

HABITAT SELECTION BY NEWLY METAMORPHOSED GREAT BASIN SPADEFOOTS (*SPEA INTERMONTANA*): A MICROCOSM STUDY

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Abstract.—Wetlands and their surrounding upland areas provide crucial habitat for the Great Basin Spadefoot (*Spea intermontana*), a species at risk in the grasslands of the southern interior of British Columbia, Canada. Understanding habitat selection and how these animals respond to change is crucial in the creation and implementation of conservation plans for the Great Basin Spadefoot. Little is known about the habitat selection of the Great Basin Spadefoot as they transition from aquatic larvae to terrestrial animals. The objective of this study was to determine microhabitat preferences of newly metamorphosed Great Basin Spadefoots. The small size of the metamorphs (18.7 mm SVL \pm 2.8 mm (SD); n = 130) and 0.66 g \pm 0.33 g (n = 130) precluded telemetry, so we conducted 13 simple habitat selection trials within four artificial enclosures. The trials were run in four batches over a 36-h period in the field near a spawning site. At release in the enclosures, the metamorphs immediately dispersed into all four habitat types (e.g., dry-bare, dry-cover, moist-bare, moist-cover). After 12 h, 75% of the metamorphs were located in moist-cover habitat, indicating a preference for that habitat. At the 36-h time period, it was clear that metamorphs were selecting for moist-cover habitat (79%, $P < 0.001$). Favourable habitat attributes for metamorphic spadefoots may be more specific than that of adults, requiring a more complex, holistic approach to habitat management for the Great Basin Spadefoot.

Key Words.—amphibian; British Columbia; conservation; cover; desiccation; grasslands; juvenile; larval emergence.

INTRODUCTION

Habitat selection by juvenile animals may differ substantially from that of adults, particularly for species where parental care is nonexistent or only occurs for very short periods of time (McHugh et al. 2011; Pereira et al. 2019; Delancey and Islam 2019). In situations where there is no parental care, juvenile animals should demonstrate habitat associations and preferences critical to immediate survival and, ultimately, successful recruitment into the population (Patrick et al. 2008). Amphibians provide striking examples of habitat associations: individuals transforming from aquatic larvae to terrestrial animals will abruptly face a different suite of environmental conditions, and the ability to find appropriate habitat may be imperative to survival (Rittenhouse et al. 2008). Understanding habitat selection during this stage of development is important to designing and implementing conservation strategies that do not focus solely on adult habitat needs (Biek et al. 2002; Vonesh and De la Cruz 2002).

North American spadefoots (genera *Scaphiopus* and *Spea*) are terrestrial, burrowing amphibians associated with arid or semi-arid habitats. North American spadefoots rely on two distinct habitats to survive: water bodies for breeding and tadpole development and terrestrial habitat for feeding, aestivation, and hibernation (Pearson 1955). Habitat studies on North American spadefoots have focused largely on adult breeding sites (e.g., Nystrom et al. 2002; Morey and Reznick 2004). As a result,

very little is known about the habitat preference of newly metamorphosed spadefoots (metamorphs), owing in part to their small size (18.7 mm SVL \pm 2.8 SD, n = 130, and 0.66 g \pm 0.33, n = 130; our data) and cryptic nature. As post-metamorphic juveniles do not remain in the water, they are likely vulnerable to desiccation and predation upon emergence, so habitat available near the edge of water likely plays a key role in enabling some proportion of the animals to survive the critical early stages of terrestrial life (Rothermel and Semlitsch 2006; Roznik and Johnson 2009). Heinen (1993) and Baughman and Todd (2007) conducted lab experiments on recently metamorphosed anurans (American Toad, *Bufo americanus*, Southern Toad, *Bufo terrestris*, and Eastern Spadefoot, *Scaphiopus holbrookii*) and concluded that vegetative cover was chosen over bare ground, and that cover was significant in providing protection from predators; however, neither of these studies included soil moisture as a factor. Jansen et al. (2001) concluded that Eastern Spadefoot metamorphs preferred moist substrate over dry. Grover (1998) analyzed cover and soil moisture and found both to be significant in predicting abundance of both juvenile and adult terrestrial salamanders (Red-backed Salamander, *Plethodon cinereus*, and Northern Slimy Salamander, *Plethodon glutinosus*) in a Virginia forest. Further studies are clearly required to explore the relationship between cover and moisture in determining habitat selection during the critical emergence stage of amphibians. Such work can guide the creation of artificial breeding ponds or the retention of key microhabitats



