core sites, as evident by short distance movements or in some cases, no movement at all, is advantageous in that maximal energy is gained with minimal energy expenditure.

Spadefoots in my study exhibited high levels of retreat site fidelity and an apparent homing ability to find these sites. Sinsch (1990) suggests that orientation and homing in anurans is facilitated using mental maps with fixed reference points (i.e. forest silhouettes, landmarks). Considering that many 'core' sites were located in open grassland with no distinct (fine-scale) landmarks and were unrecognizable (to the human eye) from the surface of the ground, the ability to move away from a site then return and burrow into the exact spot in the ground is quite remarkable. High site fidelity and repeated use of retreats has been observed in other spadefoots species including the eastern spadefoot (*Scaphiopus holbrookii*; Pearson 1955, 1957, Johnson 2003) and common European spadefoot (*Pelobates fuscus*; Eggert 2002), as well as other species of anurans including the giant burrowing frog (Lemckert and Brassil 2003, Penman et al. 2005), Cope's gray tree frog (*Hyla chrysoscelis*; Pittman et al. 2008), gopher frog (*Rana capito*; Blihovde 2006), cane toad (*Anaxyrus marinus*; Cohen and Alford 1996), arroyo toad (*Anaxyrus microscaphus californicus*; Griffin and Case 2001) and the

Yosemite toad (Liang 2010). Not only were retreat sites used repeatedly by spadefoots in my study, activity centers were often visited more than once. This fidelity to activity centers was common in my study in contrast with Forester et al. (2006), who found that American toads rarely returned to previously used activity centers. Selection of appropriate microhabitat is essential for maintenance of ideal body temperature and moisture levels, therefore, site fidelity may suggest ideal microhabitat conditions for spadefoots at core sites (Seebacher and Alford 1999). This concept is discussed further in Chapter 3.

Movement in Relation to Weather

In this study, the overall influence of temperature, relative humidity and precipitation on spadefoot movement was not readily obvious. Movement distances showed weak positive correlations with average daily relative humidity and precipitation, and nighttime relative humidity was only marginally useful in predicting whether a spadefoot changed locations overnight. These results contrast previous studies, in which connections between environmental factors and amphibian movement were clearly demonstrated (Sexton et al. 1990, Sinsch 1990, Seebacher and Alford 2002, Greenberg and Tanner 2005). Sinsch (1988) suggests that the effect of weather factors on movement is only clearly detected when those factors approach the tolerance limit of the individual. Given that, at best, weak correlations between these factors were identified, I suggest that the range of temperature, relative humidity and precipitation occurring during my study (see Figure 1.5) did not approach this species' tolerance limits. A high tolerance for dry conditions by this species may explain the lack of correlation for precipitation and humidity; however, one might expect that temperature would approach the lower limits for spadefoots given that my study area is located at the extreme northern edge of their range.

The positive correlations seen between distance moved and both relative humidity and precipitation indicate that spadefoots may be moving primarily on nights in which their water balance can be maintained, although, a high tolerance to water loss may make this relationship difficult to demonstrate. Thorsan and Svihla (1943) examined the effect of water loss in anuran species in the genera *Scaphiopus* (southern spadefoots), *Bufo/Anaxyrus* (toads), *Hyla* (tree frogs) and *Rana* (true frogs). Eastern and western spadefoots (*Spea*

hamondii) survived the greatest degree of desiccation, being able to tolerate close to a 50% loss of their body weight in water. Although no significant pattern emerged in my study, I did observe spadefoots moving to breeding ponds after heavy rains. This suggests that although moisture cannot predict general movements over the whole active season, it may well be a good predictor for breeding activity (Sexton et al. 1990, Greenberg and Tanner 2005, Todd and Winne 2006).

Movements in Context of Northern Periphery

Spadefoots in my study do not appear to follow the trend of elongated movements at the northern periphery set by other herpetofauna. The relatively small core habitat of spadefoots near 70 Mile House, BC, as compared to other anurans, may be an indication of movement constraint at the northern edge of their range. Given the northern latitude of my study site, the active season for these animals should be shorter than elsewhere, even in southern BC, much less other locations in the core of their range (Figure 1.4). Over the 2 study seasons of my work, breeding began at the end of May, and the animals began to hibernate by the end of August (n = 3, see Chapter 3 for more information on hibernation sites). During this relatively short period, spadefoots have to consume enough food to obtain sufficient energy reserves for hibernation. The time necessary to do this is variable among spadefoot species: Dimmitt and Ruibal (1980) found that Great Basin spadefoots could consume up to 18% of body weight in one feeding, while Couch's spadefoots (*Scaphiopus couchi*) were observed consuming up to 55 % of body weight. While the amount Great Basin spadefoots can consume may be lower than Couch's spadefoots, it likely still allows individuals to gain enough energy in a short time for hibernation, thus eliminating the need for a prolonged post-breeding foraging season.

An alternative explanation to the short movements, small home range size and short active season demonstrated by animals in my study is that spadefoots as a group of anurans share these traits. Although additional data on Great Basin spadefoots do not exist (to my knowledge), Ruibal et al. (1969) suggested that western spadefoots have a very short active season in Arizona, hibernating in early September, and emerging in early July, and eastern spadefoots have been observed to have very small home ranges (Pearson 1955, 1957). I

hypothesize that the fossorial nature of spadefoots may lead to this trait. This group of anurans can essentially create their own retreat and/or hibernation sites, thus eliminating, at least partially, the need for long movements in search of appropriate sites, and allowing individuals to maintain energy reserves needed for hibernation.

The data collected in this study provide much needed background information on the ecology of Great Basin spadefoots. This species' unique ability to create suitable retreat sites by burrowing into the soil may influence their ability to endure the northern climate experienced by spadefoots in my study. Core habitat and movement data from other anuran species at the northern edge of their range as well as from Great Basin spadefoots in the core of their range are needed in order to further investigate the influence of climate on the northern peripheral population of spadefoots near 70 Mile House, BC.

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**CHAPTER 3 • FINE-SCALE HABITAT SELECTION OF THE GREAT BASIN
SPADEFoot (*SPEA INTERMONTANA*) AT THE NORTHERN LIMIT OF ITS
RANGE IN BRITISH COLUMBIA, CANADA**

INTRODUCTION

Habitat loss and/or degradation are the most significant threats to the persistence of amphibian populations (Semlitsch 2002, Stuart et al. 2004, Blaustein et al. 2011). Given this, it is becoming increasingly important to understand how these animals respond to their environment and what (species specific) habitat factors are important for survival. This challenge is made more difficult by the fact that the majority of amphibians exhibit a biphasic life cycle, requiring both aquatic and terrestrial habitat for various life stages. Within the terrestrial environment, many significant activities occur, including foraging, aestivation, migration, dispersal and over-wintering (Semlitsch 2008). For some species, such as anurans occupying arid habitats, individuals may be associated with water bodies only for a short time during the breeding period.

Terrestrial habitat use and requirements have been studied significantly less than those in the aquatic phase, despite the importance of both habitat phases in the persistence of populations (Marsh and Trenham 2001, Regosin et al. 2003, Semlitsch 2008). The reason for this imbalance is likely due in part to the difficulty of conducting terrestrial amphibian studies. Amphibians often gather *en masse* at water bodies where breeding and larval development take place, but they can be considerably more difficult to locate and observe during the terrestrial portion of their life cycle.

Selection of suitable microhabitat during the terrestrial phase is critical for amphibians. Given their physiology, amphibians must select locations that allow for maintenance of suitable body temperature and avoidance of desiccation (Prest and Pough 1989, Huey 1991, Seebacher and Alford 2002). Microhabitat selection has been demonstrated for a variety of amphibian species including Jefferson and spotted salamanders (*Ambystoma jeffersonianum* and *A. maculatum*; Faccio 2003), wood frogs (*Rana sylvatica*; Baldwin et al. 2006), western toads (*Bufo boreas*; Bull 2006) and common European spadefoots (*Pelobates fuscus*; Eggert 2002).

North American spadefoots (Family Scaphiopodidae) are a group of anurans that are notably terrestrial. Species from this group originated in desert environments where there is often an absence of standing water. Larval development period for this taxa ranges from 2 - 8 weeks, being the shortest among anurans (Buchholz et al. 2002). Aside from this period and a brief breeding season, these animals spend the rest of their lives in terrestrial habitat, further indicating the importance of understanding terrestrial habitat requirements.

As with all spadefoots, comprehensive knowledge of habitat use and preferences are lacking for the Great Basin spadefoot (*Spea intermontana*). This species is a wide ranging anuran found throughout the inter-montane region between the Rocky Mountains and the Coastal Ranges of Western North America (Matsuda et al. 2006). It is typically associated with desert-like environments in the southern portions of its range and semi-arid grassland or shrub-steppe towards the northern range periphery. Great Basin spadefoots spend the majority of their time underground in self made burrows or, to a lesser extent, those created by small mammals (Matsuda et al. 2006); these locations are hereafter termed 'retreat sites'. Retreat site selection at the fine scale is likely critical to survival (Huey and Kingsolver 1989, Huey 1991, Seebacher and Alford 1999). The paucity of information for this group may be attributed to their short and some-what unpredictable breeding seasons, fossorial nature and nocturnal habits, all of which render spadefoots a challenging group to study.

