Occupancy, Abundance, and Summer Ecology of the Western Tiger Salamander (*Ambystoma mavortium* Baird) in the Beaver Hills, Alberta

by

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Abstract

The western tiger salamander (*Ambystoma mavortium* Baird) is a 'species of special concern' in the Canadian prairie provinces. Potential declines caused by habitat loss and fragmentation, emergent diseases, and fish stocking are reasons cited for this species conservation status. However, little data exist about the ecology, distribution, and abundance of this species in Canada, where the species reaches the northern extent of its global range. In the Beaver Hills of Alberta, I examined occupancy, abundance, and summer habitat of the western tiger salamander. In 2013, I surveyed potential breeding ponds for salamander occurrence and abundance and characterized the distribution of populations in relation to terrestrial habitat variables with generalized linear regression. In 2014, I conducted season-long capture-mark-recapture (CMR) studies at three study sites to characterize seasonal activity patterns of adults and larvae and population sizes. I then compared CMR density estimates among sites to relative counts observed during my low-intensity survey method to determine if counts from low-intensity surveys suitably characterized salamander population densities among sites. In 2013 and 2014, I tested the effect of baited funnel traps on adult and larval capture success, as ambystomatid salamanders are difficult to detect. The distribution of salamander populations was significantly related to northern pocket gopher density (*Thomomys talpoides* Richardson) adjacent to wetlands, but not land cover composition. Density when present was not significantly related to any terrestrial habitat features. Counts (from low-intensity surveys) accurately characterized population density, although density estimates were very imprecise. Seasonal pond-use patterns indicate that post-metamorphic individuals remain in wetlands to forage after breeding, which is atypical among ambystomatid salamanders. Lastly, baiting funnel traps did not affect capture success of post-metamorphic individuals, but light-baited traps captured significantly more larval individuals than non-baited traps. The key findings of this study are that salamander populations likely depend on small mammal burrows to overwinter and that wetlands are important summer habitat for post-metamorphic individuals. Further, baited minnow traps differentially affect distinct life stages of western tiger salamanders, and likely other ambystomatid salamanders.

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Chapter 1: General Introduction

Context

The western tiger salamander (*Ambystoma mavortium* Baird) is federally designated "a species of special concern" in Alberta, Saskatchewan, and Manitoba (hereafter, the prairie provinces) because of habitat loss and fragmentation, emergent diseases, and in some cases, fish stocking (COSEWIC 2012). However, there is little evidence for actual declines in populations or in the number of individuals within populations. Like many other pond-breeding amphibians, ambystomatid salamanders require interconnected aquatic and terrestrial habitats with a few exceptions, as some species are permanently aquatic (Petranka 1998). Adults breed and lay eggs in aquatic habitat, usually fishless ponds and wetlands, then return to forage and overwinter in the terrestrial habitat adjacent to the breeding wetland. From the eggs, gilled larvae hatch and remain in wetlands until metamorphosis, after which they emerge as air-breathing, terrestrial individuals. A single wetland and the adjacent terrestrial habitat will typically support an entire population, which is defined as the breeding adults, non-breeding adults, terrestrial juveniles, and aquatic larvae inhabiting a wetland. Alteration or loss of terrestrial or aquatic habitat can disrupt life-cycle processes and result in the extirpation of populations, making ambystomatid salamanders and other pond-breeding amphibians particularly vulnerable to habitat loss and alteration (Harper et al. 2008).

Populations of the western tiger salamander in the prairie provinces are thought to be declining but the extent of declines is unknown because no distribution, abundance, or ecological data exist for these populations. Whether western tiger salamanders have suffered a decline in the area of their occupied range or suffered a decline in number of adult individuals per population is unknown but both would be particularly useful for determining the future status of the species within the Committee on the Status of Endangered Wildlife in Canada (hereafter, COSEWIC) framework. Habitat data for western tiger salamanders are lacking, in part, because the species was only recently recognized as distinct from the eastern tiger salamander (*A. tigrinum* Green) (Shaffer & McKnight 1996) and because the species is difficult to detect on land. Ambystomatid salamanders are not ideal candidates for transect counts, point counts, radio-telemetry, or other traditional terrestrial vertebrate sampling methods because of their small size (relative to other vertebrates), delicate skin, fossorial habits, and lack of vocalizations. To date, no surveys have been conducted in the prairie provinces to assess the extent and patterns of western tiger salamander distribution, and most aspects of their ecology have been gleaned from populations in the United States that often inhabit completely different ecosystems. However, distribution and abundance data, along with basic ecological data for prairie populations are necessary to guide future status assessments and potential management efforts.

The Beaver Hills/Cooking Lake Moraine, Alberta (hereafter, the Beaver Hills) is an ideal region to assess the distribution of western tiger salamander populations in relation to terrestrial habitat types and simultaneously provide baseline distribution and habitat data for a "species of special concern" that has never been systematically surveyed in the prairie provinces. The region contains thousands of potential breeding wetlands within a heterogeneous landscape, offering a unique opportunity to separate the influence of aquatic and terrestrial habitat characteristics on the species' distribution. The Beaver Hills lie along the northern edge of the western tiger salamander's global distribution. The vegetation in this area is classified as dry southern boreal mixed-wood forest, which is found nowhere in the species distribution outside of Canada. This transition zone between drier prairies to the south and the continuous boreal forests to the north is highly variable offering a mixture of forested and grassland environments for salamanders to choose from. The region also contains thousands of potentially suitable pothole wetlands that include known and possible salamander breeding sites.

Study organism

The western tiger salamander (Figure 1) is among the largest of all terrestrial salamanders in North America (Adult size: 7.6 – 16.5 cm, SVL). The species occurs from the Canadian prairie provinces southwards to the Mexican Plateau (including: Sonora, Chihuaha, Durango, Mexico State, and Nuevo Leon), and eastwards from Arizona to Oklahoma and southwestern Minnesota (Petranka 1998; Stebbins 2003). A disjunct group of populations occurs in the Columbia Basin of Washington, Oregon, Idaho, and south-central British Columbia. In the prairie provinces, western tiger salamanders are the only salamander present except for extreme western Alberta, where the easternmost populations of the long-toed salamander (*Ambystoma macrodactylum* Baird) overlap with those of western tiger salamanders along the eastern slopes of the Rocky Mountain foothills (Russell and Bauer 2000). The western tiger salamander was recently recognized as distinct from the eastern tiger salamander via molecular methods (Shaffer & McKnight 1996) and is comprised of four subspecies, two of which occur in Canada: the blotched tiger salamander (*A.m. melanostictum* Baird) (Alberta & southern Saskatchewan) and the gray tiger salamander (*A.m. diaboli* Dunn) (central Saskatchewan and Manitoba). Within the Beaver Hills, tiger salamanders occur alongside the boreal chorus frog (*Pseudacris maculata* Agassiz), the wood frog (*Lithobates sylvaticus* LeConte), the boreal toad (*Anaxyrus boreas* Baird and Girard), and occasionally, the Canadian toad (*Anaxyrus hemiophrys* Cope).

Thesis Outline

In the following three data chapters, I provide distribution, abundance, and basic ecological and natural history data for the western tiger salamander in the Beaver Hills, Alberta. Each chapter is presented as a stand-alone study, thus some figures and background information are repeated. In chapter 2, I examine the distribution and abundance of western tiger salamanders in relation to terrestrial habitat features. My primary questions were: (1) What terrestrial vegetation features characterize western tiger salamander habitat? (2) Do low-intensity survey counts suitably reflect density of pond-using individuals?, and (3) Can we estimate the number of populations (wetlands supporting salamanders) and the number of individual salamanders in the Beaver Hills? I addressed these questions by surveying 40 potential breeding wetlands and then relating occupancy and density of salamanders across wetlands to adjacent terrestrial habitat characteristics. I then compared survey counts to population density estimates based on capture-mark-recapture techniques and extrapolated occupancy and abundance patterns to available, appropriate wetlands across the Beaver Hills. I also evaluated the influence of imperfect detection on proposed occupancy patterns.

In Chapter 3, I examine the summer aquatic habitat-use of post-metamorphic salamanders following spring breeding efforts. My primary question was: Do seasonal pond-use patterns of post-metamorphic individuals reflect prolonged summer foraging in wetlands after breeding efforts? I addressed this question by characterizing adult and larval pond-use patterns and determining if adult pond-use patterns reflected foraging, as evidenced by weight gain in recaptured individuals. I also report demographic data for populations, such as sex ratios, evidence of sexual dimorphism, and juvenile productivity (juveniles per female), which are poorly known for the species in Canada.

In Chapter 4, I discuss the effect of baiting aquatic funnel traps on capture success of post-metamorphic and larval salamanders in wetlands. Post-metamorphic ambystomatid salamanders are notoriously cryptic and difficult to detect, thus many research efforts are a trade-off between monitoring few individuals across many sites or many individuals in a few sites (Semlitsch 1981; Trenham 2001; Steen et al. 2006; Searcy et al. 2013; Scott et al. 2013). Baiting has the potential to increase detections and sample size with minimal effort, allowing research efforts to potentially focus resources on sampling additional sites. My primary question was: Does baiting aquatic funnel traps increase capture success of salamanders? I addressed this question by comparing capture success of baited traps with non-baited traps for two baits anecdotally reported to attract salamanders.

My study provides important baseline data for western tiger salamander populations in the prairie provinces, which are currently lacking. These data will be useful for assessing future declines in distribution or abundance of the species. Further, these data provide region-specific life-history data that will be useful for potential management efforts and guidelines aimed towards conserving tiger salamander habitat in Canada.

Figure

Figure 1.1. a) A western tiger salamander (*Ambystoma mavortium*) post-metamorphic adult, and b) larva. Photos by Kyle Welsh.

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Chapter 2: Occupancy and Abundance of the Western Tiger Salamander (*Ambystoma mavortium* Baird) at the Northern Limit of its Distribution in North-Central Alberta

Introduction

The western tiger salamander (*Ambystoma mavortium* Baird) is federally designated "a species of special concern" in Alberta, Saskatchewan, and Manitoba (hereafter, the prairie provinces) because of concerns that habitat loss and fragmentation, emergent diseases (e.g. *Ambystoma tigrinum* virus and Chytrid fungus (Chytridiomycota)), and in some cases, fish stocking may be leading to declines (COSEWIC 2012). Declines however are only predicted and have not been verified because little data exist regarding the distribution and abundance of western tiger salamanders in these provinces. Degradation of upland (terrestrial) habitat is listed as a reason for decline in Canadian populations (COSEWIC 2012) but upland habitat has never been systematically described for Canadian boreal or prairie populations. The terrestrial habitat and distribution of western tiger salamanders needs further examination to identify potentially critical habitat elements for these populations and to provide baseline data to assess future trends.

Intensive small-scale studies of tiger salamanders and other ambystomatid species (mole salamanders) have demonstrated that terrestrial habitat for these salamanders is usually in the form of subterranean runways and tunnels of various small mammal species (*A. mavortium*: [Hamilton Jr. 1946; Lomolino & Smith 2003; Richardson et al. 2000; Shipley & Reading 2006; Vaughan 1961]; *A. tigrinum* Green & *californiense* Gray: [Loredo et al. 2006; Madison & Farrand 1998; Pittman 2005; Steen et al. 2006; Trenham 2001]; other species: [Faccio 2003; Graeter et al. 2008; Semlitsch 1981; Kleeberger & Werner 1983; Madison 1997; Johnston 2000]). However, the terrestrial ecology of ambystomatid salamanders also needs evaluation at a larger spatial scale in order to understand distribution patterns of multiple populations rather than individuals within a single population. I defined a single population as the group of breeding and non-breeding adult, juvenile, and larval salamanders inhabiting a single breeding wetland and adjacent upland habitat. Many pond-breeding amphibian populations exist within highly variable metapopulations within which frequent extinction and recolonization of single populations and associated breeding sites is natural (see Smith & Green [2005] for a review). Therefore, caution is warranted when scaling highly variable small-scale and single-population patterns up to a landscape level that encompasses many populations (Petranka et al. 2004).

The western tiger salamander, like other tiger salamanders, is generally considered a ‘grassland’ species (Petranka 1998). This relationship is evident in much of the prairie provinces where the species occurs in short-grass and mixed-grass prairie ecosystems (COSEWIC 2012). Other Canadian populations occur in a region characterized by Great Basin shrub-steppe grasslands (bunchgrass-sagebrush) in south-central British Columbia. However, some populations in the prairie provinces occur in aspen parkland and dry southern boreal mixedwood forest matrices that have vegetation characteristic of the transition zone between the prairies to the south and continuous boreal forests to the north. This transition zone is a heterogeneous landscape with elements of native prairie grassland, cattle pasture, and agriculture embedded within a largely forested matrix (see ‘Study Area’ for details).

The distribution of western tiger salamander populations within this transition zone might be limited by the availability of grassland patches. However, terrestrial vegetation composition might not significantly influence the distribution of populations in this region, as the species occurs in a wide variety of ecosystems other than grasslands throughout their continental range including deserts and alpine conifer forests (Petranka 1998; Stebbins 2003). Gray et al. (2004) demonstrated that agricultural development adjacent to breeding ponds did not significantly influence western tiger salamander occupancy of wetlands in Texas (*A. tigrinum* at the time of publication), suggesting that western tiger salamander choice of terrestrial vegetation may be flexible if adjacent to wetlands that are suitable for breeding. However, the likelihood of western tiger salamander presence in a wetland increased with distance from forests in Wyoming (Bartelt et al. 2011), suggesting that the species prefers specific vegetation types near wetlands, likely in the form of grasslands. Inferences from related species are inconsistent, as California tiger salamanders (*A. californiense*) are strongly tied to grassland ecosystems (Trenham 2001; Orloff 2011; Searcy et al. 2013) while eastern tiger salamander (*A. tigrinum*) distribution is not significantly related to any specific type of terrestrial vegetation (Brodman 2010; Herwig et al. 2013; Knutson et al. 2004). To my knowledge, no studies have examined the distribution of western tiger salamander populations in boreal/prairie Canada, particularly where terrestrial vegetation is highly variable within the transition zone between the northern prairies and southern boreal mixedwood forest.

The Beaver Hills, Alberta, (Figure 2.1) lie within a disjunct patch of dry southern boreal mixedwood forest and is an ideal location to examine the distribution of western tiger salamanders within the prairie/boreal transition zone because the effect of terrestrial habitat on the distribution of populations can be isolated from that of aquatic habitat. Much of the existing literature on tiger salamander distributions, and that of other ambystomatid salamanders, focuses on aquatic habitat characteristics rather than terrestrial characteristics. This research has repeatedly demonstrated the importance of fishless water bodies with long hydro-periods as a factor influencing ambystomatid occupancy and abundance patterns (Cosentino et al. 2011; Drake et al. 2014; Goldberg & Waits 2009; Herwig et al. 2013; Maurer et al. 2014; Semlitsch et al. 2015). The Beaver Hills lie within the prairie pothole region and harbor numerous permanent and semi-permanent wetlands with a sufficiently long hydro-period for larval salamander development (n= 3,057 wetlands (apprx.)). These wetlands are typically fishless (excluding some larger lakes), likely because of poor connectivity and frequent winter hypoxia (Cosentino et al. 2011; Peterka 1989). Salinity can be highly variable among wetlands in the Beaver Hills and ranges from 16-899 µS (Nicholson 1995). However, Klaver et al. (2013) found that salinity did not significantly influence western tiger salamander occupancy of wetlands in Wyoming, where available wetlands showed a greater range in salinity (10-1,300 µS) than is found in the Beaver Hills. Among the pothole wetlands in the Beaver Hills, those that are semi-permanent or permanent and lack fish populations should provide suitable breeding habitat for the species, presumably when adjacent to suitable terrestrial habitat. Given the high abundance of potential aquatic habitat, the distribution of these northern peripheral populations might be disproportionately driven by the availability of winter refugia. This relationship would be expected of ectothermic tetrapods living in an area at the edge of its physiological limitations versus southern populations near the species' core range (Mitcheletti & Storfer 2015; Soule 1973). This study provides much needed evaluation of the importance of specific terrestrial habitat features for western tiger salamanders, and the influence of terrestrial habitat on the distribution and abundance of ambystomatid salamander populations while controlling for aquatic habitat quality.

Studies across a spatial extent that encompasses multiple populations rely on the fundamental assumption that the observed relative abundance and occurrence of organisms accurately reflect the true occupancy and relative abundance across the region of interest (Smith & Petranka 2000; Houze & Chandler 2002). For practicality, large-scale studies typically use short-term or low intensity sampling methods at multiple sites rather than intensive sampling at only a few sites (Goldberg & Waits 2009; Herwig et al. 2013; Jacobs & Houlahan 2011). The relationship between short-term catches and actual population densities is seldom validated in amphibian studies (Dodd & Dorazio 2004). More work is needed that validates the accuracy of low-intensity sampling methods relative to fully enumerated amphibian populations or intensive Capture-Mark-Recapture (CMR) studies that more accurately estimate population size and density. Low intensity survey counts that accurately characterize density and/or abundance will be useful for long-term and large-scale monitoring efforts and distribution studies because they require less effort and resources at each site.