FIGURE 1. Location of the study site for microhabitat selection of metamorphic Great Basin Spadefoots (*Spea intermontana*) in the semi-arid grasslands in the Thompson River Valley, approximately 10 km west of Kamloops, British Columbia, Canada. A natural spadefoot breeding pond is located in the center of the photo. The four microcosms (arenas) are located to the right of the breeding pond, within the fenced enclosure. (Photographed by Jo-Anne Hales).

during habitat restoration or other land management.

The Great Basin Spadefoot (*Spea intermontana*) ranges further north than any other spadefoot in North America, occupying the semi-arid grasslands of British Columbia (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2007; BCSIRAWG 2017). This ecosystem makes up < 1% of British Columbia and has been affected over many decades by various forms of both anthropogenic and natural disturbance, substantially altering the habitat (Wikeem and Wikeem 2004). This includes a dramatic decrease (63%) in grassland ephemeral ponds (Coelho 2015) used by Great Basin Spadefoots. Cattle grazing and water use also has degraded the habitat around many of the remaining ponds (Jones et al. 2011; Teuber et al. 2013). Previous research on the Great Basin Spadefoot in British Columbia is limited and primarily restricted to the movement and breeding ecology of adults (Garner 2012; Ashpole et al. 2014).

Given the small size of metamorphic spadefoots, we hypothesized that newly metamorphosed animals would select habitat that provided cover in the warm, dry climate in the semi-arid grasslands of British Columbia. In this study, we report on a microcosm experiment used to investigate microhabitat preferences of newly metamorphosed Great Basin Spadefoots. The ultimate purpose of this work was to provide information that would help shape emerging guidelines for the rehabilitation, protection, and creation of Great Basin Spadefoot habitat on the British Columbia interior landscape.

METHODS

Study site.—This study took place throughout August 2014 in the semi-arid grasslands in the Thompson River Valley, approximately 10 km west of Kamloops, British Columbia, Canada (50°41'38"N, 120°32'7"W). Typically, summers in the Kamloops area are warm and dry (Chilton 1981). In 2014, Kamloops average daily temperatures in June, July, and August ranged from 11.2° C to 25.8° C, 14.6° C to 32.2° C, and 15.1° C to 29.7° C, respectively (http://climate.weather.gc.ca/index_e.html#access). Total precipitation in June, July, and August was 31.4 mm, 30.5mm, and 51.1 mm, respectively (http://climate.weather.gc.ca/index_e.html#access). Ephemeral alkaline ponds and wetlands are sporadic on the landscape, a feature typical of this zone (Meidinger and Pojar 1991). Due to current and historical cattle grazing, Big Sagebrush (*Artemisia tridentata*), Cheatgrass (*Bromus tectorum*), and Knapweed (*Centaurea sp.*) dominate upland sites. The elevation of the study site is about 643 m. We conducted this work outdoors, in close proximity (< 10 m) to a known breeding pond of Great Basin Spadefoots (Fig. 1) where tadpole development naturally occurred. This outdoor location was open to fluctuating ambient temperature and humidity, and the diurnal cycle.