I studied the terrestrial ecology of the Great Basin spadefoot at the extreme northern limit of the species' range near 70 Mile House in south-central British Columbia (BC), Canada. This particular area is of interest for a number of reasons, one being its northern location. It is unknown whether suitable habitat is limited for spadefoots at this site. Ectotherms in a peripheral environment, including amphibians, may require a more narrow set of habitat criteria to meet their physiological needs, therefore, useable sites may be a limiting factor for spadefoots at the northern edge of their geographic range (Thomas et al. 1998, Oliver et al. 2009). Another reason this area is of interest is its potential for Great Basin spadefoot conservation and management. The study area consists mainly of government-owned land, thus the conservation and land management potential is greater than in southern BC where urban development and agriculture (vineyards and fruit orchards) are ubiquitous.

My objective in this chapter is to investigate habitat selection by Great Basin spadefoots during the terrestrial portion of their active season. Specifically, I aim to (1) identify vegetation categories and ground-cover features that are important for spadefoot retreat site selection, (2) determine if there are differences between retreat sites used only once and those visited multiple times (hereafter termed 'core sites'), and (3) identify and characterize hibernation sites. Through the identification of disproportionately used resource units, I am able to infer those factors most important for site selection, and thus identify critical aspects of spadefoot habitat.

METHODS

Study Area

My research was conducted during May - August in 2009 and in 2010, in the area west of 70 Mile House in south-central British Columbia, Canada (51°18'11" N, 121°23'51" W). Average monthly temperature during this period ranges from 9.4°C in May to 15.2°C in July, with average lows from 2°C in May to 7.4°C in July. Just over half of the total annual precipitation in this region comes from thunderstorms during the four months in which Great Basin spadefoots are typically active (May – August; see Figure 1.5). The landscape here is a mixture of grasslands, wetlands and upland forests, comprised mainly of lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Open range cattle-grazing is the most prevalent land-use followed by timber harvesting in selected pockets of forest. Aside from these activities, there are minimal anthropogenic disturbances in this area.

Radio-telemetry

Spadefoots were captured by hand at ponds during breeding season, or opportunistically pre/post-breeding on roads and open areas surrounding breeding sites. Captured individuals were weighed to the nearest 0.1 g to determine suitability for transmitter attachment. Depending on the weight of the animal, the telemetry package consisted of either a 0.70 g (16 day life) or an 0.85 g (21 day life) BD-2 external radio-transmitter (Holohil, Carp, ON) attached to a Flexi-fix™ harness. The transmitter-harness package weighed 0.9-1.0 g and did not exceed 6 % of the individual's body weight, with most weighing < 5 % as suggested by

Bartelt and Peterson (2000) for western toads (*Anaxyrus boreas*). Two or 3 days before the battery was set to expire, the animal was briefly re-captured and refitted with a new transmitter, provided that no injuries were evident. Animals that received transmitters were hydrated in a bucket of water prior to release to replace any fluids expelled during handling. The transmitter attachment process took 5-15 minutes.

Telemetered individuals were tracked for varying durations (4 – 90 days) from 10-Jun until 7-Sept 2009 and 17-May until 26-Aug 2010. Individuals were located every 1 to 3 days (average = 1.5). To avoid unnecessary disturbance to the animal, relocations took place during daylight hours when spadefoots were in retreats (see Chapter 2). Each location was marked and Universal Transverse Mercator (UTM) coordinates were recorded with a Garmin 76CX handheld GPS unit.

Retreat Analysis

I recorded the dominant habitat-type, as a representation of macro habitat, within a 10 m radius circular plot surrounding retreat sites of telemetered individuals (Table 3.1). All locations on land where individuals spent the daylight hours were considered retreats. Microhabitat characteristics (as shown in Table 3.1) were recorded as a percentage of ground cover from a bird's eye view (i.e. summing to 100%). These were assessed at two scales of circular plots surrounding the spadefoot retreat site: 0.4 m radius and 1.5 m radius. Spearman rank correlation was used to assess the relationship between micro-habitat characteristics and the time spent in each retreat.

Random habitat plots were established at all scales and were used to collect comparative data on habitat availability. Habitat variables within random plots were assessed in the same way as used sites. At the smallest scale (0.4 m radius) three same-sized random habitat plots were established. The center of each random plot was located 1.1 m from each used habitat plot. A randomly chosen bearing was used to place the first plot; subsequent plots were located 120° from the previous (Figure 3.1). This scale represents the microhabitat choices available to the individual at that location; by assessing resource selection at this scale we are looking at whether habitat features are different within a 1.5 m radius, and if spadefoots respond to

Table 3.1. Description of measured habitat variables at the macro and microhabitat scale.

Scale	Variable	Description
Habitat-type (macro)	Grassland	Grass-dominated.
	Forest	Tree-dominated landscape. Mainly trembling aspen and logepole pine (<i>Pinus contorta</i>)
	Shrubland	Shrub covered areas. Dominant species include scrub birch (<i>Betula glandulosa</i>) and kinnikinnik (<i>Arctostaphylos uva-ursi</i>)
	Interface	The transition area between open grassland and forest. We considered any retreats within 10 m of open grassland to be located within interface habitat
	Forest path	Any path going through a tree dominated area. Path could be made by livestock, wildlife or vehicles
	Grassland path	Any path going through open grassland. Path could be made by livestock, wildlife or vehicles.
	Wetland	Area with standing water or with wetland vegetation (i.e. rushes or sedges) indicating a dried wetland
Habitat variables (micro)	Grass	Grasses
	Bare	Open soil
	Litter	All dead non-woody vegetation (i.e. leaves, pine needle, grass) and animal droppings (ie. Cow patties, moose pellets)
	Rock	All sizes of rock
	Shrub	Low-growing woody vegetation, dominant species include scrub birch (<i>Betula glandulosa</i>) and kinnikinnik (<i>Arctostaphylos uva-ursi</i>)
	Herb	All non-woody vegetation that is NOT a grass
	Coarse woody debris	Includes sticks, twigs, and logs without attached roots or branches that were less than 300 cm ² (bird's eye view)
	Tree	Live or dead standing trees
	Fallen tree	Any fallen trees with attached branches and /or exposed roots, or > 300 cm ²
	Moss, lichen, fungi	Moss, lichen or fungi covered soil
	Water	Standing water
Mud	Exposed wet soil	

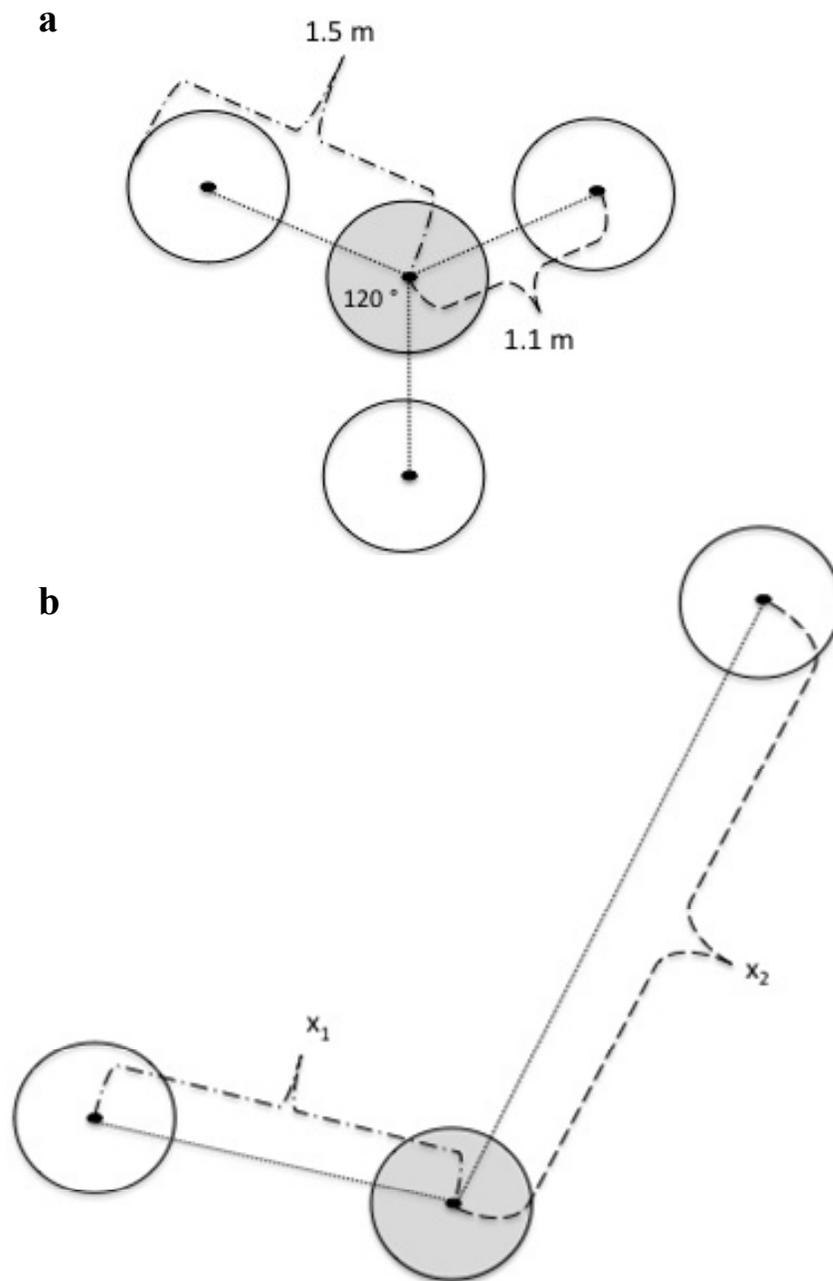


Figure 3.1. Schematic of study design for a) 0.4 m radius plots and b) 1.5 m radius plots. Grey circles represent spadefoot retreat locations and white circles are randomly chosen plots. x_1 and x_2 represent random distances from the retreat site.