The objectives of my study were (1) characterize the occurrence and abundance of western tiger salamanders in the Beaver Hills in relation to terrestrial habitat features in 2013, (2) compare relative density (catch per unit effort (CPUE)) of salamanders from the 2013 survey to rigorous capture-mark-recapture (CMR) population estimates in 2014, and (3) use occurrence and abundance data from objectives 1 & 2 to estimate the number of populations and the number of post-metamorphic individuals in the Beaver Hills.

I addressed the first objective by sampling potentially suitable breeding ponds with highly variable terrestrial habitat composition in 2013 and relating salamander occurrence and density at a wetland to adjacent terrestrial habitat variables with generalized linear regression. I predicted that salamander presence and density would be negatively related to the proportion of forested habitat because tiger salamanders are commonly characterized as 'grassland species' (Petranka 1998), because other Canadian populations in British Columbia occur in a semi-arid grassland system (COSEWIC 2012), and because the likelihood of western tiger salamanders' occupancy of wetlands in Wyoming was significantly positively related to distance from forests (Bartelt et al. 2011). I addressed the second objective by conducting a season-long CMR study in 2014 at a subset of study sites where salamanders occurred in 2013 to estimate true density, then compared this estimate to densities (CPUE) among the same sites surveyed in 2013. I predicted that salamander counts derived from low-intensity surveys in 2013 would reflect true differences in salamander population density, as estimated with CMR methods. Lastly, I addressed the third objective by extrapolating 2014 CMR population size and density estimates to wetlands across the study area based on estimated occupancy patterns observed in 2013. Information on distribution, abundance, and terrestrial habitat preferences of the western tiger salamander is important for future status assessments (e.g. COSEWIC), where the decline in area occupied by a species or a decline in the number of individuals are often the key criteria for determining conservation status.

Study area

The Beaver Hills/Cooking Lake moraine (Figure 2.1) encompasses 1572 km^2 and lies directly east of Edmonton, Alberta, Canada. The area is along the northern edge of the prairie pothole region and contains thousands of pothole wetlands and larger shallow lakes (n=3,057; Natural Resources Canada 2007) that range in size from 0.006 to 2,749 ha. The moraine rises over 790 m above the surrounding aspen parkland and supports a patch of dry southern boreal mixed-wood forest. Dry southern boreal mixed-wood forests experience cooler average annual temperatures (1.1 degree Celsius) and higher average annual rainfall (461 mm) than the surrounding aspen parkland and prairie plateau (Natural Regions Committee 2006). The terrestrial landscape is heterogeneous and includes natural grassland, shrubland, agriculture, and grazing land within a forested matrix. Forests are predominately deciduous poplar species (*Populus tremuloides* Michx. and *Populus balsamifera* L.) interspersed with spruce (*Picea mariana* [Mill.] Britton, Sterns & Poggenb. and *Picea glauca* [Moench] Voss (Natural Regions Committee 2006). The dominant understory is beaked hazel (*Corylus cornuta* Marshall), low-bush cranberry (*Viburnum edule* Michx.), and Saskatoon (*Amelanchier alnifolia* Nutt). Native grasslands are fescue prairie (*Festuca* L. spp.). Open shrublands are dominated by willow (*Salix* L. spp.) and rose (*Rosa* L. spp.). The primary crops in cultivated areas include forage crops and grains, specifically barley, legumes, and canola. Poor soil and climate conditions have limited the extent of agricultural development to only 24% of the moraine proper, with the remainder comprised of 45% forests, 27% grassland/grazing land, and 4% urban development. Greater than 22% of the natural and grazing land is protected within parks: Elk Island National Park, Cooking Lake-Blackfoot Provincial Park and Recreation Area, Ministik Bird Sanctuary, and Miquelon Lakes Provincial Park.

Methods – Distribution and Density Survey

Site Selection and Terrestrial Habitat Variables

Each study site was a single wetland and the adjacent terrestrial habitat within 200 metres of the wetland's edge, which represented the area estimated to encompass an entire salamander population (Figure 2). Terrestrial habitat was defined as the adjacent upland habitat within 200 m of the water's edge, as this area likely encompasses the upland foraging and overwintering habitat of most breeding individuals within a population of pond-breeding amphibians, including ambystomatid salamanders (Brodman 2010; Porej et al. 2004; Semlitsch 1998). Sites with overlapping terrestrial habitat were not sampled. Habitat within each 200 m terrestrial zone was classified by percent land cover in ArcGIS10.1 (data source: Agriculture and Agri-foods Canada 2012). Study sites were selected to maximize heterogeneity in terrestrial habitat and to minimize heterogeneity in wetland hydro-period and size. Wetlands in the study area were stratified to semi-permanent and permanent wetlands (Zoltai & Vitt 1995) less than or equal to 7 ha in size. A wetland's permanence was assessed with aerial imagery or a site was included if on the first visit most of the wetland area was open water ringed by cattails (*Typha* L. spp.). A size limit of 7 ha was chosen based on the range of previously known western tiger salamander breeding wetlands (n=14) in the study area, which ranged from 0.282 to 12.637 ha (incidental observations from previous students, Paszkowski lab). Study sites were randomly selected from available wetlands with adjacent land cover composition greater than 90% forest and/or open grassland habitat. Sites with rare (e.g. barren rock) and anthropogenic adjacent land cover (e.g. urban development, etc.) were excluded to minimize the number of variables used in analysis. Forested land cover was defined as deciduous, coniferous, and mixed forest stands. Open land cover was defined as native grassland, shrubland, and pasture used for cattle grazing. Forested lands cleared for grazing were the only anthropogenic land cover included within this study because they resembled and were often visually indistinguishable from natural grasslands, and likely provide similar habitat for salamanders. Forty wetlands were randomly selected from the available in ArcGIS along a gradient of land cover composition ranging from 3 to 99 % forest (Figure 3). Average wetland size was 1.26 ha and ranged from 0.04 to 6.09 ha.

Northern Pocket Gopher Activity Surveys

Northern pocket gopher (*Thomomys talpoides* Richardson) activity was also characterized as salamander habitat and was defined as the density of tunnel excavation mounds per ha within 30 m of the wetland edge. Excavation mounds of pocket gophers are indicative of their extensive subterranean tunnel systems and were used to represent the subterranean small-mammal burrow networks available to salamanders. Western tiger salamanders are known to use these burrows, likely to forage, overwinter, and/or avoid desiccation (Hamilton Jr. 1946; Lomolino & Smith 2003; Richardson et al. 2000; Shipley & Reading 2006; Vaughan 1961). Terrestrial juveniles and adults were observed in the excavation mounds themselves (personal observations).

Total mound counts were conducted once at each site in 2014. Multiple mounds were considered distinct if separated by undisturbed ground, with distinct mounds sometimes separated by less than 20 cm (approx.). Time constraints limited mound count efforts to within 30 m of the water's edge. Pocket gopher excavation mounds were selected as a metric for burrowing mammal tunnel networks because they are large, conspicuous, and strongly correlated with subterranean tunnel density (Pearson r = 0.72, data not shown). Other larger burrowing mammals present on the landscape were Richardson's ground squirrel (*Urocitellus richardsonii* Sabine) and American badger (*Taxidea taxus* Schreber), neither of which was encountered at study sites in 2013 or 2014. Burrow networks created by smaller tunneling mammals (family: Cricetidae (Fischer)) were not surveyed because they were difficult to detect in dense summer growth across large areas, although ambystomatid salamanders have been documented using them (Faccio 2003; Graeter et al. 2008; Semlitsch 1981; Kleeberger & Werner 1983; Madison 1997; Johnston 2000).

Aquatic Sampling for Salamanders

Each of the 40 wetlands was sampled for salamanders in May, June, and July 2013 with aquatic drift fences and minnow trap arrays. This sampling period reflects peak salamander activity in the Beaver Hills when adults, larvae, or both are using aquatic habitats. Sites were sampled three times (once each month) to increase detection probability. Trapping began when pond ice receded enough to place traps in water during the first week of May. An array consisting of 10 Gee minnow traps (length = 42 cm, diameter = 22.9 cm, mesh size = 6.35 mm) and a single, larger modified minnow trap (height = 76.2 cm, width = 45.7 cm, depth = 50.8 cm, mesh size = 6.35 mm) (Figure 4) placed along an aquatic drift fence (synthetic fiber silt fence, height = 0.9 m, length

= 10 m) was placed in the wetland during each trapping event. The drift fence was positioned perpendicular to the shoreline in shallow water with the modified trap set at the deepest end and two Gee traps fastened horizontally along either side of the fence (Figure 5). The shoreline location for trap placement was selected randomly and changed with each visit. The remaining six Gee traps were spread evenly around the pond margin and attached to stakes in shallow water with airspace in the top of the traps. Traps were placed among emergent vegetation (*Typha* spp.) when possible. The design of the modified minnow trap and aquatic drift fence allowed sampling of the entire water column at depths up to 30 cm while maintaining airspace for captured salamanders and air breathing by-catch animals (muskrats, ducks, gartersnakes, etc.). Traps were set in the afternoon and checked the following morning. Trapping effort was constant among sites and captures reflected catch per unit effort (CPUE), a measure of density, with the area being defined as the wetland area in each pond that was effectively sampled with this trapping array. Individual salamanders were classified as adults or larvae based on the presence or absence of external gills.

Terrestrial Sampling for Salamanders

In 2014, all study sites (n=40) were revisited and sampled for terrestrial salamander activity in northern pocket gopher excavation mounds. Each site was visited once during June or July and all excavation mounds within 30 m of the pond margin were raked to find terrestrial salamanders. Excavation mounds were thoroughly combed with a potato rake to uncover salamanders hiding within the mounds. This method was selected because five individuals were found in four separate pocket gopher mounds in September 2013 adjacent to wetlands inhabited by western tiger salamanders (personal observation). Gee minnow traps (n=15; see ‘Aquatic Sampling for Salamanders’ for trap dimensions) were set in subterranean foraging tunnels to trap salamanders (Figure 6) at sites with salamander populations. Traps were covered with sod and soil after placement to prevent light penetration into the tunnels. These horizontal tunnels were approximately 10 - 20 cm deep. Traps within tunnels were set continuously for anywhere between 1 and 10 nights between 20 May and 15 August (96 trapping days) and were checked for salamanders in the morning and then moved to new tunnels. In September 2014, terrestrial surveys were conducted at three sites (GS, S1, S3) using a homemade portable PIT-tag scanning unit (max detection depth in soil: 74 cm) (Atkinson-Adams 2015) to detect pit-tagged individuals (see 'CMR methods' for marking details). Each of the three sites was surveyed twice for PIT-tagged individuals by walking in a zigzag pattern through the upland habitat within 200 m of the wetland edge with the portable scanning unit. All available terrestrial habitats were surveyed proportionally during surveys for marked individuals. Survey effort was increased immediately adjacent to points where salamanders were detected. Detected salamanders were excavated upon detection.

Statistical Analysis - Generalized Linear Regression

Salamander detection (presence/absence) and density when present (counts) for 2013 were modeled as a function of terrestrial habitat variables with generalized linear regression (program R). Salamander detection was defined as the presence of post-metamorphic individuals (hereafter, adults) and/or larvae during the sampling season. The presence of eggs was disregarded for analysis because eggs were only detected twice and at sites where larvae and adults were also detected. Salamander density when present was defined as the season's total CPUE of adults when present (counts). I used Firth's penalized maximum-likelihood logistic regression for presence/absence models because it is suitable for small sample sizes and is robust to model fitting errors associated with data separation (Albert & Anderson 1984; Heinze & Schemper 2002). Data separation occurred when one highly predictive variable prevented model convergence by completely separating the response variable and thus prevented the creation of a descriptive model for the data. Salamander density when present was modeled with zero-truncated negative binomial regression. Three candidate models with different combinations of the two habitat variables ((1) land cover; (2) pocket gopher density; (3) land cover + pocket gopher density) were fitted to presence/absence and count data and then assessed for model fit with a likelihood ratio test (LRT), where models were considered a good fit if they explained significantly more variation than a model with no environmental covariates at alpha = 0.05. Percent forest was selected as the land cover variable for use in each model and was strongly negatively correlated with percent open habitat within the 200 m buffer (Pearson r = -0.94). Other land cover categories (excluded from analysis) were temporary wetlands. Preliminary analysis using percent open habitat as the land cover variable in place of percent forest had consistent and complementary results. Missing northern pocket gopher data for two sites were estimated with Bayesian multiple imputation (package 'Amelia', statistical program R) after preliminary analysis revealed no difference in results with different imputation methods or record removal.

Statistical Analysis - Occupancy Models

Western tiger salamander detection (presence/absence) was also modeled with terrestrial habitat variables using single-season occupancy models in program PRESENCE to account for potential bias resulting from imperfect detectability. Species detection during a survey is a product of the species being present (occupancy = ψ) and being detectable by the investigator (detectability = p). Failure to detect a species when it is present can bias or underestimate occupancy by organisms with detectability less than one, like salamanders (MacKenzie et al. 2002). PRESENCE provides a framework to more accurately estimate species occupancy at a site by using temporally replicated site surveys to separate the effect of imperfect detectability from detection. Occupancy was modeled with terrestrial habitat variables and detectability was modeled with larval presence/absence, as overall salamander detection likely increased among surveys when larvae were present in the pond (July) compared to detectability during surveys when only post-metamorphic individuals were present (May and June). The 'larval presence/absence variable' was characterized by dividing the sampling period into a binary variable based on the time period that larvae were in the pond (July) or were not yet detected (May-

June). Three candidate models with site (ψ) and survey (p) predictor variables, and one without, were fitted to the data and ranked with AIC. The saturated model containing all predictor variables was assessed for goodness of fit (GOF) with a Pearson's chi-square test and a parametric bootstrap procedure (MacKenzie & Bailey 2004). The coefficient standard errors (S.E.) were adjusted in all candidate models for overdispersion (c-hat = 1.27) with the following equation:

$$\text{S.E.}_{\text{adj}} = \text{S.E.} * \sqrt{\text{c-hat}}.$$

Models were then ranked by QAIC to account for overdispersion:

$$\text{QAIC} = (-2\text{loglik}/\text{c-hat}) + k$$

where loglik is the maximized log-likelihood and k is the number of parameters, including c-hat (Burnham & Anderson 2002). The best model was selected as that with the lowest QAIC and site variables interpreted as significant at alpha = 0.05. Any model < Δ2 QAIC of the best model was deemed plausible and also interpreted (Burnham & Anderson 2002).

Methods – Capture Mark Recapture (CMR)

CMR Study Site Descriptions

Sites GS, S1, and S3 were chosen for CMR analysis in 2014 from among the 20 wetlands where western tiger salamanders were detected in 2013. These sites were selected because they had variable population densities (S1: 1 adult; GS: 10 adults; S3: 20 adults, Table 1) in 2013 surveys (hereafter, 2013 coarse relative abundance estimates). Sites S1 and S3 were natural pothole wetlands and site GS was a naturalized, flooded gravel pit. All wetlands were fishless and the adjacent land cover was natural or grazed, as defined by land cover without anthropogenic or agricultural development (cropland). As with sites selected for 2013 surveys, upland habitat converted to cattle pasture was grouped with natural grasslands because they were visually indistinguishable from each other and both natural grassland and cleared forest stands are typically used for grazing in this region. All three sites held water for the entirety of 2013 and 2014, although site S3 retracted considerably in 2013 (apprx. 80%) and likely experiences years where it dries completely by fall. Sites S1 and S3 had extensive areas of emergent vegetation (*Typha* spp.) along the entire pond margin and site GS had minimal emergent vegetation that was concentrated along the northern edge of the pond margin. Aquatic productivity was measured in September 2013 as total nitrogen (N µg/L) and total phosphorus (P µg/L). Total nitrogen for sites GS, S1, and S3 were 580 µg/L, 2,004 µg/L, and 6,720 µg/L, respectively. Total phosphorus for sites GS, S1, and S3 were 11 µg/L, 32 µg/L, and 626 µg/L, respectively.

Sampling Design

In 2014, trap arrays were deployed continuously at sites GS, S1, and S3 from 15 May to 23 July and checked every 1-2 days for a total of 44 sampling events. The sampling period reflects the time period during which post-metamorphic salamanders were found using aquatic habitat in 2013 but truncated to reduce bias from non-random en mass salamander movements to and from the sampling area, specifically during spring breeding migrations and larval dispersal and recruitment in the fall. Trapping effort was scaled for pond size by placing Gee minnow traps evenly along the shoreline in 30 m intervals. Newly captured individuals were surgically implanted with unique passive integrated transponder tags (PIT-tags) before release and recaptured individuals were identified at each trapping event. Individual capture probability was assumed to be constant between samplings. The population size of adult salamanders was estimated for each site using Full-likelihood Closed models with equal individual encounter (p) and recapture (c) probability in program MARK. Although a completely closed system is not realistic for most wild systems, closed models should be suitable for ambystomatid salamanders because populations are typically characterized by very low immigration and emigration, owing to high site fidelity of individuals to their natal ponds, excluding the dispersal of young of year individuals (Gamble et al. 2007). Because the sampling period does not overlap with breeding movements or larval recruitment and dispersal, any salamander movement to or from the sampling area within the sampling period was assumed to be random foraging behavior. Deaths were a possibility and were considered random. Population estimates pertain to the population of pond-using individuals plus non-breeders within the population that did not enter the pond. This definition of population is synonymous with 'population' as defined elsewhere in this document. Further, this definition of population is synonymous with the 'superpopulation' defined by Kendall (1999), which is robust to violations in model closure assumptions. Because not all adults migrate to breeding wetlands each year (Semlitsch 1983), this definition of population should better characterize the group of individuals inhabiting a single breeding wetland and the adjacent terrestrial habitat.