Microcosm (arena) construction.—We established four enclosures (i.e., microcosms) using plastic arenas

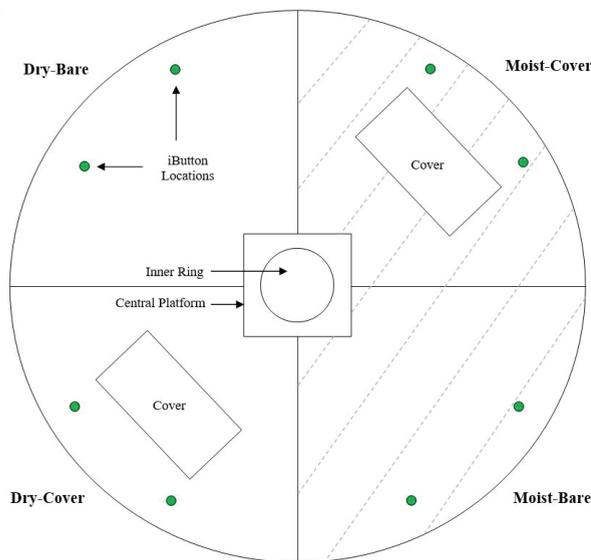


FIGURE 2. Schematic of artificial enclosure (i.e., microcosm) divided into four habitat types (e.g., dry-bare, dry-cover, moist-bare, moist-cover) to investigate microhabitat selection by newly metamorphosed Great Basin Spadefoots (*Spea intermontana*) in the Thompson River Valley, British Columbia, Canada. Enclosure diameter was 1.2 m. Dashed grey lines define the half of the enclosure that was moistened with water.

(children wading pools) approximately 1.2 m diameter with a wall height of approximate 20 cm. We divided each microcosm into four quadrants (surface area of one quadrant = 0.6 m²) with a central platform of rigid, translucent plastic (about 27 × 27 cm) and inner ring of the same material (about 23 × 23 cm; Fig. 2, 3). We placed the central platform and inner ring at the center of the arena and prevented the metamorphs from burrowing into the soil and entering the quadrants prior to release. Across these quadrants, we established four microhabitat types: dry-bare, dry-cover, moist-bare, and moist-cover. We filled each arena to a depth of 5 cm (volume = 0.06 m³) with a 1:1 mixture of sand and silt obtained from a local gold mining operation (about 4 km south of study site), which was stockpiling the materials for tailings dam construction. We applied 2 L of deionized water to the half of the microcosm containing moist habitat. After water application, soil saturation was visibly evident (Fig. 3). Subsequent applications of water occurred at the 12 h observation to maintain moisture in the soil. We used plastic dividers to prevent moisture from seeping into the dry treatments, but we took care to ensure that there were no physical surface barriers for the metamorphs between the moist and dry halves. Following Baughman and Todd (2007), we used a fresh soil mixture in each trial. The soil mixture was sifted prior to being placed into the arena to ensure all large particles were removed. Light raking ensured an even surface prior to commencement of the trial. We placed pine cover boards (about 15 × 15 × 1 cm) in two of the four quadrants to create covered habitats (pine naturally occurs at the study site and we acquired cover boards locally). We raised

the boards about 2.5 cm above the soil with wooden sticks and positioned stones on top of the cover boards to ensure stability. During the trials, we covered each arena with a metal screen (about 1.5 × 0.8 cm mesh) fine enough to prevent predators from entering the pools and to prevent metamorphs from escaping, but coarse enough to prevent shading.

We sequentially rotated each arena 0°, 90°, 180°, and 270° at the start of each trial to avoid bias in directional orientation. Following Heinen (1993) and Baughman and Todd (2007), the rotation of the arenas also controlled for other possible stimuli in the surrounding environment (e.g., presence of a wetland, direction of the sun). To collect comparative soil temperatures, we buried two Maxim Integrated iButton Thermochron® temperature data loggers (Model DS1921G, San Jose, California, USA) 2.5 cm deep along the outside edge of each quadrant (Fig. 2, 3). These loggers recorded soil temperatures every 1 h over the 36-h time period. Data from the loggers allowed us to determine whether soil temperatures across the four treatment quadrants differed significantly and therefore possibly exerted an effect on the metamorphs.