varying habitat features at this scale. Two random sites were paired with each 1.5 m radius plot. These plots were located at a random bearing and a random distance between 3.0 – 100.0 m from the used sites. The distance was > 3.0 m to avoid overlap with the used location and < 100.0 m to represent the maximum single night movement distance. See Figure 3.1 for a schematic of the study design.

Ground cover variables within the random plots and the plots at spadefoot locations were compared using generalized linear mixed models ('*glmer*' function, in the package *lme4*, R Version 12.2.0 (<http://www.r-project.org/>)). Observations of spadefoots in aquatic habitat during breeding were not included in habitat analysis. Ground cover variables were considered fixed effects and random effects were attributed to each individual. Random effects were included in the models to control for imbalance in the number of observations per individual and the effects of repeated measures on individuals (i.e. non-independence) (Breslow and Clayton 1993, Bennington and Thayne 1994, Gillies et al. 2006). I ran one model per explanatory variable as a preliminary analysis to yield 12 candidate models. Model selection follows an information-theoretic approach as outlined in Burnham and Anderson (2000). Akaike's Second-Order Information Criterion (AIC_c) for small samples was used to determine the most parsimonious model. Akaike weights (w_i) were used to examine the relative importance of variables as they represent the probability of that model being the most likely candidate (Burnham and Anderson 2000). AIC_c differences (Δ_i) between models were used as level of support for each model. Models with $> 10 \Delta_i$ were omitted from the final candidate set of models. Model averaging was conducted to obtain parameter estimates based on the final candidate set of models (Burnham and Anderson 2000).

Retreats were categorized as single use, core, hibernation or random sites. Single use retreats were locations used by spadefoots only once. During this time, the animal was present in the same location each morning. Core retreats were defined as those returned to one or more times per season, meaning the individual travelled to other retreat sites or a breeding pond, then returned to a previously-used site. Certain individuals had core retreats that were so predictable that that I was able to relocate three spadefoots whose transmitters had failed based solely on previous knowledge of their preferred retreats. These retreats may share common characteristics that deem them suitable for repeated or preferential use. Wilcoxon

rank sum tests were conducted to test if habitat characteristics (bare ground, rock and shrub) differed among retreat categories (single use, core and random).

Hibernation sites were suspected when an individual was present at the same site for an extended period of time (> 7 days) after August 15th and were confirmed as such when an individual was located more than 0.6 m underground (observed when dug up for transmitter changes). Due to small sample size ($n = 3$) these sites were excluded from Spearman rank correlation and Wilcoxon rank sum tests. These sites were included in generalized linear mixed model analyses.

RESULTS

I captured 55 spadefoots by hand, both opportunistically (on paths or in open areas surrounding breeding sites) or during pond edge searches. Nineteen adult spadefoots were large enough for transmitter attachment. Of these animals, 8 were captured at the pond and 11 were encountered opportunistically on land.

Habitat characteristics were measured at 133 spadefoot retreat sites. For the 1.5 plot, habitat characteristics were measured at an additional 266 paired random locations, and at 399 paired random locations for the 0.4 m radius plot. A summary of tracking statistics for all 19 telemetered individuals is provided in Table 3.2. Linear regression analysis indicated a highly significant positive relationship (adjusted $R^2 = 0.56$, $P < 0.001$) between tracking duration and number of observed retreats per animal (Figure 3.2). All told, I observed 96 single-use sites, 34 core sites and 3 hibernation sites.

The majority of retreat and random sites were located in the open grassland habitat-type, followed by forest habitat-type. Grassland and forest path habitat-types were used at a higher proportion than in random locations, while grassland interface, grassland path, wetland, and shrub-covered areas were used less frequently than random. There was no difference in the proportion of used and random plots located in forest habitat-type (Figure 3.3).

Table 3.2. Spadefoot identification code, weights (g), snout to vent length (SVL) (mm), tracking dates (MM/DD) and duration (days), number of telemetry relocations (fixes), total number of retreat sites, core retreat sites and fate of telemetered individuals. Weights and SVL were recorded at initial capture. Within the ID codes, ‘M’ represents males, ‘F’ represents females, numbers beginning with ‘1’ (i.e. SF101) were tracked in 2009, and those beginning with ‘2’ (i.e. SM203) were tracked in 2010.

ID	Mass	Start	End	Days	Fixes	Retreats	Core
SM101	17.8	06/16	06/25	11	14	2	1
SM102	17.2	06/16	07/25	41	49	5	1
SM103	17.6	06/16	07/19	35	31	6	2
SM104	19.4	07/03	09/07	67	73	15	5
SF101	17.7	06/16	06/19	4	4	1	0
SF102	21.7	06/22	07/28	37	41	7	0
SF103	23.3	07/17	09/01	47	51	4	1
SM201	15.9	05/17	07/14	58	42	16	0
SM202	16.8	05/17	07/05	49	36	6	4
SM203	16.4	05/18	07/30	73	49	8	4
SM204	17.2	05/27	08/26	90	59	20	3
SM205	19.7	06/02	08/24	83	54	17	7
SM206	18	06/02	08/12	71	31	9	5
SM207	21.8	06/02	08/23	82	50	10	3
SM208	18.8	06/17	06/27	10	6	2	-
SF201	19.5	05/18	07/24	67	45	17	3
SF202	18	05/26	06/13	18	9	1	-
SF203	29.1	05/27	06/14	18	8	2	-
SF204	26.4	05/31	08/24	85	55	22	1
Average	19.6			49.5	37.2	9.0	2.1
Total				946	707	170	40

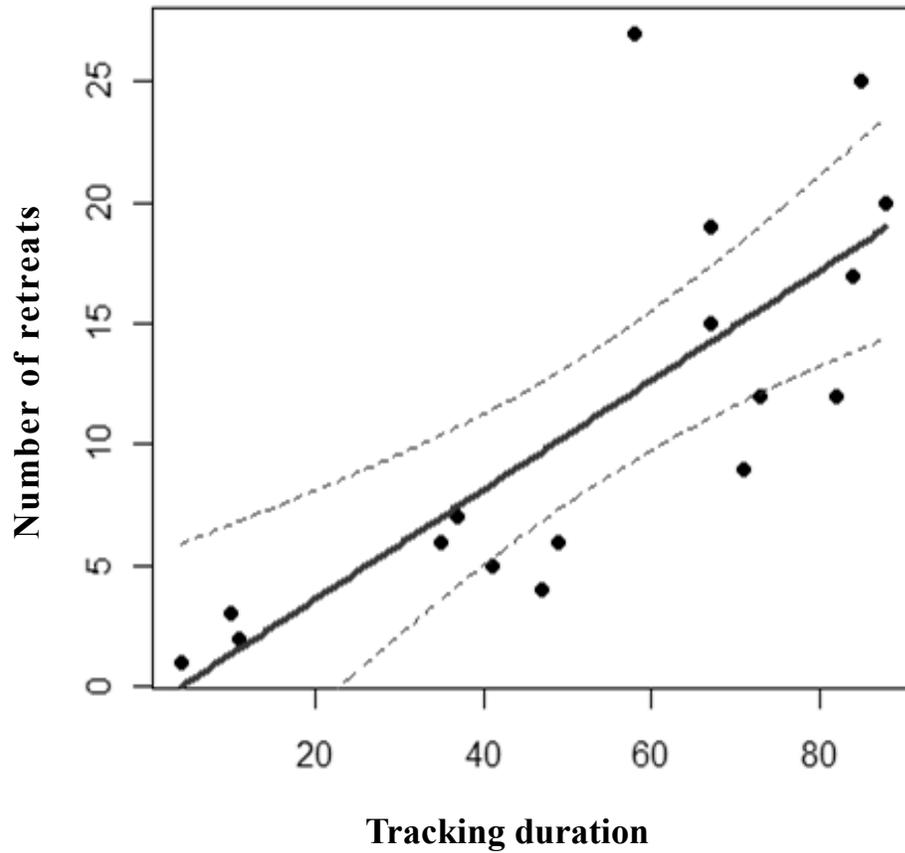


Figure 3.2. Scatterplot showing the relationship between the number of spadefoot retreats used by each study individual and the number of days each individual was tracked. The dashed lines show the 95% confidence intervals for the regression analysis (adjusted $R^2 = 0.56$, $P < 0.001$).