Population estimates were standardized by wetland area to estimate the density of salamanders at each site because there is some evidence to suggest that wetland size influences density of pond-breeding amphibians (Semlitsch et al. 2015). Densities were compared qualitatively among the three sites with 2013 counts and 2014 CMR estimates to determine if 2013 counts reflected actual densities, thus validating the use of CPUE generated from low intensity sampling designs as representative of sampled populations.

Methods – Occurrence and Abundance Estimates for Entire Study Area

The minimum number of wetlands occupied by western tiger salamanders in the Beaver Hills was estimated by applying the 95% confidence interval of the site occupancy estimate (ψ) in the best occupancy model to the total number of available wetlands within the study area. Available wetlands were stratified to the criteria for sampled wetlands and were those with areas less than 7 ha and with greater than 90% forested and/or open adjacent land cover within 200 m of the wetland edge (n = 1,137).

The minimum number of adult western tiger salamanders in the Beaver Hills was estimated via 4 methods: (1) extrapolating the minimum population size of the smallest population among the three CMR study sites (lower 95% CI) to the estimated number of occupied wetlands, (2) extrapolating the average minimum population size (lower 95% CI) among the three CMR study sites to the estimated number of occupied wetlands, (3) extrapolating the minimum density of the least dense study site among the three CMR sites to the estimated area of occupied wetlands, and (4) extrapolating the average minimum density among the three CMR study sites to the area of occupied wetlands. Methods 3 and 4 were used to account for variation in wetland size.

Results - Distribution and Density Survey

Northern Pocket Gopher Activity Surveys

Northern pocket gopher mounds were detected at 45% of sites (n=18) with an average density of 600 mounds/ha, ranging from 30 to 4,300 mounds/ha (Table 1). The high densities observed at some sites (see P16, GS, and P6) were likely a reflection of the relatively limited suitable habitat that was heavily used by pocket gophers at those particular sites, and is probably not realistic of actual pocket gopher abundance at those sites (Smallwood & Morrison 1999). Mounds were typically in open habitat or along the ecotone between open and forested habitats. No pocket gopher mounds were detected in forested habitat. However, pocket gopher mound density within 30 m of the wetland edge was not strongly correlated with land cover (percent forest) within 200 m of the wetland edge (Pearson's r = -0.32). To avoid a potentially significant relationship driven by a few high values, pocket gopher density data were transformed (ln+1) during preliminary analysis and also modeled as binary presence/absence when regressed against salamander detection and abundance. Pocket gopher data were then modeled as raw abundance of mounds during preliminary analysis to account for misrepresentative values derived from scaling counts for density, but this did not significantly influence model results. Therefore, non-transformed pocket gopher density data were used for analysis because transformations did not significantly change relationships or interpretations.

Aquatic Sampling for Salamanders

Salamanders were detected at 50% of sites for all three months combined, with detection at 20%, 28%, and 40% of sites in May, June and July, respectively. Eighteen percent, 27%, and 55% of individuals were captured in May, June, and July, respectively. All larvae were caught in July and represented 29% of monthly captures and 16% of total captures (Table 1). Both larvae and adults were captured at 12.5% of the sites, adults only at 32.5%, and larvae only at 5%. Ninety-four percent of all salamanders were captured in modified traps or Gee traps along the aquatic drift fence and the remaining 6% were captured in "satellite" Gee traps without a drift fence.

Terrestrial Sampling for Salamanders

A total of 2,687 pocket gopher excavation mounds were raked in June and July 2014 at sites occupied by pocket gophers (Table 1) and no salamanders were found. No vertebrates were found in mounds except for a single wood frog (*Lithobates sylvaticus* LeConte) that was found in an excavation mound less than 2 m from the water's edge at site GS. Traps placed inside tunnels were mostly ineffective for trapping salamanders because pocket gophers quickly plugged trap entrances, which likely prevented salamanders from entering. Every trap was completely plugged on both sides at every trapping event, regardless of the amount of time a trap was open. However, one juvenile salamander was captured in a subterranean funnel trap at site S1 on 5 June, at a distance of 21 m from the wetland edge. Of the 112 PIT-tagged individuals, nine individuals were detected during terrestrial surveys with PIT-telemetry. Of those nine, three detections were PIT-tags without dead or living salamanders. These tags could have been rejected implants encysted and pushed out by the salamander or remnants after the salamanders had died and/or completely decayed or predated upon. Two detections were dead and decayed salamander carcasses, and one was a dead recently metamorphosed individual with partially receded gills. The remaining three individuals were live salamanders (two young of year, one adult). All nine individuals detected with PIT-telemetry were found underground in or immediately adjacent to pocket gopher tunnels or excavation mounds. No salamanders were detected in forested areas. Several mounds were haphazardly raked at site S3 in September 2014 and three young-of- year western tiger salamanders were found.

Statistical Analysis: Generalized Linear Regression

Salamander detection (presence/absence) and density (when present) were not significantly related to adjacent land-cover composition in any suitable model (Table 2.2). Firth's logistic regression indicated that salamander detection was influenced by pocket gopher density adjacent to wetlands and this terrestrial variable was the only significant factor in either of the two presence/absence models that provided reasonable model fit (Table 2.2). In contrast, generalized linear regression of count data indicated that pocket gopher density did not explain salamander density, and no terrestrial habitat model described these count data accurately.

Statistical Analysis: Occupancy Models

Occupancy analysis results were consistent with those of generalized linear regression, as the best models indicated that salamander occupancy was not significantly influenced by adjacent land cover, but was significantly related to pocket gopher density within 30 m of the wetland edge (Table 2.3). The best models also indicated that the likelihood of salamander detection increased significantly in July when catchable larvae were present in the wetland (Table 2.3). Imperfect and variable detectability did not significantly influence the relationship between site occupancy and adjacent terrestrial habitat.

Capture-Mark-Recapture

In 2014, 112 individuals were captured and marked across the three study sites, and 52 salamanders were recaptured for a total of 103 recapture events. Fifteen individuals were captured and eight recaptured at site GS. Forty-four individuals were captured and 10 recaptured at site S1. Fifty-three individuals were captured and 34 recaptured at site S3. From lowest to highest, the population size estimates were: site GS = 16 (16-28), site S3 = 58 (54-68), and site S1 = 122 (79-218). Also from lowest to highest, population densities (post-metamorphic individuals/ha) were: site S1 = 53 (34-94), site GS = 114 (114-200), and site S3 = 138 (129-162).

Occurrence and Abundance Estimates for Entire Study Area

The best occupancy model for describing salamander occurrence was not selected as the most suitable for predicting the minimum number of occupied wetlands within the study area because data for the site variable that significantly explained salamander occurrence (pocket gopher density) were unavailable for non-surveyed wetlands. The occupancy model with no terrestrial habitat variables and with larval presence/absence as the detectability variable was therefore selected as the most suitable model because it provided an estimate for the proportion of occupied wetlands after accounting for changing detectability, which increased the occupancy estimate to 0.55 (0.37-0.71, 95% CI) from the naïve estimate of 0.50. The total number of semi-permanent and permanent wetlands with an area < 7 ha and with > 90% adjacent forest/open habitat in the Beaver Hills was 1,137, therefore the estimated number of wetlands occupied by western tiger salamanders in the Beaver Hills was 625 (420 – 811, 95% CI).

The minimum population size of post-metamorphic western tiger salamanders among sites was 16 individuals at site GS, as predicted by the lower 95% confidence interval of the population size estimate. The average minimum population size among the three sites, as predicted by the lower 95% confidence intervals (CI), was 50 individuals. The minimum density and average minimum density among the three sites, as predicted by the lower 95% CI for the population size estimates, was 34 salamanders/ha (site S1) and 91 salamanders/ha, respectively. The total combined area of suitable wetlands was 24,336.82 ha and the proportion of wetland area occupied by salamanders was estimated as 9,004.62 – 17,279.14 ha. The minimum number of post-metamorphic individuals as estimated by each method were: (1) 10,000 (6,720-12,976), (2) 31,250 (21,000-40,550), (3) 306,157-587,491, and (4) 819,420-1,572,401 (Table 4).

Discussion

The distribution of western tiger salamander populations in the Beaver Hills was significantly influenced by the density of northern pocket gopher excavation mounds adjacent to breeding wetlands but was not significantly influenced by the composition of adjacent land cover. However, neither pocket gopher activity nor adjacent land cover explained salamander density at breeding wetlands. The positive relationship between western tiger salamander presence and northern pocket gopher activity in north-central Alberta was not surprising given the extensive evidence demonstrating the use of mammal burrows by ambystomatid salamanders (see Hamilton Jr. 1946; Lomolino & Smith 2003; Richardson et al. 2000; Shipley & Reading 2006; Vaughan 1961; Loredo et al. 1996; Madison & Farrand 1998; Pittman 2005; Steen et al. 2006; Trenham 2001; Faccio 2003; Graeter et al. 2008; Semlitsch 1981; Madison 1997; Johnston 2000). In total, all 18 salamanders encountered in terrestrial habitat were found in or immediately adjacent to northern pocket gopher activity. Unmarked juvenile and adult western tiger salamanders (n = 8) were found in pocket gopher excavation mounds during the fall of 2013 and 2014. Additionally, each of the nine PIT-tagged individuals that were detected in September 2014 with PIT-telemetry was found underground directly under or within one meter of northern pocket gopher burrow entrances and excavation mounds. A single individual was captured in a minnow trap that was buried in a pocket gopher tunnel. These observations, combined with the significant positive relationship between salamander distribution and pocket gopher density suggest that western tiger salamanders in prairie provinces and elsewhere in Canada are using habitats created by northern pocket gophers and that this habitat feature might be required for many populations to persist, although not all sites with salamander populations had detectable pocket gopher activity within 30 m of the wetland edge (Table 2.1). The individual salamander found in a pocket gopher tunnel was trapped in June and all those in excavation mounds were found in September, suggesting that at least some proportion of salamanders use the gopher tunnels as terrestrial foraging habitat in the summer and a larger proportion use them as winter refugia beginning in the fall.

Pocket gopher activity and land cover were not strongly correlated (Pearson's r = -0.32), which is surprising because pocket gophers typically inhabit open areas like fields and meadows, and no pocket gopher activity was found within forested land cover during this study. This mismatch between pocket gopher activity and land cover could be because the two variables were measured at different scales, with pocket gopher activity assessed within 30 m of the wetland edge and land cover characterized within 200 m. Also, pocket gopher activity varied among occupied sites with extensive open grasslands sometimes having similar pocket gopher abundances to those of much smaller meadows originating from beaver (*Castor Canadensis* Kuhl) activity or drought in an otherwise forested habitat (personal observation). In other cases, the inverse was true. For example, site S3 and GS were located in comparable landscapes with 58% and 53% forest cover, respectively, but pocket gopher mound density was 200/ha at S3 and 4300 /ha at GS (Table 1). Site G43 harbored a population of western tiger salamanders and was occupied by northern pocket gophers at a density of 150 mounds/ha although the adjacent terrestrial land-cover was 99% forest (Table 1). At this site, the wetland existed within a predominately forested tract but had upland meadow immediately adjacent to a portion of the water's edge and where pocket gophers were active. Although related to salamander occurrence, it is unclear to what degree individuals or populations rely on habitat features created by pocket gophers. However, 16 of 20 sites where tiger salamanders were present also had northern pocket gopher activity whereas only two of the 20 sites without salamanders had pocket gopher activity. Root holes and other small mammal burrows might also provide habitat for western tiger salamanders in the prairie provinces, as they do for other forest-dwelling ambystomatid salamanders (Faccio 2003; Madison 1997; Johnston 2000).

The 2013 survey suggested that sites S1, GS, and S3 had low (3 counts), medium (10 counts), and high (21 counts) relative abundance of post-metamorphic salamanders, respectively. This was consistent with rigorous CMR density estimates among sites where S1 had 53(34-94, 95% CI) individuals/ha, site GS had 114(114-200) individuals/ha, and site S3 had 138(129-162) individuals/ha. These data suggest that CPUE in the form of counts were correlated with true density, although imprecisely. Therefore, I argue that counts of pond-using amphibians during low intensity surveys can be used as an index that is reasonably correlated with relative abundance among sites during a given year and can be used to monitor trends through time, although they assuredly lack precision. However, short-term trends should be interpreted with caution because yearly variation in population size is likely normal (Green 2003; Marsh 2001).

I have no evidence to suggest that western tiger salamanders in north-central Alberta occur in lower abundances than do tiger salamanders elsewhere. Western tiger salamander population sizes (including non-breeders) in the Beaver Hills (GS: 16 (16-28, 95% CI); S1: 122 (79-218, 95% CI); and S3: 58 (54-68, 95% CI)) were similar to population estimates of breeding adult eastern tiger salamanders in two ponds (location: South Carolina) that averaged 87 and 24 breeding adults, respectively (Semlitsch 1983), although the proportion of non-breeding individuals is unknown. The effective population size, a subset of the entire population at a site, among 10 populations (location: California) of California tiger salamanders in ranged from 11 to 64 individuals (smaller wetland size range than: 0.04-1.54 ha) (Wang et al. 2011). These data suggest that habitat quality is likely similar in the Beaver Hills compared to that inhabited by other tiger salamanders. However, these studies all estimate distinct subsets of the entire population at a site (effective population size or breeding adults) and are not directly comparable with my data, which includes breeders, non-breeders, and post-metamorphic juveniles.

Occupancy estimates of western tiger salamanders in the Beaver Hills (0.55 (0.37 – 0.71, 95%CI)) were higher overall than occupancy of western tiger salamanders in Grand Teton and Yellowstone National Parks;

where wetland occupancy ranged from 0 to <0.3 between 2004 and 2011, but was similar among beaver-influenced ponds in 2002 (Hossack et al. 2015). In other studies from Yellowstone NP, western tiger salamander occupancy ranged between 0.073 – 0.15 (Klaver et al. 2013; Gould et al. 2012), which is much lower than occupancy estimates in this study. Occupancy of western tiger salamanders in the Beaver Hills is also higher than that of eastern tiger salamanders in Minnesota, where occupancy varied between 0.27 – 0.35 among candidate models (MacKenzie et al. 2003). These patterns suggest that a higher proportion of wetlands in the prairie/boreal transition zone are suitable for tiger salamanders than elsewhere in the range of western tiger salamanders and related eastern tiger salamanders, or that other studies sampled a wider range of wetlands of which a higher proportion might have been unsuitable for salamanders.

Minimum estimates for the area occupied and the number of adult individuals are important for future status assessments (COSEWIC), where a decline in the range and/or the number of mature individuals is the criteria for assigning a species conservation status. The most recent COSEWIC status assessment (2012) elevated western tiger salamander populations in the prairie provinces to ‘special concern’ status from ‘not at risk’. Declines in the number of western tiger salamander populations or the number of individuals within those populations have not been described because the data do not exist, but declines have been inferred based on stocking of trout and loss of wetlands and terrestrial habitat due to increasing urbanization and agriculture (COSEWIC 2012). At the time the status report was written, there were no estimates for western tiger salamander population size and the index of area occupied (IAO) was limited to known sites, as distribution patterns (occupancy) were unknown for populations in the prairie provinces and could not be projected to sites with unknown presence. My research indicates that wetland occupancy is high in the Beaver Hills region (0.55 (0.37-0.71, 95% CI). Extrapolation to other areas of western Canada should be done cautiously but my results might suggest western tiger salamander abundance throughout the prairie provinces may be higher than previously thought, although I have no data for regions outside of the Beaver Hills.