Metamorph introduction.—The average size of the metamorphs used in this study at emergence from the water was 18.7 mm SVL ± 2.8 SD (n = 130) and 0.66 g ± 0.33 (n = 130). We fenced two natal ponds (about 2.5 km and about 900 m from microcosms) when tadpoles neared the later stages of metamorphosis to capture the spadefoots immediately upon emergence from the water. We hand captured metamorphs in the evening (about 2000) inside these fences less than 45 min before each series of trials was about to begin. We only selected individuals that had completely absorbed their tail into their body (i.e., Gosner stage 46; Gosner 1960) and that we observed to be physically able to move onto land. We transported animals to the arenas in small plastic containers. Once at the arenas, we weighed individuals (g) on a portable electronic scale (Model 1250BKEF, Salter Housewares Canada Inc., Burlington, Ontario, Canada), measured their snout-vent length (SVL), and tagged them on the right, hind foot using manual injection fluorescent yellow Visible Implant Elastomer (VIE; Northwest Marine Technology, Inc., Shaw Island, Washington, USA). We used the VIE marker to ensure individuals participated in only one trial and were not later recaptured from the natal pond and retested. Each trial consisted of 10 newly metamorphosed spadefoots being introduced into the center of each of the four microcosm arenas. Metamorphs were removed from the arenas and immediately released back into their original natal pond once each trial was complete.

Microhabitat analysis.—We conducted 13 trials (i.e., one set of 10 spadefoots in an enclosure = one trial), run in four batches (i.e., four arenas used simultaneously).



FIGURE 3. Photographs of artificial enclosures (i.e., microcosms) divided into four habitat types (e.g., dry-bare, dry-cover, moist-bare, moist-cover) to investigate microhabitat selection by newly metamorphosed Great Basin Spadefoots (*Spea intermontana*) in the Thompson River Valley, British Columbia, Canada. A natural spadefoot breeding pond is located within the fenced enclosure, adjacent to the microcosms. (Photographed by Janessa Ekman, left, and Jo-Anne Hales, right).

Each batch took place over two nights, spanning 36 h from start to finish. Prior to initial release into the arena, as per Baughman and Todd (2007), we placed the metamorphs on the central platform and covered them within the inner ring for 10 min, allowing time for the individuals to partially adjust to their surroundings. We then removed the inner ring and cover and visually monitored metamorphs until each had left the central platform and entered one of the four habitat quadrants, which was typically an immediate response. We recorded the location of each metamorph, according to quadrant association, at three time periods: At release, 12 h, and 36 h. At release was defined as the exact moment each individual left the inner ring and entered a quadrant. Our rationale for the later time periods was to provide ample time (including two night periods) for the metamorphs to explore, adjust, and choose a position within their new surroundings.

To determine locations of the metamorphs in the arenas at 12 h and 36 h, we removed the screen gently to prevent disturbance and we completed a visual inspection. When necessary, we briefly removed cover boards and counted the metamorphs. Once we accounted for all 10 individuals in each arena, we gently repositioned cover boards and screens. Extreme care was taken to acquire individual locations as quickly as possible with no disturbance to either the metamorph or the arena. We gently unearthed metamorphs if no sighting could be made but evidence of a burrow existed; we promptly re-covered these metamorphs with soil.

Statistical analysis.—We performed statistical analysis using R 3.2.5 (R Core Team, 2015). Prior to conducting analysis, the categorical variables were appropriately designated using the ordered (for ordered categorical [ordinal] variables, e.g., trial number, time period) and factor (for categorical [nominal] variables, e.g., direction, habitat-type) functions (Kabacoff 2011; Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J-S.S. White. 2011. GLMMs in action: gene-by-environment interaction in total fruit production of wild populations of *Arabidopsis thaliana*, revised version, part 1. Available from www.cell.com/cms/attachment/601623/4742452/mmc1.pdf [Accessed 1 December 2015]). We tested for correlation among our predictor variables (i.e., direction, cover type, soil temperature) by calculating a Generalized Variance Inflation Factor (GVIF) following Zuur et al. (2012) and Fox and Monette (1992). The GVIF measures how much the variance of a predictor is increased due to linear dependence with other predictors. As recommended by Zuur et al. (2010), we used a GVIF value of three as the pre-selected threshold (indicating no collinearity), versus the higher (and more flexible) value of ten used by Montgomery and Peck (1992).