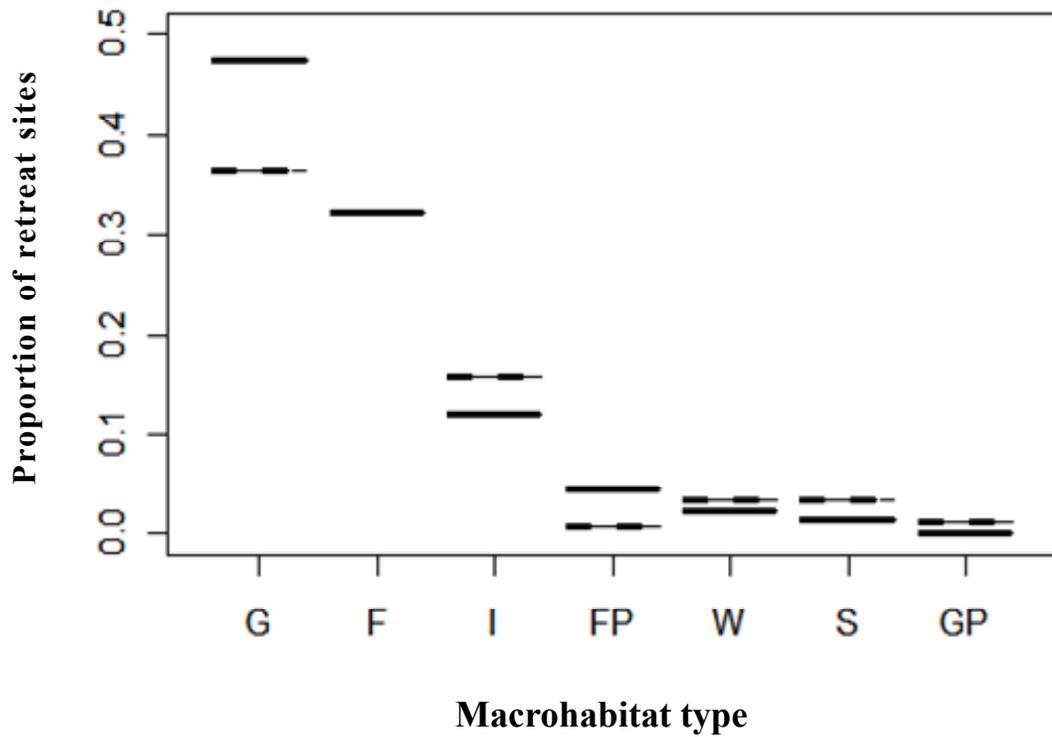


Figure 3.3. Proportion of retreat sites (solid line) and random plots (dashed line) located in each macrohabitat type: grass (G), forest (F), grassland-forest interface (I), forest path (FP), wetland (W), shrubland (S), grassland path (GP).

For the 0.4 m radius plots, I ran univariate mixed-effects models for each measured ground cover variable as well as a null model containing only random effects (i.e. the intercept, but no fixed effects). The AIC_c values for all models were very close (all $\Delta_i < 1.98$) with the null model being the strongest (lowest AIC_c). This suggests that none of the ground cover variables were relatively effective predictors for used sites at this scale.

For the 1.5 m radius plots, I ran univariate mixed-effects models for each variable. The AIC_c value for model 'bare' had a w_i value of 1 which was 23.3 points lower than the next ranked model. I ran bivariate models, each of which contained 'bare' and one of the 11 other variables (i.e. bare + rock, bare + tree, etc.). Of the resulting 11 models, the top two carried a w_i of 0.34 and 0.31 respectively, and the Δ_i (0.17) was very small between the two. The next highest ranked model had an w_i of 0.06 and a Δ_i of 3.51; therefore, I chose the variables contained in the top two ranking models (bare, rock and moss/lichen/fungi) to create my final candidate set of models (Table 3.3). Model averaged estimates of top habitat variables are shown in Table 3.4.

The proportion of bare ground and rock were positively correlated to the amount of time spent at each location, while the relationship for moss/lichen/fungi was slightly negative. The only significant relationship was observed with bare ground ($\rho = 0.09$, $p < 0.001$).

No significant differences between core sites and single-use sites were seen in terms of proportion of bare, rock or moss/lichen/fungi ground cover (Figure 3.4). Significant differences were observed between random sites and single-use sites for bare ($V = 3367$, $p < 0.00001$), random sites and core sites for bare ($V = 429.5$, $p < 0.01$), and random sites and single-use sites for rock ($V = 246$, $p < 0.01$).

Table 3.3. Final candidate set of mixed effects models for habitat use at the 1.5 m radius scale. Variables include bare ground (B), rock (R) and moss/lichen/fungi (MLF).

Model	FIXED EFFECTS			RANDOM EFFECTS					
	Bare	Rock	MLF	Intercept	Variance	SD	AIC_c	Δ_i	w_i
B + R + MLF	0.030	0.041	-0.530	-1.238	3.02e ⁻¹²	1.74e ⁻⁶	474.35	0	0.68
B + R	0.031	0.039		-1.285	0	0	477.42	3.07	0.15
B + MLF	0.032		-.0464	-1.186	3.71e ⁻¹²	1.93e ⁻⁶	477.59	3.24	0.14
B	0.032			-1.23	0	0	480.36	6.01	0.03

Table 3.4. Model-averaged estimates of variables included in the top candidate models, bare ground, rock and MLF (moss, lichen or fungi).

	Bare	Rock	MLF
Unconditional model-averaged estimate	0.0307	0.0405	-0.5193
Unconditional standard error	0.0059	0.0188	0.4016

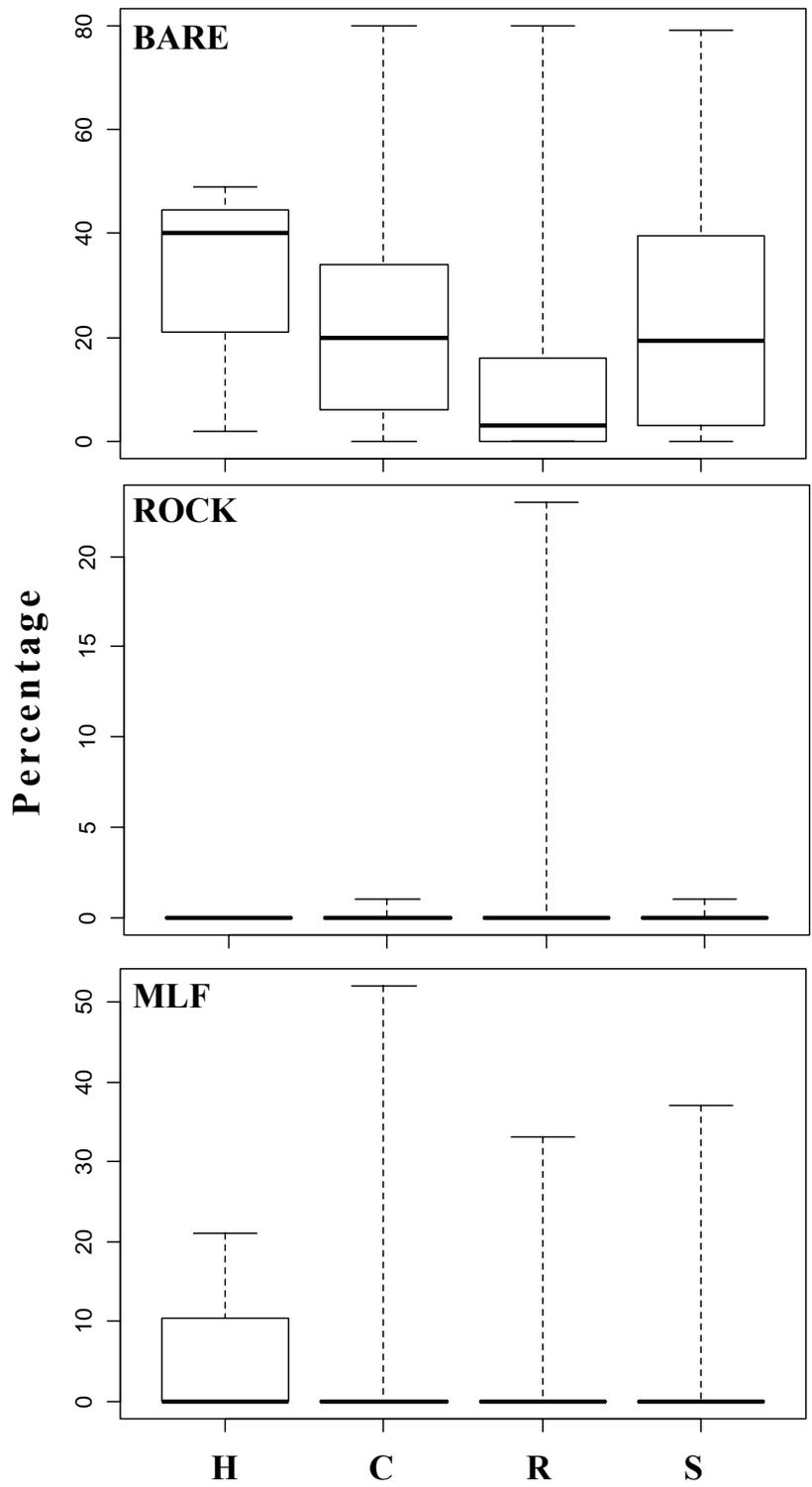


Figure 3.4. Top-ranking habitat variables (bare, rock, and moss, lichen and/or fungi) shown as percentage of ground cover at hibernation sites (H), core retreat sites (C), random habitat plots (R) and single-use retreat sites (S).