The minimum number of wetlands inhabited by western tiger salamanders in the Beaver Hills was estimated based on occupancy patterns observed within wetlands within a specified size range and land cover criteria, and could not be meaningfully applied to the hundreds of wetlands outside these criteria. My estimate should be viewed as conservative because there are known populations that exist at sites that fall outside of these criteria. For example, western tiger salamanders were detected in a 20 ha lake, demonstrating that salamanders do occur in wetlands much larger than those in this study (<7 ha) (pers. observation). Western tiger salamanders have also been documented in wetlands where fishes occurred (C. Paszkowski, University of Alberta, pers. comm.). Western tiger salamanders were detected in wetlands within the city of Edmonton, suggesting that they will also use sites with less than 90% forest/open adjacent terrestrial habitat (Scheffers 2010; pers. observation). Previously, the number of occupied wetlands across the prairie provinces was estimated as >500 (COSEWIC 2012). Based on my data, the projected number of occupied wetlands in the Beaver Hills alone was 625 (420 – 811, 95% CI), suggesting that the overall number of occupied sites in the prairie provinces was grossly underestimated and must be far greater than 500. However, occupancy patterns and wetland density likely vary across ecoregions within the three provinces. Although not tested in this study, trout stocking was not observed at any sites, and is likely rare in most of the small eutrophic pothole wetlands occupied by western tiger salamanders in the prairie provinces. Very few of these sites support fish communities. I argue that western tiger salamander occurrence and abundance is likely quite high in the prairie provinces and that loss of breeding habitat via fish stocking is not likely a serious concern in most of the small wetlands inhabited by tiger salamanders in this area.

Estimates of the minimum number of post-metamorphic western tiger salamanders in the Beaver Hills were coarse for the reasons listed above regarding wetland inclusion and because population sizes and densities were estimated based on the lower 95% confidence intervals at study sites and thus were conservative. I took this approach to err on the side of caution when describing patterns of a listed species, and because studied wetlands (CMR sites) had equal representation by low, medium, and high-density salamander populations, while the true proportion of high-density sites might not be equal to that of low-density sites across the landscape. I only used three study sites to generate population densities and these may or may not be representative of the study region as a whole. The estimates based on population size (minimum population size and average minimum population size) might be more realistic than those estimated by density (minimum observed density and average observed density), as larger wetlands do not necessarily harbor more individuals (Semlitsch et al. 2015). Researchers should exercise caution when projecting abundance and density estimates to additional wetlands because estimates can be highly variable based on the method of extrapolation.

Management recommendations and future monitoring

Management guidelines for western tiger salamanders in the prairie provinces should ensure the preservation of northern pocket gophers in upland habitat adjacent to wetlands rather than infer salamander habitat based on adjacent land cover composition. My study suggests that land cover is a poor proxy for tiger salamander terrestrial habitat. This likely also applies to other areas within the prairie provinces where northern pocket gophers and tiger salamanders coexist. Other burrowing mammals, notably Richardson's and thirteen-lined (*Ictidomys tridecemlineatus* Mitchill) ground squirrels inhabiting these provinces should also be considered as potentially providing suitable habitat to western tiger salamanders. Western tiger salamanders in Saskatchewan have even been observed in black-tailed prairie dog holes (*Cynomys ludovicianus* Ord) (Parks Canada, pers. comm.).

Future surveys should be conducted to establish occupancy and abundance patterns in regions outside of the prairie/boreal transition zone in the prairie provinces, particularly the mixed-grass and short-grass prairie. Long-term datasets are crucial for understanding trends in highly variable amphibian populations (Pechmann et al. 1991), therefore additional surveys will be beneficial before judging a decline in area occupied or the number of individuals. Accounting for imperfect detection did not significantly influence the interpretation of site variables in relation to salamander occurrence or density. This indicates that future surveys for western tiger salamanders should allocate sampling effort towards more sites rather than repeat visits to fewer sites. Any future surveys for western tiger salamanders and other ambystomatid salamanders should use aquatic drift fences when trapping. Aquatic traps along drift fences were much more effective than free floating minnow traps, with 94% of salamanders in 2013 captured along the drift fence. A single drift fence was used in this study design (2013) but a second could easily be installed in less than 10 minutes, and would likely greatly increase the probability of detecting salamander presence in lieu of setting additional free-floating minnow traps. PIT-telemetry was useful for detecting terrestrial individuals while mound raking and subterranean trapping was futile. Future studies of terrestrial ambystomatid salamanders should consider PIT-tagging and PIT-telemetry as efficient and reliable methods. PIT-telemetry is particularly effective in ‘open’ areas (without trees or dense shrubs), as surveyors can cover ground very quickly. Future studies should focus on the effect that urban and agricultural development has on western tiger salamander occupancy and abundance patterns, as these are listed as potential causes for decline.

Tables and Figures

Table 2.1. Capture totals (L = larva, A = adult) and terrestrial habitat characteristics (%F = % forest cover within 200 m of wetland edge, PGD = pocket gopher density within 30 m of wetland edge (mounds/ha)) for 2013 study sites (n=40). Dotted horizontal line separates sites with and without detections. Sites selected for 2014 Mark-Capture-Recapture are designated with an asterisk.

Site	May	June	July		Total		Comb. Total	Terrestrial Habitat		Wetland Area (ha)
			L	A	L	A		%F	PGD	
S3*	1	7	1	12	1	20	21	58	200	0.42
P8	2	2	-	8	-	12	12	53	500	0.52
P16	4	1	3	3	3	8	11	33	2600	0.04
GS*	6	3	-	1	-	10	10	53	4300	0.14
G43	-	3	4	1	4	4	8	99	150	1.78
P20	-	2	-	3	-	5	5	65	-	0.45
P2	1	1	-	2	-	4	4	3	240	0.39
S1*	1	-	2	-	2	1	3	14	98	2.31
P15	-	-	2	1	2	1	3	48	-	0.18
P13	-	2	-	1	-	3	3	51	76	0.17
PT10	-	1	-	1	-	2	2	9	800	0.30
PT11	-	-	-	2	-	2	2	45	300	0.97
P6	-	2	-	-	-	2	2	71	1200	0.19
G22	-	-	2	-	2	-	2	88	73	1.05
G10	-	-	-	1	-	1	1	5	170	0.85
P23	1	-	-	-	-	1	1	19	-	0.18
G25	-	1	-	-	-	1	1	39	100	0.45
G46	-	-	-	1	-	1	1	86	50	2.28
G36	1	-	-	-	-	1	1	89	60	1.43
P19	-	-	1	-	1	-	1	91	-	4.05
P11	-	-	-	-	-	-	-	5	-	0.38
P18	-	-	-	-	-	-	-	28	43	0.30
G33	-	-	-	-	-	-	-	36	-	6.09
P22	-	-	-	-	-	-	-	47	-	0.46
PT13	-	-	-	-	-	-	-	51	-	5.51
P7	-	-	-	-	-	-	-	56	-	0.11
P24	-	-	-	-	-	-	-	63	-	1.90
G48	-	-	-	-	-	-	-	64	-	0.32
G19	-	-	-	-	-	-	-	64	-	0.86
P21	-	-	-	-	-	-	-	64	-	3.12
P4	-	-	-	-	-	-	-	65	-	0.50
G42	-	-	-	-	-	-	-	71	-	3.88
G31	-	-	-	-	-	-	-	77	-	3.23
G28	-	-	-	-	-	-	-	78	-	0.72
P10	-	-	-	-	-	-	-	79	34	0.41
G15	-	-	-	-	-	-	-	86	-	0.80
P12	-	-	-	-	-	-	-	88	-	1.14
G27	-	-	-	-	-	-	-	89	-	0.42
G13	-	-	-	-	-	-	-	90	-	2.05
G14	-	-	-	-	-	-	-	94	-	0.21
Total	17	25	15	37	15	79	94			

Table 2.2. Generalized linear models for salamander presence/absence (Firth's logistic regression) and abundance of adults when present (zero-truncated negative binomial regression on count data). Table shows the independent variables and the Likelihood Ratio Test for each model (to evaluate the fit of the model with a chi-square statistic, χ^2). Significant models are in bold and the likelihood ratio test is denoted with an asterisk (*). Significant independent variables within a model are also denoted with an asterisk and the direction of influence on the response variable is denoted as positive (+) or negative (-). PGD = pocket gopher density (mounds/ha), %F =% forest cover within 200 m of wetland edge.

Presence/Absence (logistic regression)

			Likelihood Ratio Test		
Model	Variables in model	p	χ^2	df	p
1	PGD (+)	<0.001*	19.99	1	<0.001*
2	%F (-)	0.059	3.58	1	0.059
3	PGD (+)	<0.001*	19.37	2	<0.001*
	%F (-)	0.58			

Abundance when present (zero-truncated negative binomial regression)

			Likelihood Ratio Test		
Model	Variables in model	p	χ^2	df	p
1	PGD (+)	0.27	1.49	1	0.22
2	%F (+)	0.61	0.119	1	0.73
3	PGD (+)	0.15	1.91	2	0.38
	%F (+)	0.44			

Table 2.3. Model results for occupancy and detectability of western tiger salamanders in program PRESENCE. ψ is the probability that a species is present and p is the probability that a species is detected at an occupied site. Best models (a=0.05) are in bold and their significant habitat variables are denoted with an asterisk (*). Explanatory variables for each parameter in a model are in parentheses. PGD = pocket gopher density (mounds/ha); %F = % forest cover within 200 m of wetland edge; p(lar) = detectability is binomial variable for time period where overall species detectability varies between prelarvae season (May-June) and larvae season (July). S.E. = adjusted standard error (s.e. * √c-hat). $\Delta QAIC = QAIC_i - QAIC_{min}$.

Model	QAIC	ΔQAIC	Habitat variable	coefficient	S.E.	95% CI
ψ(PGD),p(lar)	86.85	0.00	PGD *	2.43	0.86	0.74 – 4.12
ψ(PGD+%F),p(lar)	88.41	1.56	PGD *	2.44	0.93	0.62 – 4.26
			%F	-0.01	0.03	-0.03 – 0.09
ψ(%F),p(lar)	103.92	17.07	%F	-0.02	0.01	-0.01 – 0.03
ψ(.),p(lar)	104.94	18.09				

Table 2.3 cont'd.

detectability variable	coefficient	S.E.	95% CI
lar*	1.38	1.37	0.01 – 2.75
lar*	1.37	1.36	0.01 – 2.73
lar	1.27	1.31	-0.04 – 2.58
lar	1.27	1.31	-0.04 – 2.58

Table 2.4. The minimum population size of post-metamorphic western tiger salamanders in the Beaver Hills as estimated by four methods.

Method	Number of individuals (95% CI)	Pop. size	Number of Occupied wetlands (95% CI)
Min_{abs}	10,000 (6,720 – 12,976)	16 (site GS)	625 (420 – 811)
Min_{avg}	31,250 (21,000 – 40,550)	50	625 (420 – 811)
		Density	Area of Occupied wetlands
Density_{abs}	306,157 – 587,491	34/ha (site S1)	9,004.62 – 17,279.14 ha
Density_{avg}	819,420 – 1,572,401	91/ha	9,004.62 – 17,279.14 ha

Min_{abs} = The absolute minimum, based on the lower 95% CI from the smallest estimated population size of western tiger salamanders among all three sites.
Min_{avg} = The average minimum, based on the mean lower 95% CI of estimated individuals among all three sites.
Density_{abs} = The absolute lowest density, based on the lower 95% CI of the lowest estimated density of $\text{salamanders/ha}_{wetland}$ among the three sites.
Density_{avg} = The average lowest density, based on the mean lower 95% CI of the minimum density of $\text{salamanders/ha}_{wetland}$ among the three sites.

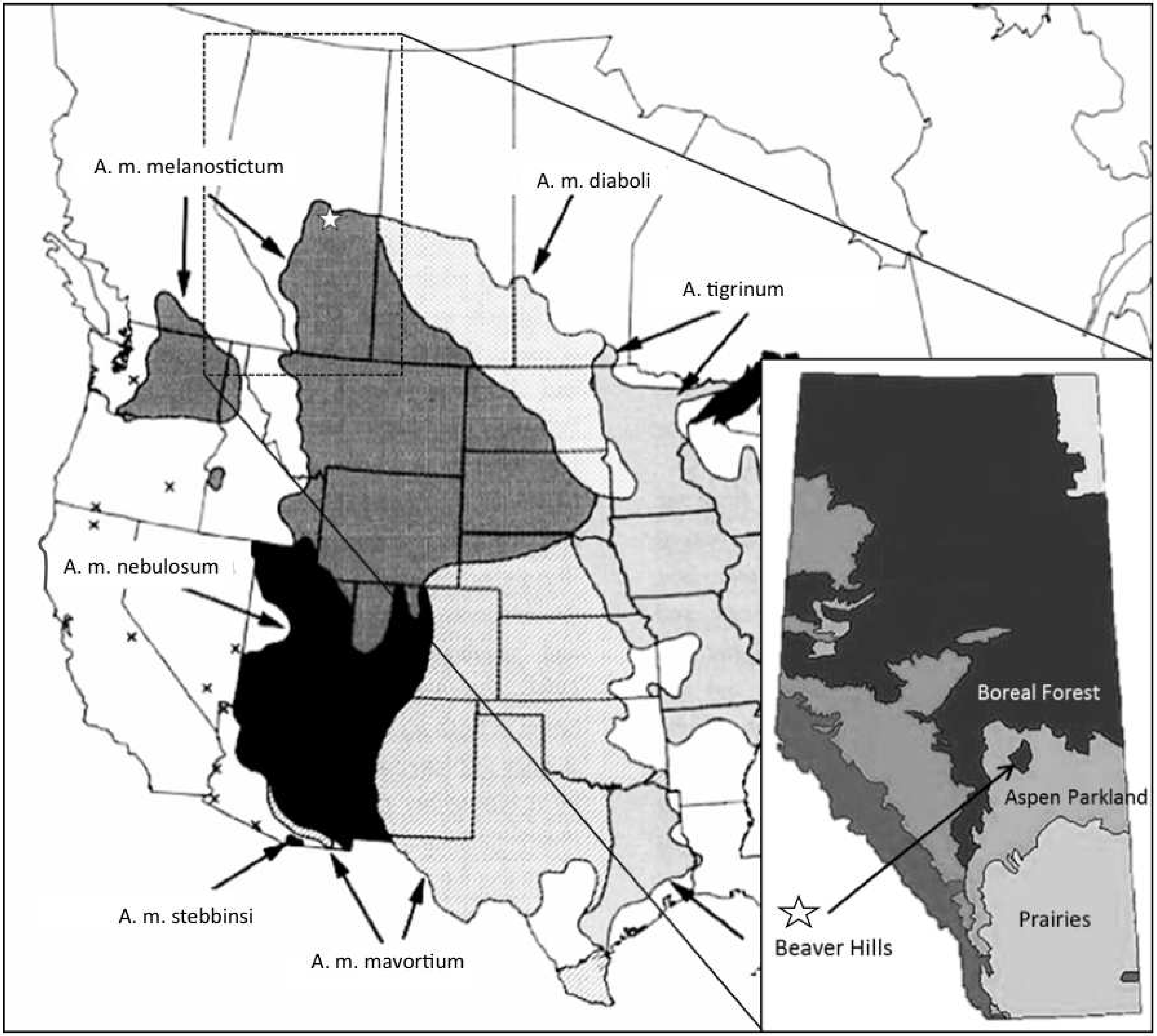

Figure 2.1. Study site location (white star) in relation to the continental distribution of the Western Tiger Salamander (*Ambystoma mavortium*). Inset: The Beaver Hills/Cooking Lake Moraine in Alberta, a disjunct patch of boreal forest surrounded by Aspen Parkland (modified from Petranka 1998).