We used Fisher's Exact Tests using the lattice package in R (Sarkar 2008) to explore if metamorphs exhibited equal preference for the four habitat types and directionality in each arena. The results indicated whether data within each batch of trials could be pooled for a robust analysis of metamorph microhabitat preference using

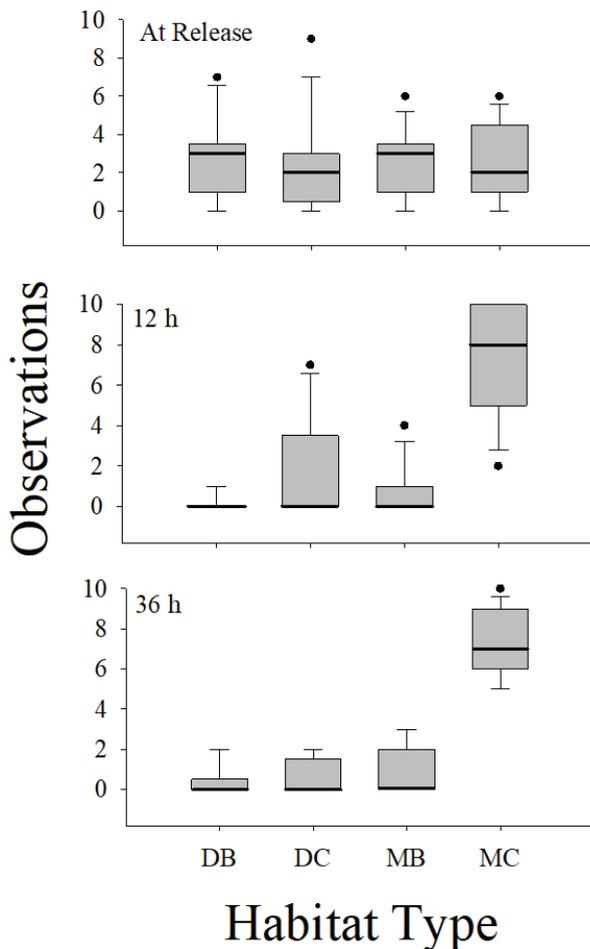


FIGURE 4. Observations of the number of metamorphic Great Basin Spadefoots (*Spea intermontana*; $n = 130$) in the four available habitat types in each arena: dry-bare (DB), dry-cover (DC), moist-bare (MB) and moist-cover (MC). The locations of the metamorphs were determined over three time periods: At Release, after 12 h, and after 36 h. A value of 7 means that seven of 10 spadefoots in a trial ($n = 10$ spadefoots per trial; $n = 13$ trials) selected the given habitat type. Closed circle = outliers, shaded box = interquartile range, dark horizontal bar = median, top horizontal bar = greatest value excluding outliers, and the bottom horizontal bar = least value excluding outliers.

Pearson’s Chi-squared Tests in the lattice package in R (Sarkar 2008). We analyzed the zero-inflated, grouped, non-normal count data with mixed effects using a zero-inflated Poisson (ZIP) Generalized Linear Mixed Model (GLMM; Bolker et al. 2013) to effectively predict metamorph microhabitat selection. The ZIP model accounted for the high number (38.5%) of true zeros in the count data (Lambert 1992; Zuur et al. 2009). We used the glmADMB package (Fournier et al. 2012; Skaug et al. 2015) with a loglink function to determine whether there was a relationship between the number of observations (i.e., number of metamorphs) within each quadrant for each trial and time period, and the three explanatory variables direction, habitat-type, and soil temperature. We attributed the random effects to our grouping (i.e., nesting) variables, time at 0 h, 12 h, 36 h and trial number 1,

TABLE 1. The mean soil temperature ($^{\circ}\text{C}$; \pm standard deviation) for each habitat type: dry-bare (DB), dry-cover (DC), moist-bare (MB) and moist-cover (MC), at three time periods at the study site in the Thompson River Valley, British Columbia, Canada: At release, at 12 h, and at 36 h. We used eight Maxim Integrated iButton Thermochron $\text{\textcircled{R}}$ temperature data loggers (Model DS1921G, San Jose, California, USA) to record soil temperature every hour within the artificial enclosures.