I found 4 putative hibernation sites, 1 suspected and 3 confirmed by excavating the site and locating the individual (Table 3.5). One female spadefoot (SF103) appeared to hibernate underneath a large boulder, a site where she had spent the most time during the tracking duration. The individual used this retreat from 22-Jul until her transmitter died on 1-Sep. She emerged to forage on 28-Jul, but was not seen thereafter. I was unable to conduct an excavation to determine her ultimate fate because of the physical location. A second female (SF204) burrowed into a large mound of soil that was originally created by forestry activity. The hibernation site of one male (SM204) was located upslope from a breeding pond. His location was in close proximity to a badger burrow complex, and it is suspected that he dug downwards into a badger tunnel, moved along the tunnel and then continued to dig down. A second male (SM205) entered his hibernation site in a depression at the end of a fallen tree upslope from his breeding location.

Table 3.5. Characteristics of 4 spadefoot hibernation sites including the date first observed at the site, the vertical distance underground in cm (Dv), the length of tunnel route in cm (Dt), (macro) habitat type, top two microhabitat variables (in order) measured in a 1.5 m radius plot surrounding the site, and fate of the individual. ID corresponds to the code number for each animal.

ID	Date arrived	Dv	Dt	Habitat-type	Microhabitat	Fate
SF103	22/07/09	-	-	grassland	rock, bare	Unsure
SF204	09/08/10	40	60	forest	bare, rock	Dead
SM204	21/08/10	145	-	grassland	bare, grass	Alive
SM205	25/08/10	42	60	grassland- forest interface	coarse woody debris, grass	Alive

DISCUSSION

While many species of amphibians appear to require a microhabitat with sources of protective cover, such as leaf litter, coarse woody debris, animal burrows, and rocks (Bartelt and Peterson 2000, Faccio 2003, Baldwin et al. 2006, Bull 2006, Blomquist and Hunter 2010), this study indicates selection for bare ground by Great Basin spadefoots. However, studies of other fossorial anurans have indicated the importance of bare soil: common European spadefoots selected for open areas (Eggert 2002), as did arroyo southwestern toads (*Anaxyrus microscaphus californicus*) (Griffin and Case 2001).

Burrowing likely eliminates the need for moist ground cover, as water is available in the form of soil moisture (e.g. western spadefoots (*Spea hammondi*); Ruibal et al. 1969). Higher soil moisture has been observed in bare areas than in surrounding grass covered or chaparral (shrub) zones (Davis and Mooney 1985). This observation is associated with the root systems of each zone: deeper root systems of shrub-covered areas deplete soil moisture to a greater depth than in grassland or in bare zones (Davis and Mooney 1985). Avoidance of highly-vegetated areas by spadefoots in my study may reflect selection for areas with higher soil moisture. In addition, burrowing in highly-vegetated areas with complex root systems may be difficult, hence may negatively affect the ability to seek refuge and/or reach an appropriate depth of retreat.

Site selection also may reflect foraging strategy. Spadefoots are generalist feeders and are thought to employ the 'sit and wait' predator method (Zack and Johnson 2008). Tobias et al. (2001) observed higher predation efficiency by common European spadefoots in a simulated habitat with linearly arranged structures than in a disordered habitat. He attributed this to a greater line of sight. Taking this into consideration, bare areas chosen by spadefoots in my study could provide a greater line of sight, leading to higher predation efficiency. Great Basin spadefoots also have been observed foraging in open areas (Bragg 1965). Fowler's toad was commonly found in bare areas during night time foraging, which presumably followed the 'sit and wait' strategy (Clark 1974).

Rock features were also found, to a much lesser extent, to be an important habitat factor for spadefoots. I observed the use of small mammal burrows under rocks as well as self-created

burrows adjacent to large rocks. Similarly, rocks served as an important retreat area for western spadefoots (Svihla 1953). Increased relative humidity and prey availability in burrows under rocks may influence the apparent selection for this habitat characteristic (Civantos et al. 2003). Spadefoots in my study also showed a slight selection against microhabitat containing moss, lichen and/or fungi. It is possible that the structure of these organisms may inhibit burrowing. Mosses are associated with moist, shady areas, such as forest floor, on which they can form dense mats (Parish et al. 1996). Lichens, such as the pixie-cup (*Cladonia pyxidata*; commonly encountered in my study area) can form extensive colonies on open soil and in open forests (Parish et al. 1996).

The apparent broader preference for grassland by these animals likely reflects the habitat selection of bare areas at the fine-scale. However, the proportion of sites located in forest was no different than that found randomly on the landscape, indicating that the animals were able to seek out microsites in the forest with a suitable proportion of bare ground. The observed association with forest paths may be related to a higher ease of movement in areas cleared of vegetation, such as forest service roads and game paths (on which numerous spadefoots were encountered). In a similar fashion, the microhabitat selection of desert tortoise (*Gopherus agassizii*) burrows was positively related to the proximity of gravel roads that were used as travel routes (Grandmaison et al. 2010). Therefore, movement capabilities may also be a factor in retreat site selection for Great Basin spadefoots in my study.

Selection of bare ground at the microhabitat level appears to be consistent across/among individuals as evident by very low or nil random effects. This may indicate that spadefoots, as a taxon, are quite habitat-specific at the fine scale of retreat site selection. Microhabitat preferences were more specific for burrowing sites than activity sites in arroyo southwestern toads (Griffin and Case 2001). Specificity of diurnal retreat site selection in spadefoots may reflect the relative importance of these sites. Fine scale habitat choices (that defined nest sites) in ferruginous pygmy-owls (*Glaucidium brasilianum*) showed very little variation across individuals and were connected with higher fitness and reproductive success than choices made at higher scales (Flesch and Steidl 2010). For ectotherms, fine scale selection is even more important, as site selection has direct physiological consequences (Huey 1991). Individual fitness (growth, survival, reproduction) is a reflection of the ability to carry out

important behaviours such as foraging, migration, and breeding. Maintenance of body temperature within the ideal range is necessary to perform these functions, and this is largely achieved through the selection of appropriate microhabitat (Huey and Kingsolver 1989, Huey 1991, Seebacher and Alford 1999, Kearney and Predavec 2000).

The habitat specificity observed in my study may be a behavioural adaptation of spadefoots at the northern periphery of their range. Higher habitat specificity has been observed in ectotherms at range boundaries and climatic extremes (Thomas et al. 1998, Oliver et al. 2009). In order for individuals to maintain their preferred body temperature they may become restricted to a small range of habitat features. Thus, habitat requirements in terms of aspect and vegetation structure may differ for individuals at or near their latitudinal or altitudinal limits. For example, individuals within northern peripheral populations may be confined to south-facing slopes having short vegetation, while tall vegetation and many aspects may be suitable for individuals in the core of their range (Thomas et al. 1998). For spadefoots living at their northern limits, bare areas may receive more sunlight and therefore may offer a greater opportunity for temperature regulation.

Retreat site fidelity was demonstrated by all spadefoots in my study. Similar site fidelity is quite common among anurans (Sinsch 1990), having been observed in cane toads (*Anaxyrus marinus*; Cohen and Alford 1996), arroyo toads (Griffin and Case 2001), Yosemite toads (*Anaxyrus canorus*; Liang 2010), common European spadefoots (*Pelobates fuscus*; Eggert 2002), and eastern spadefoots (*Scaphiopus holbrookii*; Johnson 2003). This behaviour was exhibited, to various degrees, by every telemetered spadefoot in my study. Although I did not detect any differences in ground cover between core sites and single use sites, some factor(s) that I failed to measure may have made the core sites more preferable. Proximity to high quality foraging habitat could be such a factor, although Bartelt et al. (2004) found that variation in prey abundance was not an important factor for site selection in western toads. Thermal qualities or soil moisture of a particular site may contribute to site selection. These characteristics may be intrinsic at that site, or the individual may actually invest resources in the site, creating a more suitable microhabitat for themselves (Cohen and Alford 1996). A study of retreat site use by cane toads showed that toads would enter a retreat site with a full

bladder, then void the water in that shelter site, creating a moister environment (Cohen and Alford 1996).