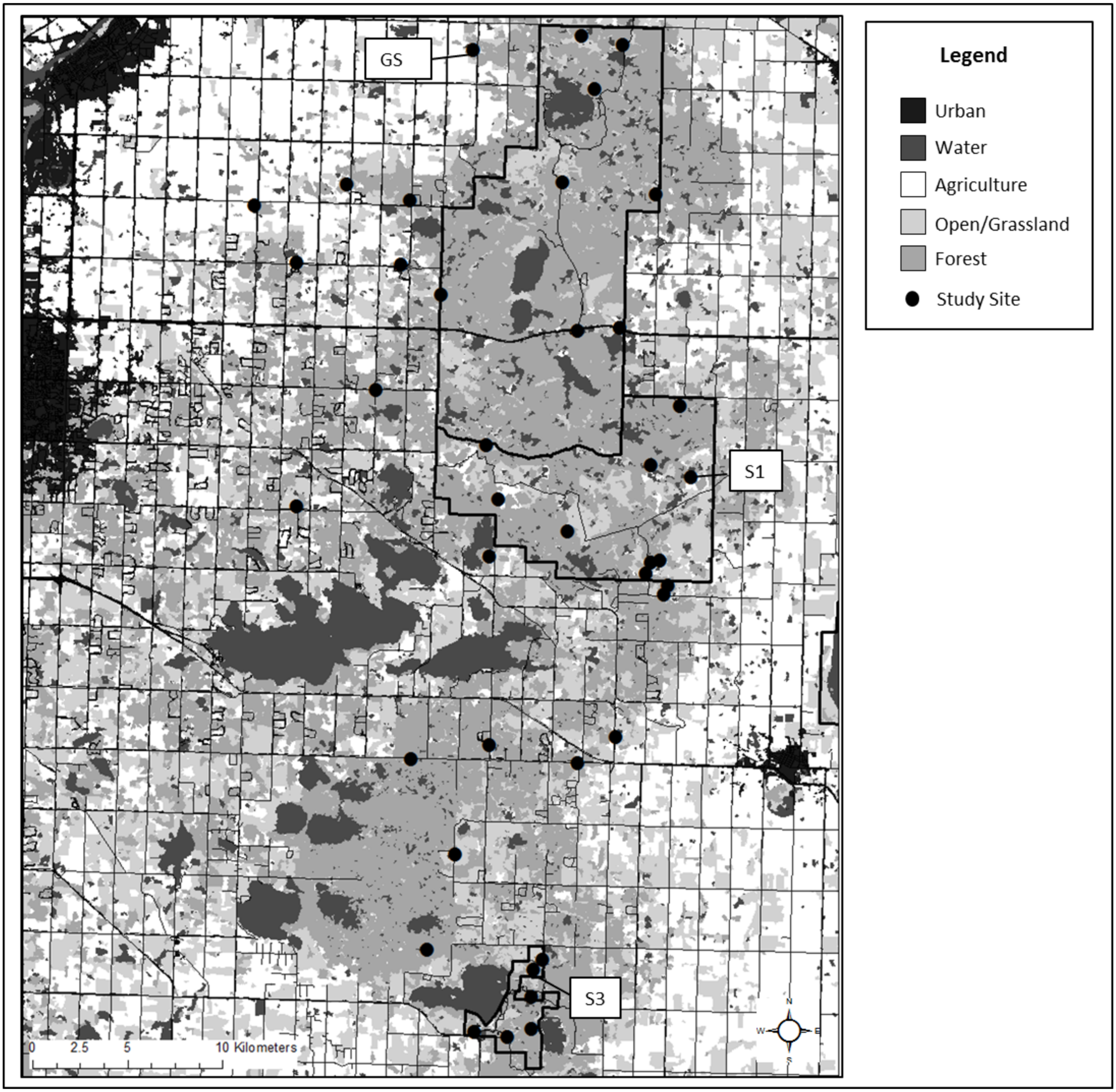

Figure 2.2. Study sites (n=40) and land cover in the Beaver Hills, Alberta. Forest = deciduous, coniferous, and mixed stands; Open/Grassland = Native grassland, shrubland, tame grassland; Agriculture is predominately wheat, barley, legumes, and Canola. The large urban area to the west of the map is the greater Edmonton metropolitan area.

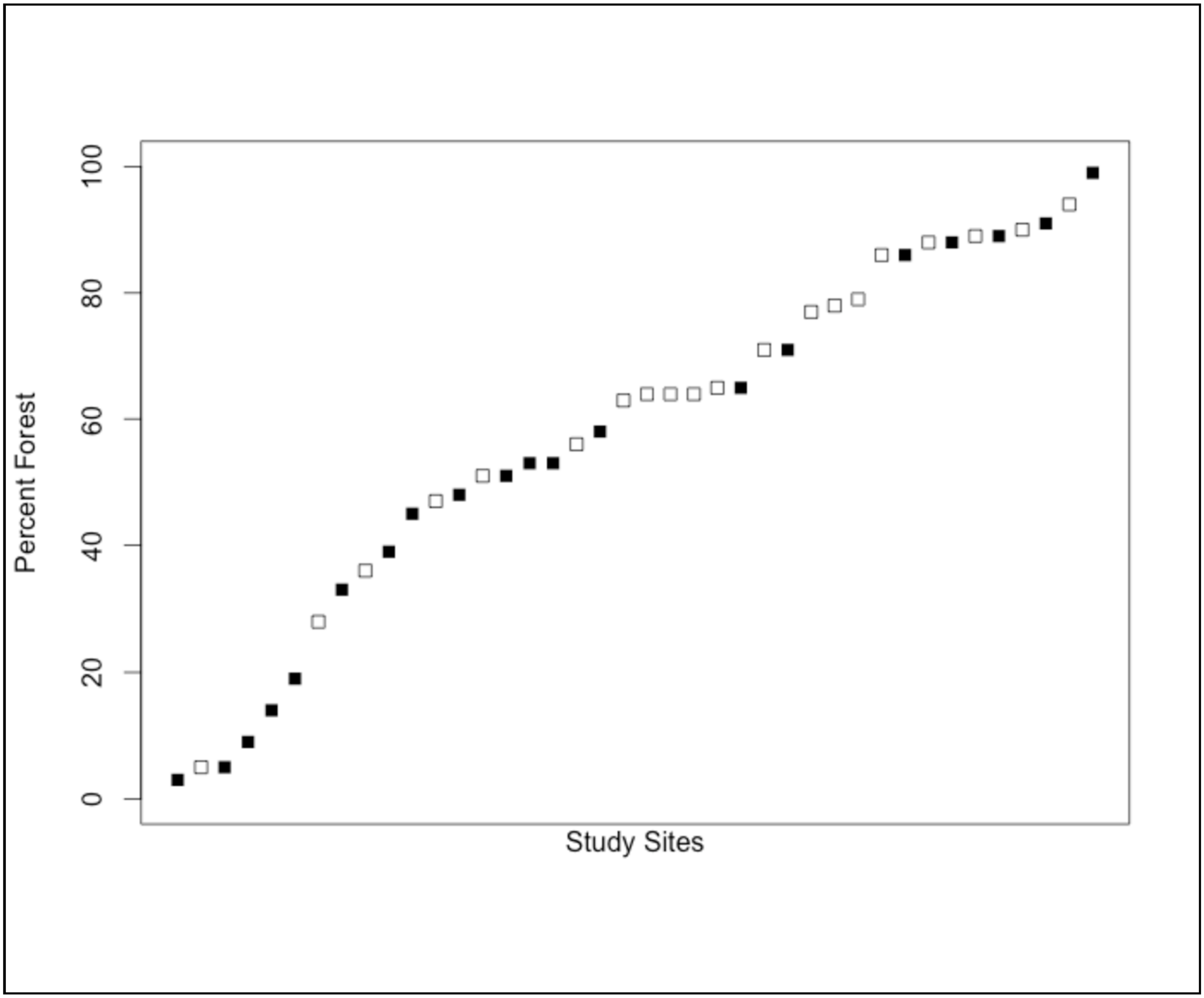

Figure 2.3. Terrestrial habitat composition, as described by land cover (% forest), within 200 m of wetland edge at each study site (n=40). Filled squares indicate sites with salamander presence. Unfilled squares indicate sites without salamander presence.

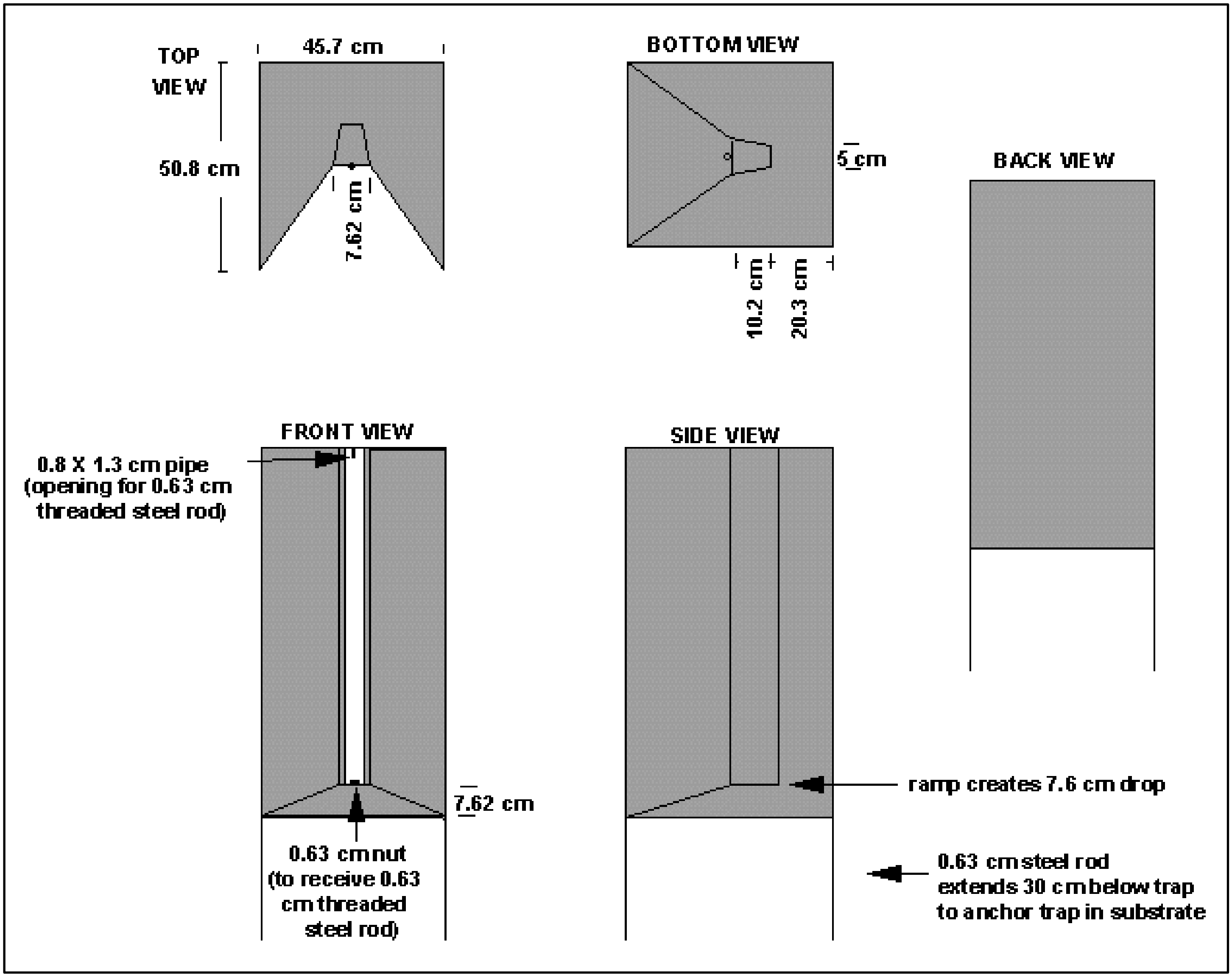

Figure 2.4. Modified minnow trap. Height = 76.2 cm; Width = 45.7 cm; Depth = 50.8 cm; Mesh size = 6.35 mm (S. Crowshoe, University of Lethbridge, pers. comm.).

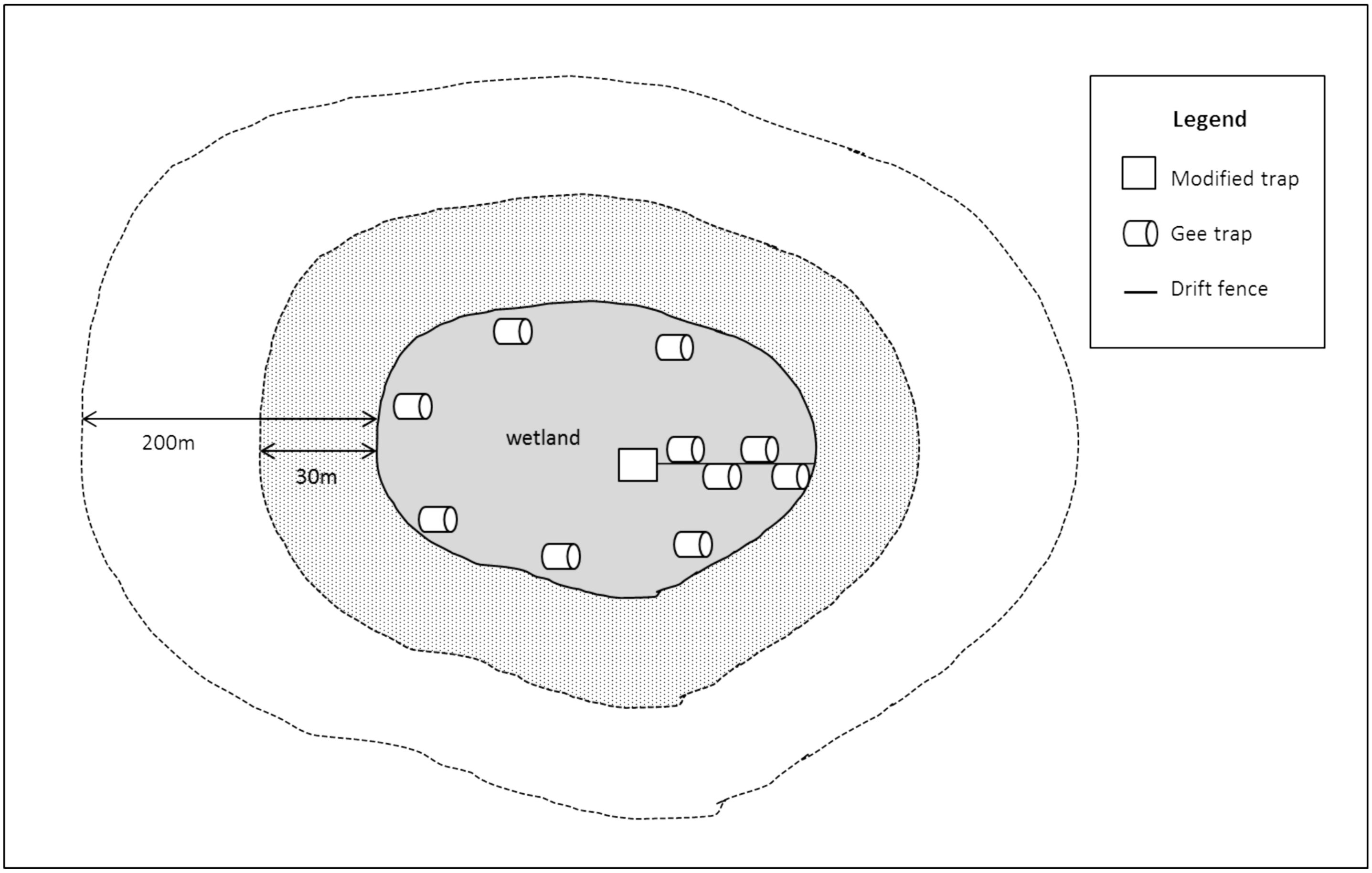

Figure 2.5. Diagram of a 2013 study site. Pocket gopher density (mounds/ha) was estimated within the 30 m terrestrial buffer (stippled) surrounding a pond. Land cover composition, as described by percent forest cover, was calculated within each 200 m buffer (open). Trap array = 1 aquatic drift fence (synthetic fabric) + 1 modified minnow trap + 10 Gee minnow traps.

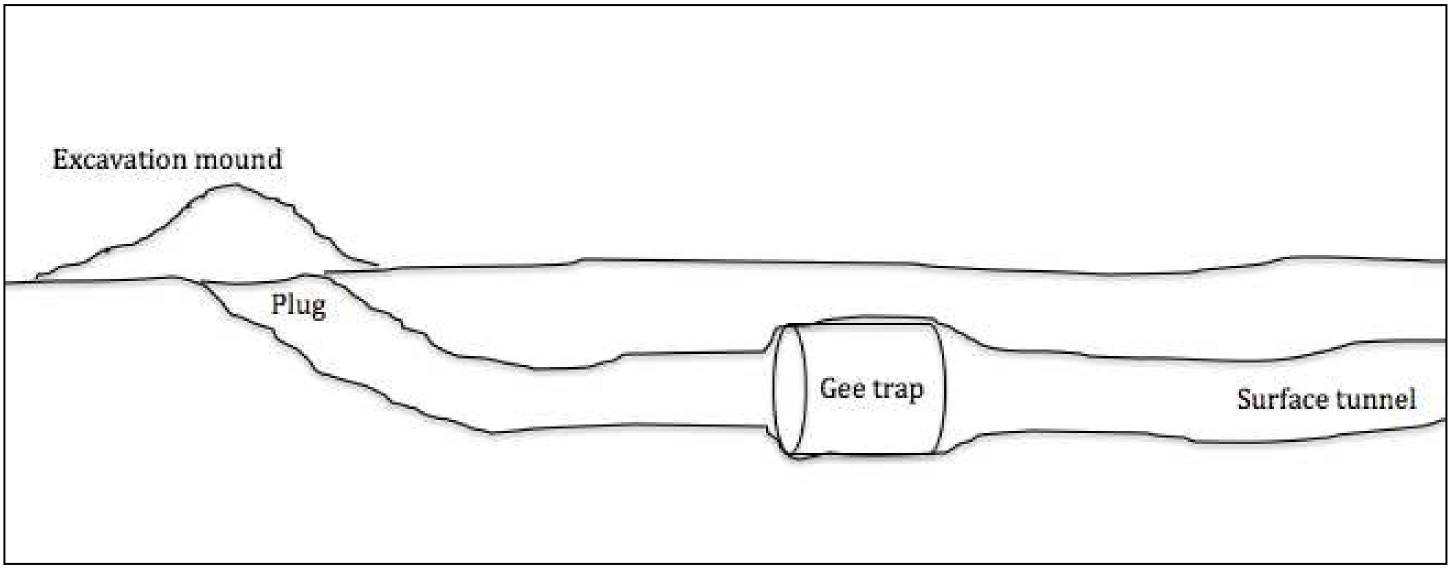

Figure 2.6. Salamander trap in subterranean tunnel of the northern pocket gopher. Within the burrow network, the surface tunnel runs parallel to the surface (apprx. depth = 10 – 20 cm).