Time Period	DB	DC	MB	MC
At release	26.1 \pm 4.9	26.6 \pm 4.9	25.5 \pm 4.8	25.6 \pm 4.6
12 h	24.5 \pm 3.1	22.9 \pm 1.5	21.1 \pm 1.6	20.6 \pm 1.8
36 h	24.6 \pm 3.3	23.0 \pm 1.9	21.8 \pm 2.2	21.7 \pm 3.1

2, 3, 4. We completed the analysis by checking the data set for overdispersion (Crawley 2002; Zuur et al 2012).

RESULTS

In total, we collected data from 13 arena trials (in four batches) and 130 animals. The mean soil temperature collected from the data loggers ranged from $20.6^{\circ} \pm 1.8^{\circ}\text{C}$ and $26.6^{\circ} \pm 4.9^{\circ}\text{C}$ at three time periods (i.e., At release, 12 h, and 36 h) and four habitat types (i.e., moist-cover, dry-bare, dry-cover, and moist-bare; Table 1). A strong trend towards the increase in the selection of the moist-cover habitat quadrant was seen over the duration of the study (Fig. 4).

Data on microhabitat choice from the 13 trials could be pooled for both cover type (Fisher’s Exact Test, $P = 0.070$) and direction (Fisher’s Exact Test, $P = 0.070$). The GVIF values for direction, cover, and soil temperature were 1.02, 1.11, and 1.09 respectively. We frequently found metamorphs ($n = 130$) concentrated in the different quadrants, which in turn resulted in the majority of quadrant counts containing zero animals.

The resulting analysis of the pooled data indicated that metamorph habitat choice was dependent on cover type ($\chi^2 = 17.82$, $df = 9$, $P = 0.037$) but independent of the direction of the arena ($\chi^2 = 7.65$, $df = 9$, $P = 0.619$). At release, the percentages of metamorphs that dispersed into the moist-cover, dry-bare, dry-cover, and moist-bare habitats were 26%, 25%, 24%, and 25%, respectively. After 12 h, 75% of the metamorphs were located in moist-cover habitat. After 36 h, 79% of metamorphs were located in moist-cover habitat rather than dry-bare, dry-cover, or moist-bare habitats. Metamorphs strongly preferred moist-cover habitat type ($z = 6.24$, $P < 0.001$, $n = 130$). All other habitat types (i.e., dry-bare, dry-cover, moist-bare), direction, and soil temperature (recorded by data loggers) were not significant (all other P s > 0.190).

DISCUSSION

Previous laboratory experiments have shown that recently metamorphosed anurans prefer some type of vegetative cover over bare ground (not including moisture as a factor; Heinen 1993; Baughman and Todd 2007), but

this study demonstrates that newly metamorphosed Great Basin Spadefoots more specifically prefer moist microhabitats with cover. Although this response is intuitive for a metamorphic amphibian entering an arid terrestrial environment, this study is the first clear demonstration for such a preference within the metamorphic stage of the Great Basin Spadefoot. Whereas this work was performed in an arena, it seems likely that metamorphs emerging from water bodies would exhibit similar behavior in a natural setting. Observations in the field support this idea: we detected metamorphs taking refuge in visibly moist soil under plywood adjacent to an evaporating pond and within moist fissures at the edges of other ponds (Hales 2018). Our results parallel those of Weintraub (1980), who found recently metamorphosed New Mexico Spadefoot (*Scaphiopus multiplicatus*) individuals under boards, in shallow retreats, cow dung, or fissures caused by drying of pond edges during the daytime. Baughman and Todd (2007) found newly metamorphosed Eastern Spadefoots preferred habitat with forest litter (i.e., cover) in laboratory experiments in South Carolina. Walston and Mullin (2008) found that juvenile amphibians in Illinois, specifically the Small-mouthed Salamander (*Ambystoma texanum*), American Toad, and Wood Frog (*Rana sylvatica*), exhibited non-random orientation moving in the direction of forested habitat versus disturbed open areas with little canopy cover. Combined, these findings suggest that many, if not most, species of amphibians transitioning from an aquatic juvenile stage to one that uses drier upland habitat would preferentially seek out moist habitat with cover.