This study provides the first in-depth investigation of spadefoot behaviour and terrestrial habitat preferences. Spadefoots located in my study area appear to be habitat specialists at the fine scale, selecting for retreat sites containing a high proportion of bare ground. Additional studies are needed to investigate if this may be attributed to their location at the northern periphery of their range, or if it is characteristic of the species throughout their range.

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CHAPTER 4 • SUMMARY AND CONCLUSIONS

SUMMARY

The overarching theme of my research was to determine the upland habitat used by spadefoots outside of the breeding season and identify important resources within that area. This broad agenda was narrowed down into the following objectives: (1) investigate terrestrial movement patterns of Great Basin spadefoots in terms of distance travelled to/from aquatic breeding sites, distance and patterns between diurnal retreat sites and distance travelled in relation to weather factors, (2) identify disproportionately-used resource units at retreat site locations, and (3) identify hibernation sites.

The most significant results of my thesis are:

- The extent of terrestrial habitat use was variable among individuals, with 136 m being the average maximum displacement from aquatic breeding sites.
- Telemetered individuals conducted many short movements and few long directed movements over the active season.
- No strong correlations were seen between weather factors and movement.
- Study animals showed a preference for open areas, both at the microhabitat scale and at the macro scale of habitat-type.

My results suggest that Great Basin spadefoots at the northern edge of their range may exhibit some differences in behaviour due to their northern location, such as habitat specificity (Thomas et al. 1998, Oliver et al. 2009), while other behaviours common to northern herpetofauna, such as elongated movements, were not observed (as compared to other anuran species; Semlitsch and Bodie 2003). The association with open grassland and bare ground at the microhabitat level suggests that spadefoots at this location are, like conspecifics further south, still tied to habitat characteristics of arid environments. Comparative data on this species are needed to further investigate this concept.

MANAGEMENT IMPLICATIONS

Great Basin spadefoots are a species at risk in Canada and British Columbia (BC), dictating the need for effective management plans. The lack of terrestrial ecological information for spadefoots is a major knowledge gap for Great Basin spadefoots (COSEWIC 2007, British Columbia Southern Interior Reptile and Amphibian Recovery Team 2008). This study provides much needed ecological information on this species and begins to close that gap.

My study area in particular presents significant opportunities for spadefoot conservation and management, as the majority of land is owned by the provincial government. Terrestrial movement and habitat-use data from this study in combination with amphibian auditory survey data already have supported the creation of 15 Wildlife Habitat Areas for this species (Garner and Packham 2011). These mapped areas include critical habitat for spadefoots and impose limitations on forestry (i.e. no road construction) and range (i.e. grazing limitations) activities, the two main land uses in my study area.

The effects of soil compaction and plant community changes from livestock grazing on spadefoot habitat quality are not known. Livestock can have a significant effect on amphibian aquatic habitat through changes in water quality or habitat structure (Sarell 2004, Schmutzer et al. 2008), however, the effect of livestock on terrestrial habitat is not clear (Burton et al. 2009). Compaction of soil by livestock may decrease availability of suitable terrestrial retreat sites, as spadefoots, particularly juveniles, require friable soil for burrowing (Oaten 2003, Sarell 2004). Overgrazing can lead to changes in plant community structure. Native bunchgrass communities, such as those favoured by spadefoots in my study, are very sensitive to overgrazing (Daubenmire 1970, Mack and Thompson 1982, Gayton 2004). Once these sites have been degraded, invasive species are more likely to take over. Invasion of sod-forming grasses, such as Kentucky bluegrass (*Poa pratensis*), is of concern given the relative importance of bare soil for spadefoot retreat sites detected in my study. Sod grass inhibited burrowing for eastern spadefoots (*Scaphiopus holbrookii*; Jansen et al. 2001). Field or experimental research should be employed to determine how spadefoot terrestrial habitat may be affected by livestock.

Forestry operations were active during the term of my study in the areas adjacent to known spadefoot breeding sites. I observed some telemetered spadefoots occupying forest habitat, although this use was not ubiquitous among all study animals. Study individuals, as well as non-telemetered spadefoots and western toads (*Anaxyrus boreas*), were often encountered on forestry roads throughout the study area. In addition to risks from habitat alteration due to logging, increased forestry-related traffic on these roads may pose a great risk to this population through increased road mortality and subsequent population declines (Fahrig et al. 1995, Mazerolle 2004). Not only did I observe nocturnal movement of spadefoots along forestry roads, but 3 individuals created retreats along the edge of a road. One such retreat site had been compacted by a vehicle (tires tracks were evident) and the individual was dead inside that retreat. In the ideal world (for spadefoots), logging would be limited during the spadefoot active season (May-August) and old logging roads would be decommissioned. However, at the present time I recommend that logging activity within 200 m of breeding sites be restricted to daytime hours in order to avoid road mortality of spadefoots and other anurans during nocturnal activity periods.

LIMITATIONS AND FUTURE RESEARCH PRIORITIES

Any wildlife researcher employing telemetry has to grapple with some form of the trade-off between number of animals tracked and number of locations obtained per animal (Millspaugh and Marzluff 2001). A larger study population yields a more accurate representation of the actual population, although more detailed information can be obtained from intensive tracking of fewer individuals (Millspaugh and Marzluff 2001). The choice should be based on which scheme would better answer one's research questions. In my study, I had a choice to track more individuals for shorter periods of time, or attempt to track fewer individuals for a longer duration. My research questions were better addressed by the latter; it allowed observations of movement to/from the breeding pond, habitat selection throughout the active season, and identification of some hibernation sites. Knowledge of movement and habitat use over the whole active season, as much as is possible, is important not only for conservation planning but for gaining an understanding of amphibian ecology (Marsh and Trenham 2001).

Telemetry-related constraints limited the number of hibernation sites I was able to observe (i.e. failed transmitters, abrasions, mortality; see Appendix A). Ultimately, identification of hibernation sites is necessary to obtain a complete picture of spadefoot habitat use, especially for northern populations that endure long, cold winters. Many anurans including Great Basin spadefoots (to our knowledge) are not freeze-tolerant, therefore, over-wintering in suitable hibernation sites is critical to survival. (Holzwardt and Hall 1984, Swanson and Graves 1995, Irwin et al. 1999). Browne and Paszkowski (2010) observed selection of certain habitat-types for hibernation sites by western toads in Northern Alberta. They concluded that suitable hibernation sites may be limited, thus further highlighting the need to identify these critical habitats. To my knowledge, there is no information on Great Basin spadefoot hibernation sites aside from the 3 confirmed hibernation sites I report on herein. Future research should aim to characterize hibernation sites in terms of microhabitat features, distance from breeding sites and associated habitat-type. Improvement of radio-telemetry equipment (i.e. smaller transmitters with longer battery lives) will likely increase the ability to gain this sort of information.

In terms of habitat analysis, I focused on microhabitat at diurnal retreat sites. These sites are particularly important for spadefoot survival (see Chapter 3) and they may indirectly reflect habitat choices made during other activities (foraging, migration). Much remains to be discovered about the nocturnal activity of spadefoots. It is unknown if spadefoots forage in close proximity to their retreat sites (Penman et al. 2008, Yetman and Ferguson 2011), if they forage widely (Strüssmann et al. 1984) or if movements are variable based on foraging success (Wiggins 1992). Future researchers may want to focus on nocturnal movements of spadefoots and the associated habitat choices. I would suggest the use of fluorescent pigments in addition to telemetry for nocturnal studies (Eggert 2002, Birchfield and Deters 2005, Rittenhouse et al. 2006). Fluorescent pigments can be used to obtain a foraging track while maintaining distance from the study individual, thus obtaining a more accurate path than with nocturnal telemetry observations alone.

CONCLUDING REMARKS

Caution must be taken when extrapolating my results to other populations in BC or elsewhere. However, the information gained from my research should be used as a baseline for future studies as knowledge gained during this study provides much needed insight into the general ecology of spadefoots at their northern extent and to the species in general. The northern population of spadefoots exists in somewhat of an atypical environment (see Chapter 1). Compared to populations elsewhere in their range, individuals in peripheral populations are likely exposed to a different combination of biotic and abiotic factors which may influence their movement and/or habitat use (Larsen 1987, Thomas et al. 1998, Sunde et al. 2001, Arvisais et al. 2002). Repeating this study in other parts of the spadefoot's geographic range, specifically in the southern part of their BC range, and in the core of their range in the US, would be desirable. Having such information would allow comparison of habitat use and movement across spatially-separated populations and better enable identification of unique traits, if any, of the northern population. On a broader level, more information is needed on amphibians at the northern edge of their range. Presumably, the life-history attributes of the animals in my study are influenced in some degree by their northern peripheral environment. Thus, their ecology may be markedly different than that seen in more southern 'typical' habitat, but this will need to be revealed by future research.