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Chapter 3: Summer Aquatic Habitat-Use by Post-Metamorphic Western Tiger Salamanders (*Ambystoma mavortium* Baird) in North-Central Alberta

Introduction

The western tiger salamander (*Ambystoma mavortium* Baird) is federally designated "a species of special concern" in Alberta, Saskatchewan, and Manitoba (hereafter, prairie provinces) because of proposed declines due to habitat loss and fragmentation, emergent diseases, and in some cases, fish stocking (COSEWIC 2012). However, the extent of decline is unknown because virtually no ecological or demographic data exist for the species in these provinces to assess trends. Specific causes of habitat loss or alteration include loss of breeding wetlands and terrestrial foraging habitat to agriculture, urban expansion, energy development, and habitat fragmentation by roads (COSEWIC 2012). Like other pond-breeding amphibians, western tiger salamanders are particularly vulnerable to habitat loss and degradation because they require terrestrial foraging and overwintering habitat adjacent to aquatic breeding habitat (Semlitsch & Jensen 2001). The loss or degradation of either habitat can disrupt life cycle processes and result in the extirpation of entire populations (Harper et al. 2008).

In general, aquatic habitats for tiger salamanders and other ambystomatid salamanders are fishless wetlands with sufficiently long hydro-periods for larval development, usually holding water for 3-7 months (COSEWIC 2012; Petranka 1998). Adult salamanders migrate to wetlands to breed and lay eggs in early spring before returning to the terrestrial environment. Aquatic eggs hatch into gilled larvae that develop and forage in wetlands until metamorphosis, after which they are thought to disperse to the surrounding upland habitat as air-breathing terrestrial juveniles. Terrestrial individuals typically forage in the upland habitat adjacent to breeding ponds throughout the summer and fall and then overwinter in subterranean retreats. A single wetland and the adjacent terrestrial habitat typically harbor an entire population of ambystomatid salamanders, which in many study areas exhibit high philopatry to their natal ponds (Gamble et al. 2007). A population includes breeding and non-breeding adults, terrestrial juveniles, and larvae.

Little is known about the ecology and habitat of western tiger salamanders in the prairie provinces, particularly where the species reaches the northern extent of its global range, and the geographical limit of the entire North American tiger salamander complex (*A. mavortium, A. tigrinum* Green*, A. californiense* Gray). Cooler and wetter than the aspen parkland, the dry southern boreal mixedwood is a largely forested transition zone between the high plains to the south and continuous boreal forests to the north, and is inhabited by western tiger salamanders only in the Canadian prairie provinces (see 'Study Area' for habitat description). In 2013, 40 wetlands were sampled across the Beaver Hills, a disjunct unit of dry southern boreal mixed-wood, to assess salamander distribution across the landscape in relation to terrestrial habitat composition (see Chapter 2). During this survey, post-metamorphic individuals were observed using aquatic habitat continuously from 3 May to 15 August, almost the entire duration of the warm season. This behavior is atypical among ambystomatid salamanders, which normally demonstrate clear and distinct migrations to and from breeding wetlands in early spring (see Williams et al. 2009; Pagnucco et al 2012; Hocking et al. 2008; Cook et al. 2006; Semlitsch et al. 1993), outside of which adults are uncommon in wetlands as they forage terrestrially.

The presence of post-metamorphic individuals in wetlands could signify that transformed individuals are using aquatic habitat to forage throughout the summer following spring breeding efforts rather than returning to the terrestrial environment. Alternately, prolonged adult presence in wetlands could be the result of staggered breeding migrations instead of the normal en masse migration in early spring (Rose & Armentrout 1976). Staggered breeding migrations would likely produce distinct cohorts of larvae, as evidenced by variation in larval size distribution and development stage. Most larval tiger salamanders reach metamorphosis within a single season, but larvae that hatch later into the season would have less time to reach metamorphosis and might overwinter in wetlands to emerge the following season. Multi-season larval development has been observed among western tiger salamanders and other ambystomatid salamanders, particularly in colder climates where larval development is slower (Wissinger & Whiteman 1992). Within the prairie pothole region, multiple larval cohorts have been observed at two sites in Alberta (S. Crowshoe, University of Lethbridge, pers. comm. 2015) and in North Dakota (Deutschman & Peterka 1988). These observations, combined with those of known paedomorphic populations in some Alberta lakes (Tyrell Lake, M. Haag, University of Alberta, pers. comm. 2012), suggest that larval wintering is possible and might occur in the dry southern boreal mixed-wood ecoregion in north-central Alberta. However, frequent winter hypoxia, occasional drying of wetlands, and complete freezing of wetlands within this region might prevent regular larval overwintering as it does with the persistence of fish communities (Peterka 1989; Herwig et al. 2010). Typical (one season) larval development would further support that any prolonged wetland occupancy by post-metamorphic individuals represents summer foraging behavior rather than staggered breeding events that produce larvae late into the summer that might attempt to overwinter.

The objective of this study was to characterize temporal patterns in aquatic habitat-use by post-metamorphic western tiger salamanders. The presence of post-metamorphic individuals in wetlands during the summer has occasionally been documented (Rose & Armentrout 1976) but has rarely been rigorously addressed to my knowledge (see Whiteman et al. 1994). These and other ecological data are lacking for western tiger salamander populations in the prairie provinces and are necessary for future status assessment and potential management efforts, particularly for the classification of critical habitat and buffer zones around breeding sites, which are typically meant to protect terrestrial habitat used by post-metamorphic individuals (Semlitsch 1998; Lehtinen et al. 1999; Porej et al. 2004). I predicted that pond-use patterns of post-metamorphic individuals would reflect prolonged summer foraging in wetlands rather than a temporary breeding presence. I interpreted the presence of a single larval cohort (indicative of synchronized spring breeding efforts) and weight gain of recaptured pond-using adults as evidence of prolonged foraging behavior in wetlands by post-metamorphic individuals rather than staggered breeding migrations. The secondary objective of this study was to provide basic demographic and ecological data, which are virtually non-existent for the western tiger salamander in north-central Alberta and elsewhere in the prairie provinces.

Study Area

The Beaver Hills/Cooking Lake moraine (Figure 1) encompasses 1572 km^2 and lies directly east of Edmonton, Alberta, Canada. The area is along the northern edge of the prairie pothole region and contains thousands of pothole wetlands and larger shallow lakes. The moraine rises over 790 m above the surrounding aspen parkland and supports a disjunct patch of dry southern boreal mixed-wood forest. Dry boreal mixed-wood forests experience cooler average temperatures (yearly average: 1.1 degree Celsius) and higher average annual rainfall (461 mm) than the surrounding aspen parkland and prairie plateau (Natural Regions Committee 2006). The terrestrial landscape is heterogeneous and includes natural grassland, shrubland, agriculture, and grazing land within a forested matrix. Native grasslands are fescue prairie (*Festuca* L. spp.). Forests are predominately deciduous poplar species (*Populus tremuloides* Michx. and *Populus balsamifera* L.) interspersed with spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Picea glauca* (Moench) Voss). The dominant understory is beaked hazel (*Corylus cornuta* Marshall), low-bush cranberry (*Viburnum edule* (Michx.) Raf.), and Saskatoon (*Amelanchier alnifolia* Nutt.). Open shrublands are dominated by willow (*Salix* L. spp.) and rose (*Rosa* L. spp.). The primary crops in cultivated areas include forage crops and grains, specifically barley, Canola, and legumes. Poor soil and climate conditions have limited the extent of agricultural development to only 24% of the moraine proper, with the remainder comprised of 45% forests, 27% grassland/grazing land, and 4% urban development. Greater than 22% of the natural and grazing land is protected within parks, namely Elk Island National Park, Cooking Lake-Blackfoot Provincial Park and Recreation Area, Ministik Bird Sanctuary, and Miquelon Lakes Provincial Park.

Site Descriptions

Three wetlands were selected for season-long salamander sampling (May-August) from among 20 with known western tiger salamander populations as discovered in 2013 during a previous salamander distribution survey within the Beaver Hills (see Chapter 2). These sites were chosen to conduct a separate mark-recapture study to estimate population size for local populations and because aquatic and adjacent terrestrial habitat characteristics represented available wetlands across the landscape. Terrestrial habitat was characterized as the adjacent land cover within 200 metres of the wetland edge, as this area likely encompasses the home range of most adult salamanders within a population (Brodman 2010; Porej et al. 2004; Semlitsch 1998). Sites S1 and S3 were natural wetlands and site GS was a retired gravel pit (Table 1). Max depth at sites GS, S1, and S3 were estimated at >2 m, >2m, and >1.3m, respectively. Each site held water for the duration of 2013 and 2014, although site S3 contracted considerably (apprx. 80%) in 2013 and likely experiences years where it dries completely by late September. All wetlands were fishless and the adjacent land cover was largely natural in composition consisting of forest and native grassland or tame pasture; no site had adjacent anthropogenic or agricultural development other than cattle grazing. Grazing lands surveyed in the study area were considered naturalized because they were visually indistinguishable from native prairie patches and likely provided similar habitat for salamanders given that both grassland types are grazed with cattle in the region. Sites S1 and S3 were within protected areas (Cooking Lake Blackfoot Provincial Park and Miquelon Lakes Provincial Park, respectively) and site GS was on land owned by Strathcona County.

Methods

Salamander Sampling

Salamanders were trapped in wetlands throughout the spring and summer of 2014 (1 May – 15 August). Trapping began as soon as pond-ice receded enough to place traps in water and pond sediments were thawed enough to allow placement of aquatic drift fences. Gee minnow traps (length = 42cm, diameter = 22.9 cm, metal mesh size = 6.35 mm) were placed along an aquatic drift fence (synthetic fiber silt fence, height = 0.9 m, length = 10 m) at 30 m intervals along the wetland margin and perpendicular to the shoreline. A single minnow trap was placed on one side of the fence. Traps were placed midway along the drift fence and tied to sticks to create airspace inside each trap. Traps were checked every 1-2 days and reset on the opposite side of the drift fence. Captured salamanders were weighed, measured, and sexed (when possible). Tail length was calculated by subtracting snout to vent length (SVL) from total length (TL). Individuals were categorized as males by the presence of vent papillae or females if lacking papillae but having swollen, rounded vents. Other terrestrial-stage individuals were categorized as juveniles if they were near in SVL to metamorphs (juvenile SVL: 5.9 – 9.7 cm; metamorph SVL: 7.8 – 9.6) and had ambiguous and small non-swollen vents and non-flattened tails. Male tiger salamanders have longer tails relative to their SVL's and females have longer overall SVL's (Williams et al. 2009; Howard 2009; Howard et al. 2007). Tail:SVL ratios were compared among known males and females with a two-tailed, equal variance t-test then used to classify post-metamorphic individuals of unknown sex. Individuals were labeled as males if their tail:SVL ratio was equal to or greater than 0.86 (0.83-0.88, 95% CI) or females if less than or equal to 0.81 (0.79-0.82, 95% CI). No individuals fell outside of these ranges. Metamorphs were defined as transformed salamanders with some evidence of receding gills or gill scars. Larvae were distinguished based on the presence of gills. The smallest larva captured was 2.2 cm (TL; SVL unmeasured), had yet to develop limbs, and was likely less than 1 week old. Larvae smaller than this could presumably avoid detection by escaping from traps or were overlooked amongst duckweed and other vegetation when traps were checked. Although frequently encountered, larvae < 23 cm TL (apprx.) could also probably escape traps, as these overlapped in size with boreal chorus frogs (*Pseudacris maculata* Agassiz), which were frequently observed escaping from traps (pers. obs.) and are less stream-lined than larval salamanders.

Marking

Passive integrated transponder (PIT) tags were used to allow identification of individual salamanders. PIT-tag implantation generally followed the procedure outlined by Ott & Scott (1999) and Connette & Semlitsch (2012). Individuals were anesthetized and surgically implanted with unique PIT-tags before release. All captured individuals were anesthetized in a pre-buffered solution of Tricaine methanesulfonate (TMS) before measuring, weighing, and implantation. Salamanders were considered anesthetized when righting behavior ceased. Salamanders were rinsed with distilled water after removal from the TMS solution to halt additional absorption. A small incision was made with a sterile scalpel in the body cavity via the ventral surface, anterior to the hind legs, and a PIT-tag was inserted (HDX 12 x 2.12 mm, weight: 0.1 g, Oregon RFID). A sterile cotton swab was used to dry the incision area before applying a liquid suture (Vetbond^{TM}) and Polysporin. Animal capture and restraint was conducted under the Animal Use Protocol 00000044, as approved by the University of Alberta Animal Care Committee. PIT-tag implantation and surgical procedures were conducted under AUP 00000501, as approved by the University of Alberta Animal Care Committee. Larval individuals were tagged in the same manner as adults, with the added procedure of having a field technician regularly flush the gills with distilled water during implantation. All salamanders were then placed with head above water in a shallow dish of distilled water to recover with larvae recovering in deeper water with gills completely submerged. Individuals recovered within 10-20 minutes and were released at their point of capture if behaving naturally and displaying no signs of injury. A minimum weight of 12 grams was arbitrarily chosen for larval salamanders before receiving a PIT-tag because of their small size. Recaptured individuals were identified with a hand-held PIT-tag scanner (Oregon RFID) at each trapping event and released after weighing and measuring.

Analysis

The number of post-metamorphic and larval individuals captured on each trapping date was plotted for all sites and by individual site to visualize the time period that they were present in aquatic habitat. The number of post-metamorphic salamander detections was compared among months with a chi-square (χ^2) goodness of fit (GOF) test to determine the period of peak pond-use. Expected values for each month were standardized based on the number of trapping events. Because 'months' are arbitrary bins for temporal data, mean and median capture dates were also calculated for post-metamorphic individuals to determine when peak pond-use occurred. I compared the size (SVL and TL) of post-metamorphic individuals among sites with a one-way analysis of variance (ANOVA) to determine if density influenced size, as study sites varied in salamander population density (Table 1). The ANOVA was restricted to adults only and results did not differ when post-metamorphic juveniles were included during preliminary analysis. The presence of distinct larval cohorts was considered evidence of staggered breeding, and thus a potential reason for prolonged pond-use by post-metamorphic individuals. The range of capture dates and size distributions of larvae were used to determine the existence of multiple cohorts via the detection of any larvae in May (when adults and eggs were first detected) or any abnormally large larvae before July. In 2013, egg masses were detected on 6 May. In 2014, egg masses were detected on 11 May and hatched within three weeks. Any larvae present in wetlands during May would almost certainly have overwintered the previous year. Abnormally large larvae were >13 g (apprx. SVL: 3.5 – 7.9 cm) before 1 July, based on capture data from 2013 from a survey of 40 wetlands, where all larvae were captured after 19 June and larvae >13 g were only detected after 8 July. Larvae >13 g before 1 July were considered too large to have likely hatched this year and were thus identified as hatchlings from the previous year. The mean larva capture date was used to determine when the largest number of trappable larvae was present in the wetland, hereafter called peak larval period.

Results

Demographic Statistics

A total of 502 individual salamanders were captured among the three sites in 2014 (Table 2). Thirty three percent of the total number of individuals captured were from site GS (n=126), 25% at site S1 (n=123), and 42% at site S3 (n=213) (Table 2). One hundred and nineteen individuals were terrestrial stage adults or juveniles, six were in the process of metamorphosis, and 377 were larvae. Juvenile production, as characterized by the number of larvae in wetland per female observed, was highest in site GS (16.1 larvae/female), intermediate at site S3 (7.1 larvae/female), and lowest at site S1 (2.8 larvae/female) (Table 2). The overall adult sex ratio (M:F) was 1:2.3 among all sites and was biased towards females at each site: site GS = 1:2.3, site S1 = 1:3.8, and site S3 = 1:1.7 (Table 2). As predicted, tail:SVL ratio was significantly higher in males (mean = 0.86, s.e. = 0.01, n=22) than in females (mean = 0.81, s.e. = 0.06, n = 52) (t= 2.46, df= 72, p= 0.0003). Nine of the 83 adults were sexed based on tail:SVL (Females = 6, Males = 3). Mean SVL of post-metamorphic adults (excluding juveniles) at site GS, S1, and S3 was 10.5 (s.d.=0.9), 10.6 (s.d.=1), and 10.9 (s.d.=0.8), respectively. Mean TL of post-metamorphic adults at sites GS, S1, and S3 was 18.9 (s.d.=2.4), 19.2 (s.d.=2), and 20.1 (s.d.=1.9), respectively. SVL and TL of post-metamorphic adult salamanders did not differ significantly among study sites (SVL: F=1.801, df=2,80, p=0.172; TL: F=2.465, df=2,80, p=0.0914).