Garner (2012) studied upland habitat selection of Great Basin Spadefoots near their northern range limit (about 110 km northwest of the present study). Using telemetered adult animals, Garner (2012) found selection for daytime retreat sites that contained a relatively high proportion of bare ground. Superficially, this seems to suggest a very different pattern of habitat selection between adults and emerging newly metamorphosed Great Basin Spadefoots (i.e., habitat preferences might change or shift as the animals ages). The Garner (2012) study site, however, was situated within a cooler, moister ecosystem than the present study, suggesting the animals may have been more limited by heat and thus selected for bare (warmer) ground in which to bury. In 2014, average daily temperatures near the Garner (2012) study site in June, July, and August ranged from 3.9–17.9° C, 6.6–24.0° C, and 6.2–23.3° C, respectively (http://climate.weather.gc.ca/index_e.html#access). Total precipitation in June, July, and August was 36.5 mm, 49.7mm, and 17.4 mm, respectively (http://climate.weather.gc.ca/index_e.html#access). Further, the smaller surface area-to-volume ratio of adult animals may enable them to remain buried underground for long periods of time, retaining and/or absorbing soil moisture through their permeable skin (Ruibal et al. 1969). Metamorphs, being much smaller in size, likely have a lower tolerance for

dry conditions, and therefore have different habitat requirements. This study did not examine all factors (e.g., food availability, body condition) that could influence the terrestrial habitat choice of newly metamorphosed spadefoots, but it did determine that, given the conditions provided in the arena, moist habitat with cover is preferred directly following metamorphosis.

This work has important implications for the management of the Great Basin Spadefoot, particularly in the semi-arid grasslands of British Columbia. Given the results of this study and the Environment and Climate Change Canada (ECCC; 2017) recovery strategy, we recommend retaining or establishing breeding water bodies with natural or artificial cover material (e.g., plants, coarse woody debris, cover boards) situated along the immediate perimeter of the pond edge to provide shelter and moisture. Such conditions should increase the quality of suitable terrestrial microhabitats for vulnerable, newly metamorphosed spadefoots. The presence of cover features may be extended over larger areas surrounding water bodies to provide additional resources for both newly metamorphic and adult Great Basin Spadefoots as they disperse from the breeding pond (ECCC 2017; Hales 2018). Breeding ponds should be protected (e.g., fencing, enclosures) from sources of disturbance (e.g., cattle, development). Metamorph mortality caused by cattle disturbance (e.g., metamorphs trapped in hoof prints along pond edge) was observed by the author at Great Basin Spadefoot breeding ponds throughout the study. Livestock use of water bodies and riparian areas can also leave shorelines and neighboring habitat devoid of vegetation and other cover (Cragg 2007).

Technology (particularly telemetry) currently restricts our knowledge of upland habitat requirements for metamorphs of the Great Basin Spadefoot. Knowledge of the dispersal phase for these animals is particularly limited: the distance travelled from the breeding pond upon metamorphosis, daytime retreat site locations and types, and hibernation locations are virtually unknown for juvenile Great Basin Spadefoots. Inventive methods will need to be employed to collect these sorts of data. For example, Popescu and Hunter (2011) tracked movement and recorded habitat preferences of newly metamorphosed Wood Frogs using runway enclosures with pitfall traps and tracking stations. Similar methods may be needed to further our understanding of habitat requirements for spadefoots across all life-history stages.

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