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APPENDIX A • USE OF RADIO-TRANSMITTER HARNESSSES FOR ANURANS AS AN ALTERNATIVE TO TRADITIONAL BELT DESIGN

INTRODUCTION

Radio-telemetry is a widely used wildlife monitoring technique. It allows researchers to follow the movement paths of individual animals, obtaining detailed information on critical life history activities as well as habitat associations, home range, movement patterns and more (Millsbaugh and Marzluff 2001). Radio-telemetry with amphibians, specifically anurans, has allowed researchers to collect much needed information on the habits of individuals outside of the (relatively) well-studied aquatic life-history stages. For a variety of anurans this information may include migration paths, dispersal distances, over-wintering locations, and upland foraging areas, all of which are necessary for the complete understanding of a particular species and the creation of effective management plans (Marsh and Trenham 2001). Radio tracking of anurans has been growing in popularity, as it provides a tool to obtain information otherwise unattainable to researchers. While this method is facilitating a (much needed) increase in our understanding of anuran ecology, it is still relatively novel and not without constraints. In particular, the sensitive nature of anuran skin and the animals' small size provide two main logistic hurdles for applying telemetry on this group of animals.

Amphibian skin is quite delicate and can be easily injured by external attachment of radio transmitters. Numerous techniques have been employed for radio-telemetry of anurans with the most common being the 'belt' method, whereby the transmitter is attached to the animal through a belt around its waist (e.g. Rathbun and Murphey 1996, Bartelt and Peterson 2000, Griffin and Case 2001, Bull 2006). Belts have been made out of a variety of materials, including (but not limited to) aluminium ball and chain (Rathbun and Murphey 1996), plastic tubing (Bartelt and Peterson 2000), glass beads on fine elastic (Muths 2003), and ribbon (Bull and Hayes 2001, McAllister et al. 2004). This method has shown success, although skin abrasions can be a common occurrence using transmitter belts (Bartelt and Peterson 2000). Inhibition of movement, via catching on vegetation, or the transmitter slipping ventrally after initial placement on the dorsum is also a concern when using externally attached transmitters (Rathbun and Murphey 1996, Bartelt and Peterson 2000).

An alternative method of radio-transmitter attachment is implantation. Using this method, a transmitter is surgically implanted into the abdominal cavity or underneath the skin of the animal near the abdomen (eg. Seebacher and Alford 1999, Eggert 2002, Lemckert and Brassil 2003, Blihovde 2006, Yetman and Ferguson 2011). While this process has been used successfully, it is relatively invasive. Anaesthetic is used during the implantation process, either general or local, and the animal is held for observation after the procedure (Seebacher and Alford 1999, Eggert 2002, Lemckert and Brassil 2003, Blihovde 2006, Yetman and Ferguson 2011). Presumably, the main motivations behind transmitter implantation are avoidance of external injuries and of movement inhibition from the external attachment device.

Fossorial anurans, and other highly terrestrial anurans, may be particularly susceptible to the negative afflictions of externally attached transmitters. These animals must be able to dig burrows and/or retreat into underground borrows created by other organisms, and may spend the majority of their time underground. Implantable radio-transmitters are commonly used in studies on fossorial anurans, presumably so burrowing and movement are not inhibited by an externally attached transmitter (Seebacher and Alford 1999, Eggert 2002, Lemckert and Brassil 2003, Blihovde 2006, Yetman and Ferguson 2011). Implantation may avoid abrasion and movement-related issues, but without a whip antenna, the resultant limited signal range of 20 – 60 m will hinder the relocation of implanted individuals (Eggert 2002, Blihovde 2006). Further, the surgical procedure and the degree of invasiveness often prevents tracking animals for more than one transmitter cycle (Bartelt and Peterson 2000, Eggert 2002). This can be problematic for smaller anurans.

The size of anurans often necessitates using transmitters that have a relatively short lifespan, but see Yetman and Ferguson (2011) for an example of long-term telemetry on a large anuran. Batteries typically contribute the majority of weight in a transmitter package (transmitter plus attachment device). Therefore transmitters needed for smaller animals have, by default, shorter life spans than those used on larger animals. Richards et al. (1994) recommend that radio-transmitter packages, which include the transmitter itself and the attachment device, should be less than 10 % of an individual's weight, but improvements in technology have resulted in 5 % or less being considered the new standard (Bartelt and Peterson 2000). The brief longevity of transmitters suitable for smaller anurans (i.e. 16–21

days) means that in order to track anurans for extended periods, the transmitters need to be exchanged for new ones during the study period (e.g. Rathbun and Murphey 1996, McAllister et al. 2004). For externally attached transmitters, this exchange is relatively simple, however, it does require the animal to be captured and handled one or more times after the initial capture. When using implanted transmitters the procedure becomes more complicated and ethical questions arise.

Great Basin spadefoots (*Spea intermontana*) are small, mainly terrestrial, nocturnal, fossorial amphibians. These characteristics have rendered them a particularly challenging anuran to study, thus there is very little in the literature about their terrestrial habits. For this thesis, I sought to collect data on upland habitat use for the animal over their entire active season (approx. 4 months). These data were considered critical to crafting and evaluating management plans for the species. Transmitters suitable (i.e. < 5 % of body weight) for individuals of this species in my study area lasted a maximum of 21 days (BD-2 external radio-transmitter, Holohil, Carp, ON). Given the fossorial nature of spadefoots, implantation of radio transmitters was considered, however, multiple transmitters per individual were clearly needed to track individuals longer than 21 days and repeated surgical implantations were not an option. I outline herein an external transmitter attachment design that deviates from the traditional 'belt' design, in that a novel material is used and the design is slightly modified from that used elsewhere (Bartelt and Peterson 2000, Griffin and Case 2001, Bull 2006). The procedure was generally successful, and provided essential data on the ecology of animals in this population.

MATERIAL & DESIGN

Opsite™ FlexiFix™ transparent film was used to make the transmitter attachment device. This thin, smooth material is a waterproof, adhesive wrap used to treat humans with burns or other injuries. It can be folded and rolled, thus allowing it to be formed into soft 'cords' that can be used for belting transmitters to anurans. Prior to the field study, FlexiFix™, polyethylene tubing and silk ribbon were tested as attachment materials on spadefoots housed in captivity (Teichman unpublished raw data). This pilot study indicated that FlexiFix™ would be the most suitable for field use. Leg straps were subsequently added to the belt design to create a harness-type device (Figure A.1). The leg straps prevented the

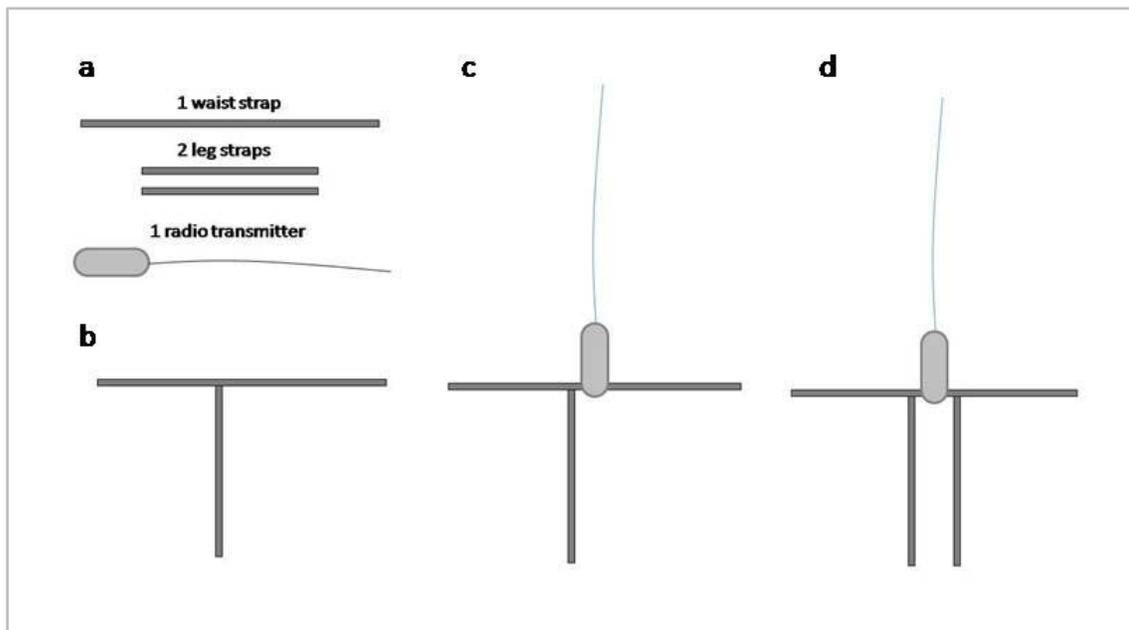


Figure A.1. Step-by-step schematic for creating the transmitter harness package: a) materials needed, b) attach one leg strap to the waist strap slightly off-centre, c) slide radio-transmitter onto waist strap, d) attach second leg strap to waist strap on the opposite side of radio transmitter. Note that step b and c are interchangeable.

transmitter from slipping ventrally and interfering with ground movement (Bartelt and Peterson 2000).