Temporal Patterns

Overall, post-metamorphic individuals were observed in wetlands from 3 May to 3 August (Figure 2). Post-metamorphic individuals were observed in aquatic habitat at site GS from 5 May to 3 August, in site S1 from 3 May to 14 July, and in site S3 from 19 May to 22 July. Total post-metamorphic salamander detections were unevenly distributed between May, June, and July, with May having significantly fewer detections than expected (n=21) and July having significantly more detections (n=78) (χ^2 = 23.38, df=2, p<<0.001). The mean and median dates of detection for post-metamorphic salamanders were 20 and 21 June, respectively. August detections were low (n=2) and excluded from analysis for post-metamorphic salamanders. Larvae were detected from 13 June to 18 August (Figure 2). Larvae were first observed on 9 and 10 July at sites GS and S1, respectively, but were seen as early as 13 June at site S3. No abnormally large larvae (>13 g before 1 July) were trapped and all larvae captured before July were <3.5 g (Figure 3). Larvae <3.5 g were not detected at sites GS and S1, but were likely present during the time period that larvae were captured in June at site S3. Larval presence peaked on 23 July (mean larval capture date), which was also the mean last date of adult detection across all three sites.

Evidence of Summer Foraging

One hundred and nineteen post-metamorphic individuals were tagged and 52 were recaptured with 30 individuals recaptured once, 9 individuals recaptured twice, 4 individuals recaptured three times, 6 individuals recaptured four times, 1 individual recaptured five times, and 2 individuals recaptured seven times (mean number of recaptures = 1.9, s.d. = 1.5). Among recaptured individuals, the mean days between initial and final capture was 23.6 (s.d. = 19.2) and ranged from 2 to 72 days, indicating the amount of time that these individuals were present in wetlands or made forays into wetlands. Mean days between initial and final capture were 29.4 (s.d.= 23.1) at site GS, 9.6 (s.d.= 7.5) at site S1, and 26.6 (s.d.= 19.2) at site S3. The minimum possible number of days between initial and final captures was 2 in most cases, as traps were typically checked every 2 days. Evidence of foraging, as characterized by weight gain between initial and final capture, was observed in 65% of all recaptured post-metamorphic individuals with an average weight increase of 24.2% (s.d. 24.3). Among adults (excluding juveniles), 73% of recaptured individuals gained weight between initial and final capture with an average weight increase of 21.7% (s.d. 22.4).

Discussion

Post-metamorphic western tiger salamanders were found in wetlands from 5 May to 3 August in 2014 and were detected more frequently in July ($\chi^2 = 23.38$, df=2, $p<0.001$), with peak usage occurring between 20 and 21 June (mean and median detection date: 20-21 June). These pond-usage patterns reflect those of 2013, where post-metamorphic individuals were found in wetlands from 3 May to 15 August. Variation in arrival/departure dates among years could be related to temperature or rainfall fluctuations (Cook et al. 2006; Sexton et al. 1990). Recaptured individuals were found using wetlands from anywhere between 2 and 72 days (mean = 23.6, s.d. = 19.2), with 65% of all post-metamorphic individuals and 73% of adults demonstrating weight gain between initial and final capture. Based on these data, I argue that post-metamorphic western tiger salamanders are using aquatic habitat as summer foraging habitat and spending prolonged amounts of time in aquatic habitat, rather than returning to adjacent upland habitat after breeding like most ambystomatid salamanders (Williams et al. 2009; Pagnucco et al 2012; Hocking et al. 2008; Cook et al. 2006; Semlitsch et al. 1993). The prolonged use of wetlands by post-metamorphic individuals is likely a foraging behavior rather than staggered breeding migration, as supported by weight gain in most recaptured individuals. This is further supported by evidence of typical (one-season) larval development rather than multi-season larval overwintering, which would be expected of some larvae hatching from eggs deposited after staggered breeding events. Eggs were only detected in early May and typically require 2-3 weeks to hatch (COSEWIC 2012), thus no young of year larvae should have been detected during May, and none were. All larvae detected before July were young of year, as characterized by their small size (<3.5 g), indicating that all larvae belonged to one cohort in 2014. These larval development patterns reflect those observed in 2013, where all larvae were captured after 19 June.

The sex ratio was skewed towards females in all sites, with an average ratio of 1:2.3 (M:F), which is very atypical among ambystomatid salamander populations and those of other pond-breeding amphibians where males are more abundant. Documented sex ratios (M:F) in tiger salamanders range from 1:1 to 5.3:1 (COSEWIC 2012; Rose 1976; Semlitsch 1983; Peckham & Dineen 1954; Sever & Dineen 1978). The higher occurrence of females in my study might indicate that more females use aquatic habitat more during the summer compared to males, perhaps to recover weight after egg-laying. The sex ratios of the entire population at each site are unknown and cannot be compared between pond-dwelling and terrestrial individuals. The mean last detection day of post-metamorphic individuals among sites was the same day as the peak larval period (23 July). This suggests that post-metamorphic individuals might be leaving wetlands to avoid competition for resources with larvae that are known to exert top-down control over aquatic food chains in prairie ecosystems (Benoy 2008; Holomuzki et al. 1994).

Extended wetland use by post-metamorphic western tiger salamanders during summer months in north-central Alberta is not surprising, although atypical among ambystomatid salamanders, because many wetlands that characterize the prairie pothole region are semi-permanent to permanent, highly productive, and lack fish (Nicholson 1995; Maurer et al. 2014; Benoy 2008). Fish populations cannot persist in many of these small wetlands because of frequent winter hypoxia (Peterka 1989) and they likely face additional extinction risks from occasional drying and low connectivity, which impedes recolonization, as in small boreal water bodies (Tonn et al. 1995). These are barriers easily avoided by terrestrially overwintering and dispersing western tiger salamanders that can leave wetlands before they freeze or dry. With the absence of fish predators, no seasonal drying, and an abundance of invertebrate foods, salamanders have less reason to return to the terrestrial environment after breeding. I argue that western tiger salamanders in the prairie/boreal transition zone occupy a niche typically occupied by fish, as Benoy (2008) demonstrated in Manitoba populations of the gray tiger salamander (*A. m. diaboli* Dunn).

Future research should examine summer aquatic habitat-use of post-metamorphic western tiger salamanders in other regions throughout their range as well as the extent of terrestrial habitat use within the dry southern boreal mixedwood ecoregion of north-central Alberta. Diet analysis and niche overlap data would be useful to determine the primary food source and foraging habitat of post-metamorphic individuals and potential resource partitioning among larval and transformed life stages. In the prairie provinces, where the western tiger salamander is a "species of special concern", potential management guidelines and future status assessment efforts should incorporate aquatic habitat as important summer foraging habitat in addition to breeding habitat. Because larval salamanders seem to complete metamorphosis within a single season, critical breeding and foraging wetlands do not necessarily need to be permanent through winter to facilitate larval overwintering.

Tables and Figures

Table 3.1. Western tiger salamander habitat characteristics and population size at three sites in boreal Alberta.

Site	Pond area	TN(µg/L)	TP(µg/L)	Hydro-period	LC	Pop. size	Pop. density
GS	0.14	580	11	Permanent	53	16(16-28)	114(114-200)
S1	2.31	2,004	32	Permanent	14	122(79-218)	53(34-94)
S3	0.42	6,720	626	Semi-permanent	58	58(54-68)	138(129-162)

TN=Total Nitrogen; TP=Total Phosphorus; LC=adjacent land cover as characterized by % forest; Pop. size= Population size of post-metamorphic individuals as estimated by Full likelihood closed models with equal capture and recapture probability (95% CI); Pop. density= Post-metamorphic salamander population size standardized by pond area (95% CI).

Table 3.2. Summary of western tiger salamander captures (excluding recaptures) among sites GS, S1, and S3 in the Beaver Hills, Alberta.

Site	Males	Females	Sex Ratio (M:F)	Juveniles	Metamorphs	Larvae	Total
GS	4	9	1:2.3	6	2	145	166
S1	8	27	1:3.8	10	2	76	123
S3	13	22	1:1.7	20	2	156	213
Total	25	58	1:2.3	36	6	377	502

Table 3.2. cont’d.

Site	Larvae/Female	Larvae/hectare(wetland)*
GS	16.1	1,036
S1	2.8	33
S3	7.1	371
Total	6.5	131

*Rounded to the nearest individual.

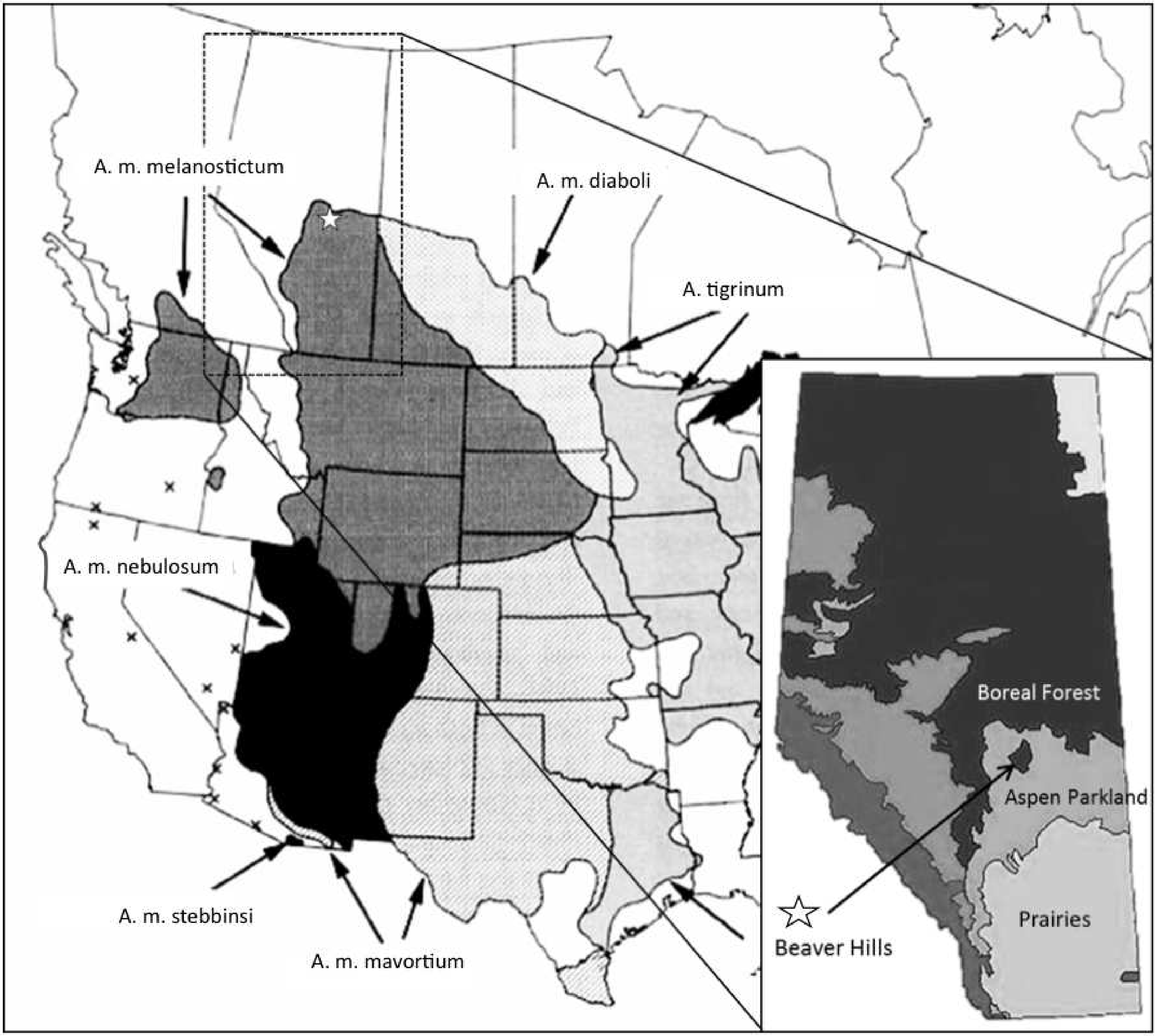

Figure 3.1. Study site location (white star) in relation to the continental distribution of the Western Tiger Salamander (*Ambystoma mavortium*). Inset: The Beaver Hills/Cooking Lake Moraine in Alberta, a disjunct patch of boreal forest surrounded by Aspen Parkland (modified from Petranka 1998).

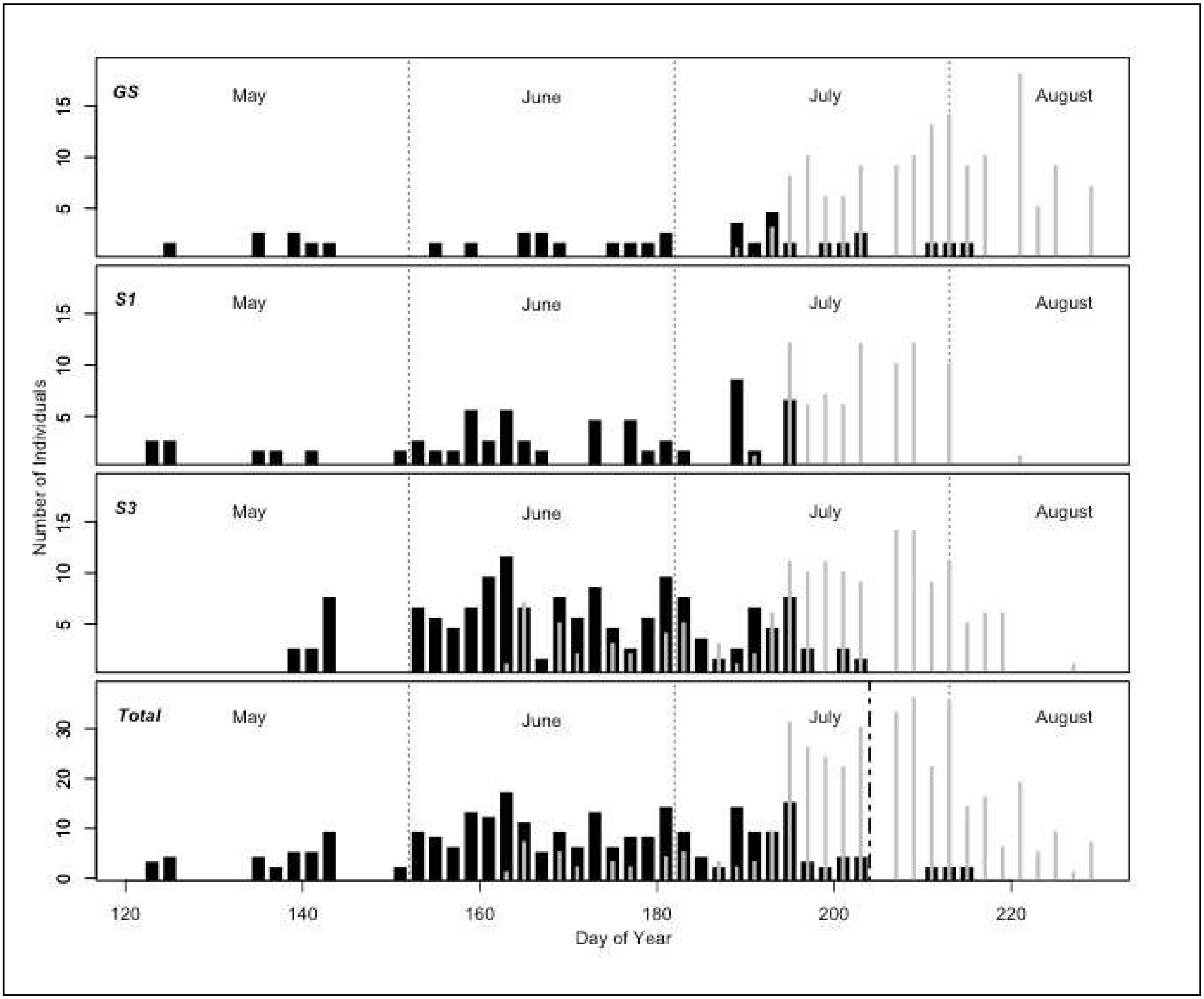

Figure 3.2. Adult (thick black bars) and larval (thin gray bars) western tiger salamander captures among sites GS, S1, S3, and combined, throughout the summer. Panel 'Total' has a different y-axis. Capture events represent two-day periods. Months are divided by a vertical dotted line. The mean last capture day of post-metamorphic salamanders and mean larvae capture date (dashed black line) are represented in panel 'Total'.