The waist and leg straps were made of 3 separate pieces of FlexiFix™: one 1.5 x 8 cm for the waist and two 1–1.5 x 5 cm for the legs. Each piece was folded into straps by peeling the white backing off and continually folding the adhesive layer back onto itself (~2.0 mm) until the entire piece has been used (see supplementary video #1). Care was taken to ensure no creases or bubbles formed in the strap, resulting in creation of a flat, smooth surface; fine-tipped tweezers were useful during this stage. A small amount of Krazy Glue® was then used to attach leg straps to the waist strap (Figure A.1). Either a 0.70 g (16 day life) or a 0.85 g (21 day life) BD-2 external radio-transmitter (Holohil, Carp, ON) was used, depending on the weight of the animal. The transmitter harness assembly is outlined in Figure A.1, as well as in supplementary videos #1–4 provided on the CD accompanying this thesis. The transmitter harnesses were constructed prior to heading into the field. The precise nature of the assembly took 30–45 min/harness on average.

DEPLOYMENT IN THE FIELD

Spadefoots were captured by hand at breeding sites or opportunistically in surrounding uplands. Suitability for transmitter attachment was based on individual body mass, as weighed to the nearest 0.1 g with a digital scale. The transmitter and harness package did not exceed 6 % of body weight and most were < 5 % (Bartelt and Peterson 2000).

Attachment of the transmitter harness required two people, one to hold the animal (ventral side up) and the other to attach the harness (Rathbun and Murphey 1996). Once the animal was in the proper position, a ‘spacer’ made of FlexiFix™ backing was placed on the belly towards the pelvic area to ensure no glue came in contact with the individual’s skin. The waistband was wrapped around the waist and secured with a small drop of glue. The fit was snug, such that it would not pull off over the animals’ hind legs, but not too tight that skin was being pinched. The leg straps were pulled through the legs and attached in the same manner. These straps fit looser than the waistband, but not so loose that the hind foot could get lodged in the harness when digging. Once the harness was in place, excess waist and leg strap was cut and all attachment points were checked to ensure the glue was dry before the

spacer was removed. Supplementary videos # 5–6 show the attachment of a transmitter harness in the field. Study animals were re-hydrated in a container of water prior to release in order to replace any fluids lost during handling. The procedure took approximately 5–15 minutes from capture to release, with a marked drop in timing as I became experienced in the technique. I took the precaution of examining the telemetered animals weekly (in Year 1) or every 2 weeks (Year 2) to ensure proper fit of belt. In doing so the animal was located at night, and handled in order to inspect the fit of the harness. If the harness fit well and no injuries were evident, the animal was released within a 1–3 minutes of capture. If abrasions/skin sores were evident the transmitter was removed, the wound was cleaned with distilled water and the animal was released. In the event of an ill-fitting harness with no skin sores, the existing harness was adjusted or a new harness was attached. Thereafter, each animal was briefly re-captured 2–3 days before the transmitter battery was set to expire and refitted with a new transmitter-harness package, provided that no injuries were evident.

RESULTS AND DISCUSSION

This method of transmitter attachment allowed tracking of 19 individuals for various durations. All telemetered spadefoots successfully ‘dug’, entered and emerged from shallow retreats throughout the summer. Average tracking duration in the first year (2009) was 34.6 ± 21.4 (standard deviation will be presented in all cases where a mean is given) days, in 2010 was 58.7 ± 28.6 days, and over both years was 49.5 ± 28.2 days. The majority of study animals ($n = 15$) were tracked over 19 days thus received multiple transmitters during the tracking duration. Study animals ventured up to 371.0 m from aquatic habitat, with the average maximum distance from breeding sites being 135.9 ± 98.2 m ($n = 12$). Spadefoot movement is discussed further in Chapter 2.

Similarly to the traditional ‘belt’ design, some problems with injuries were evident. Rubbing and/or waist abrasions, ranging from a slight chafing of the skin to cuts on the waist, were detected on 5 individuals (26 %). See Figure A.2 for a breakdown of tracking outcome in terms of abrasion. These injuries may have been caused by an improper fit of the harness (i.e. too tight or too loose) that was undetectable to the field personnel. Note that 2 individual spadefoots in this study that developed abrasions had ‘failed’ transmitters and were off the air for 10 and 18 days before being located (by knowledge of the animals' habits); therefore we

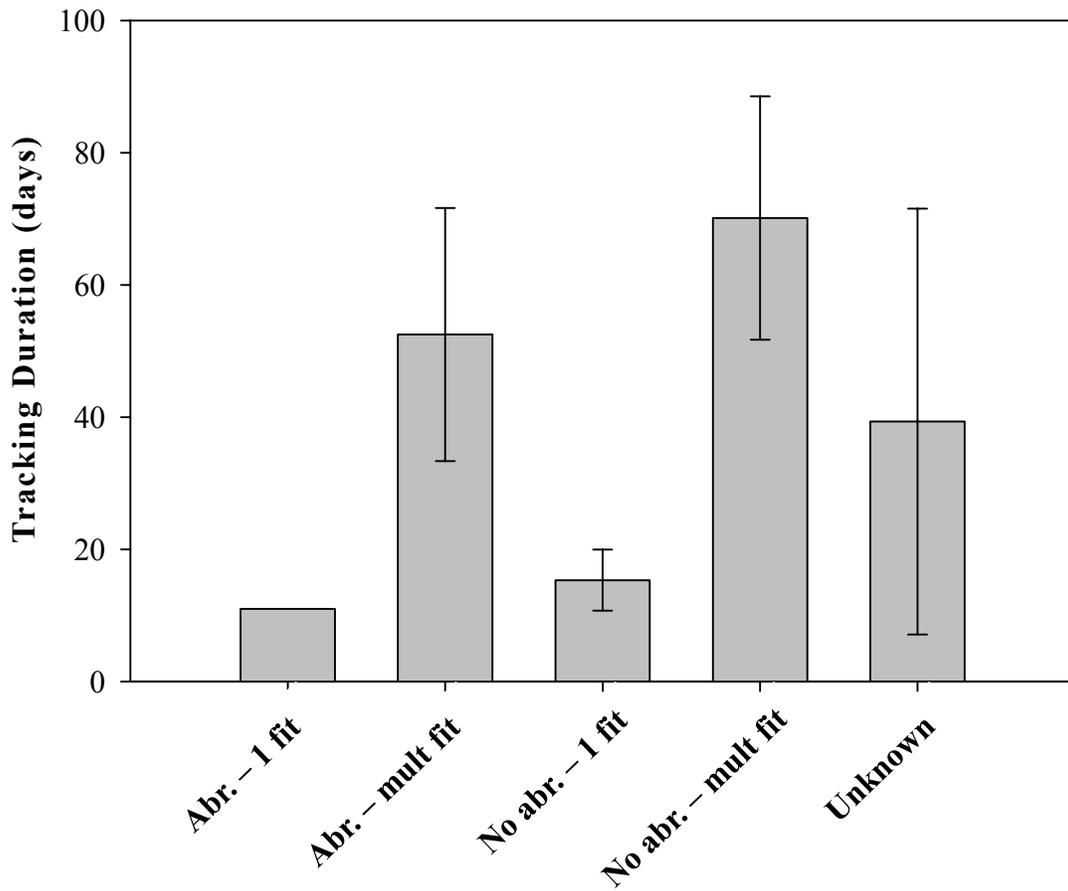


Figure A.2. Average tracking duration of Great Basin spadefoots that showed skin abrasions (Abr.) from the telemetry harness after 1 fitting ($n = 1$), abrasions after multiple fittings ($n = 4$), no abrasions after 1 fitting ($n = 3$), no abrasions after multiple fittings ($n = 8$), and those whose abrasion status was unknown ($n = 3$).

were unable to monitor the fit of their harness during those periods. The transmitter harnesses themselves appeared to be in great condition at the end of each transmitter cycle and did not show any indication of wear (i.e. fraying or shredded edges).

While researchers generally wish to disturb their study animals as little as possible, I agree with Bartelt and Peterson (2000) in that frequent assessment of a study individual's condition is necessary to ensure proper fit of belt and avoid injuries. Anurans, spadefoots in particular, can fluctuate in weight (and waist size) depending on environmental conditions and food intake (Dimmitt and Ruibal 1980), meaning that initially well-fitting harnesses/belts may become ill-fitting in a relatively short period of time. I observed both increases and decreases in weight among individuals carrying transmitters. At a minimum, I recommend checking once weekly and even more frequently if large movements are being observed. In addition, I recommend that prior to field studies, transmitter attachment should be practised in the lab to ensure ability to attach a well-fitting transmitter in the field.

It would be naïve to say that telemetry (or any other direct monitoring technique) has no effect on the behaviour of study animals. However, the trade-off between repeated disruptions to a study animals (i.e. re-capture for inspection of transmitter harness fit and for attachment of new transmitters) and operating in a complete knowledge gap may justify telemetry in many cases (such as in my thesis). Using telemetry, I detected complex movement patterns (including retreat site fidelity and an apparent homing ability to find these sites) and critical life-history behaviours (breeding attempts, entering into hibernation sites, annual migration) being conducted by the animals. The information gained from this work was hitherto unavailable for Great Basin spadefoots, and can now be utilized to craft management plans and to inform future research on this species.

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