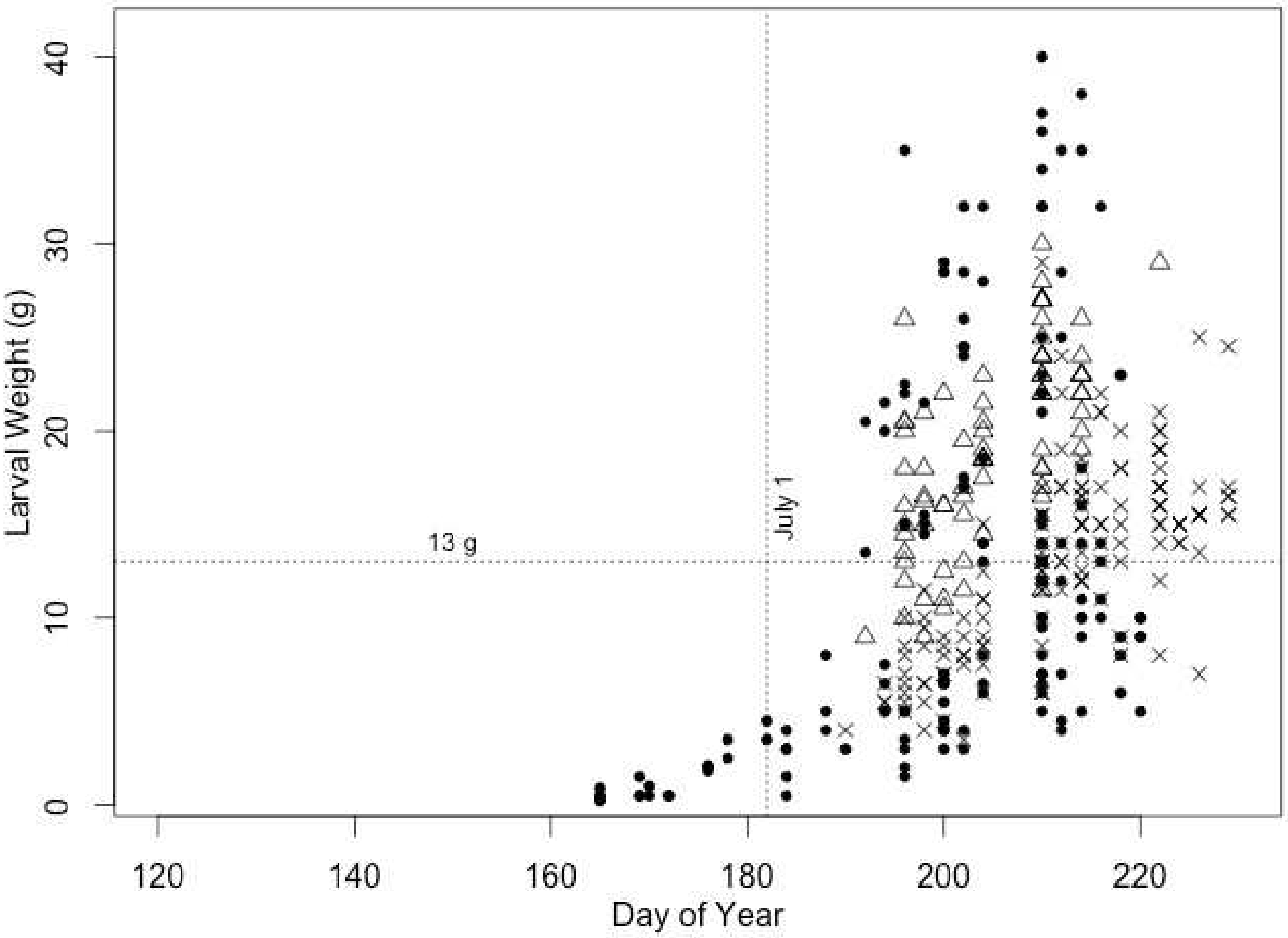

Figure 3.3. Larval (n=377) size distribution throughout the trapping period for all sites combined, indicating a single larval cohort. Site GS = "x"; Site S1 = hollow triangle; Site S3 = filled circle.

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Chapter 4: Baiting Increases Effectiveness of Aquatic Funnel Traps for Capturing Larval Western Tiger Salamanders (*Ambystoma mavortium* Baird) but not for Post-Metamorphic Individuals

Introduction

Aquatic funnel trapping is one of the most widely used sampling techniques for caudates and other amphibians (Heyer et al. 1994; Jenkins et al. 2002; Wilson & Pearman 2000). The technique is effective for sampling cryptic species that are otherwise difficult to encounter, and is relatively nondestructive to sensitive habitats and those overgrown with aquatic vegetation compared to dip-netting and seining (Johnson & Barichivich 2004). Some researchers bait funnel traps with canned pet food or meat to increase capture rates (Richardson et al. 2000) but there are few studies that directly compare trapping success of these baited traps to non-baited controls, and results have not been consistent across species. For example, Baker (2013) found that beef bait significantly increased captures of great crested newts (*Triturus cristatus* Laurenti) but had no effect for smooth newts (*Lissotriton vulgaris* L.). Bennet et al. (2012) demonstrated that glow sticks in aquatic funnel traps significantly increased capture success of larval ambystomatid salamanders (genus *Ambystoma*) and Grayson & Roe (2007) demonstrated that glow sticks significantly increased capture rates for eastern newts (*Notophthalmus viridescens* Raf.). Wilson & Pearman (2000) found that baiting aquatic funnel traps with gravid females significantly increased captures of adult rough-skinned newts (*Taricha granulosa* Skilton). Most studies evaluating the effect of baiting have focused on larval or aquatic life stages, understandably. To my knowledge, there have been no studies that examine the effect of baiting on capture success of terrestrial-stage individuals temporarily using wetlands for breeding or summer foraging in other species, particularly ambystomatid salamanders. Adult ambystomatid salamanders are difficult to detect on land because of their cryptic fossorial behavior and are typically sampled during the short period of time when adults move towards and away from breeding ponds (Semlitsch 1983; Trenham et al. 2000; Trenham & Cook 2008; Pagnucco et al. 2012). Baiting aquatic funnel traps might increase captures of post-metamorphic individuals when they are in wetlands, particularly in systems where adult salamanders remain in wetlands for several weeks to months after breeding (Rose & Armentrout 1976; personal observations). Increasing adult capture rates in aquatic habitats would allow researchers to sample more efficiently, achieving larger sample sizes, and open the possibility of including additional study sites as capturing terrestrial-stage individuals often requires intensive effort that limits studies to few sites or few individuals among many sites (Semlitsch 1981; Trenham 2001; Steen et al. 2006; Searcy et al. 2013; Scott et al. 2013).

The purpose of this study was to evaluate the efficacy of two bait types (meat and light) on capture success of post-metamorphic western tiger salamanders (*Ambystoma mavortium* Baird) during aquatic funnel-trap surveys in north-central Alberta. The western tiger salamander is a "species of special concern" in Alberta, Saskatchewan, and Manitoba (hereafter, the prairie provinces) (COSEWIC 2012), that often occurs in highly productive, soft-bottomed pothole wetlands that are choked with aquatic vegetation, making dip-netting and seining impractical for sampling individuals. Knowledge of the species in prairie Canada is poor. Populations in the Beaver Hills, a disjunct patch of southern boreal mixedwood forest in central Alberta, exhibit a pattern atypical for ambystomatid salamanders where many adults remain in wetlands for most of the summer following breeding (see Chapter 3). This setting is ideal for testing the effect of baiting funnel traps on adult capture success, because the sampling period is longer.

Methods

Gee minnow traps (length = 42 cm, diameter = 22.9 cm, metal mesh size = 6.35 mm) were baited with meat (Whiskas® canned cat food) or light (glow sticks) and paired with unbaited traps in 2013 and 2014, respectively, to determine if either baiting technique improved capture success of post-metamorphic western tiger salamanders. Sampling occurred within the framework of a larger habitat-use and distribution study, and specific trapping techniques varied slightly by year. Sampling methods for each year are presented separately.

Sampling 2013

I sampled 43 semi-permanent or permanent wetlands in the Beaver Hills for western tiger salamander presence during May, June, and July 2013. Each site was visited three times (once each month) to increase detection probability. At each visit, 10 minnow traps were placed in wetlands overnight and checked the next morning. Five of the 10 traps were baited with approximately 15 g of cat food. Two traps each were placed along either side of an aquatic drift fence (synthetic fiber silt fence, height = 0.9 m, length = 10 m) and the remaining six traps were spread evenly throughout the wetland. Traps were baited in an alternating fashion. Traps were placed in shallow water and tied to a stake to create airspace for air breathing animals.

Sampling 2014

Three wetlands with western tiger salamander populations were sampled continuously from 5 May through 15 August. Minnow traps were placed in shallow water along aquatic drift fences and tied to stakes to maintain airspace. Trap/fence arrays were placed 30 m apart to standardize trapping effort by available habitat. Traps were set in the evening and checked in the morning every 1-2 days. Traps were baited with yellow glow-sticks (dimensions: 20cm x 0.25cm (apprx.)) in an alternating fashion. Baited traps were left unbaited at every other trapping event and vice versa for traps that were initially un-baited. A total of 50 traps were trapping at all times, 25 baited and 25 un-baited.

Analysis

Capture totals were compared among baited and unbaited traps with a chi-square goodness of fit test. A separate analysis was conducted for each bait type.

Results

Thirty-four post-metamorphic individuals were captured in 2013, and 119 in 2014. Cat food was still present in baited traps when checked and glowsticks were still faintly glowing, indicating that bait was consistently present throughout each trapping session. Fewer individuals were captured in traps baited with canned cat food (n=14) than in unbaited traps (n=20), but this difference was not significant (χ^2=1.06, df=1, p=0.30). Fewer post-metamorphic individuals were captured in traps baited with glowstick (n=51) than in unbaited traps (n=68), but this difference was not significant (χ^2=2.43, df=1, p=0.12). Larval captures were not analyzed in 2013 because of few detections in minnow traps. However, larval captures (n=377 total) were significantly higher in traps baited with glowsticks in 2014 (n=208) compared to those in unbaited traps (n=169) (χ^2=8.73, df=1, p=0.031).

Discussion

Baiting aquatic funnel traps with canned cat food or glowsticks did not significantly influence capture success of post-metamorphic individuals using wetlands. However, baiting aquatic funnel traps with glowsticks did significantly improve capture rates for larvae. The ineffectiveness of cat food baiting for post-metamorphic salamanders was not surprising because caudates are typically attracted to living, moving prey. The positive effect of light baiting on capture success of larvae was consistent with results of Grayson & Roe (2007) and Bennet et al. (2012), where glowsticks increased capture success of eastern newts and larval ambystomatid salamanders, respectively. The ineffectiveness of light baiting on post-metamorphic salamanders was therefore surprising. The mismatch between adult and larval susceptibility to light bait could be due to physiological changes in vision during metamorphosis. Eastern tiger salamanders (*A. tigrinum* Green) undergo a change in photoreceptor morphology with metamorphosis that likely enhances vision in terrestrial environments (Wadas et al. 2011).

To my knowledge, this is the first study that examines the effect of bait on capture success of different caudate life stages, or the effect of baiting on western tiger salamanders. The results of this study suggest that the efficacy of baited aquatic funnel traps is inconsistent across taxa and life stages, and should be tested before implementation in aquatic surveys. Future surveys for western tiger salamanders in the prairie provinces should not waste effort in baiting traps if targeting post-metamorphic individuals but should rather allocate resources towards increasing sampling effort with additional traps. Surveys designed to establish western tiger salamander presence/absence would benefit from baiting aquatic funnel traps with glowsticks, as these devices significantly increased the likelihood of detecting larvae.

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Chapter 5: Conclusion and Summary of Findings

Proposed declines of the western tiger salamander across the prairie provinces and elsewhere in Canada have prompted the need for baseline data to gauge the extent of declines and to guide potential management efforts. In this study, I have provided occurrence, abundance, and natural history data necessary for understanding the ecology of Canadian boreal and prairie populations of the western tiger salamander, and to guide future status assessment. This study also addressed the influence of specific terrestrial habitats on the distribution of ambystomatid salamanders across a larger landscape, thus demonstrating the importance of terrestrial habitat in addition to aquatic habitat for breeding and larval development.

The likelihood of occupancy by western tiger salamanders was significantly positively related to the density of northern pocket gopher burrowing activities adjacent to wetlands. Vegetation composition, as characterized by land cover, did not significantly explain distribution. Salamander density (when the species was present) was not significantly explained by any terrestrial habitat variable. These results suggest that the small-scale (micro) habitats used by terrestrial salamanders (e.g. mammal burrows) do not always scale upwards to a larger scale (e.g. land cover) or that there is no relationship between them. More importantly, these results suggest that western tiger salamander distribution in the prairie provinces might be determined and limited largely by the occurrence and density of tunneling mammals, such as the northern pocket gopher. This indicates that salamanders are likely using the tunnel networks of these mammals to escape freezing temperatures in the winter, as further supported by the fact that all 18 terrestrial salamander detections that I made were in or immediately adjacent to pocket gopher tunnels or mounds. The importance of these burrowing mammals is not surprising, given the large amount of evidence demonstrating the commensal relationship between ambystomatid salamanders and small mammals (via tunnels) (Hamilton Jr. 1946; Lomolino & Smith 2003; Richardson et al. 2000; Shipley & Reading 2006; Vaughan 1961; Loredo et al. 2006; Madison & Farrand

1998; Pittman 2005; Steen et al. 2006; Trenham 2001; Faccio 2003; Graeter et al. 2008; Semlitsch 1981; Madison 1997; Johnston 2000).

The western tiger salamander, like the related California and eastern tiger salamanders, has traditionally been considered a 'grassland species' or a denizen of open country (Petranka 1998; Stebbins 2003). Although western tiger salamanders are well adapted to thrive in grassland and semi-arid ecosystems, my study indicates that they should not be characterized as a grassland species, but rather a species that requires micro-habitats created by burrowing mammals that are often associated with grasslands. This is similar to findings by Searcy et al. (2013), where California tiger salamanders used mammal burrows located in the driest available areas. In my study, western tiger salamanders sometimes occurred if terrestrial habitat was largely forested if some level of northern pocket gopher activity was present. Although, northern pocket gophers typically prefer open habitat, pocket gopher density was not strongly correlated with land cover in my study (Pearson's r =-0.32 (forest cover). Potential management efforts for this species in the prairie provinces should not characterize suitable habitat based on the proportion or composition of land-cover elements, but rather based on levels of pocket gopher activity.

The cryptic life history traits of ambystomatid salamanders make terrestrial detection efforts difficult, meaning that researchers are often limited to intensive surveys of few sites or low-intensity surveys of many sites (Semlitsch 1981; Trenham 2001; Steen et al. 2006; Searcy et al. 2013; Scott et al. 2013). As in other studies, terrestrial detection was low and time-intensive in my study. Only 18 individuals were detected on land during 2013 and 2014. However, my study validated the use of survey counts of adults in wetlands as a proxy for relative salamander population density. Sites S1, GS, and S3 were characterized as having low (3 counts), medium (10 counts), and high (21 counts) salamander population densities, respectively, based on low intensity surveys in 2013. Although coarse, these counts reflected more accurate measures of relative densities among sites, as estimated by capture-mark-recapture, where site S1 had 53 (34-94, 95% CI) individuals/ha, GS had 114

(114-200, 95% CI), and S3 had 138 (129-162, 95% CI). Future distribution surveys and long-term monitoring efforts of ambystomatid salamanders need not conduct intensive surveys to characterize a population in any given year, but can rather use counts of individuals from low-intensity surveys to assess general trends.

The previous status assessment of the western tiger salamander estimated the number of populations for the boreal/prairie region as >500, and estimated the probability of a decline as 'unknown' but likely (COSEWIC 2012). My study predicts that there are 625 (420-811, 95% CI) populations in the Beaver Hills alone, suggesting that the estimate of >500 occurrences is likely unrealistically low. Western tiger salamander populations are more prevalent in the Beaver Hills compared to populations in Yellowstone and populations of the eastern tiger salamander in Minnesota, as characterized by wetland occupancy estimates. The likelihood of pond occupancy in the Beaver Hills is 0.55 (0.37-0.71) compared to estimates of 0 – 0.3 in Yellowstone (Hossack et al. 2015; Klaver et al. 2013; Gould et al. 2012) and to estimates of 0.27 – 0.35 for eastern tiger salamanders in Minnesota (MacKenzie et al. 2003). Lastly regarding distribution and abundance, the minimum estimates for the number of post-metamorphic individuals in the Beaver Hills was highly variable and ranged from between 6,720 – 12,976, to 819,420 – 1,572,401, depending on the method of extrapolation, suggesting that caution is required when generating large-scale population estimates from a limited number of well documented sites. Although imprecise, these data can still be used to gauge relative declines if future estimates are made with similar methods.

I provided evidence of summer aquatic habitat-use by post-metamorphic individuals after spring breeding efforts. This is atypical ambystomatid behavior, and indicates that aquatic habitat should be considered as summer foraging habitat for at least some proportion of individuals within a population. The extensive use of wetlands after breeding likely influenced the low terrestrial detections throughout the summer, with most individuals encountered terrestrially in September, when adults were no longer observed in wetlands. Based on result presented in chapter 2, these data suggest that the significant relationship between pocket gopher tunnels and salamander occurrence likely reflects the availability of winter refugia rather than terrestrial foraging habitat, as many individuals foraged aquatically in the summer. Key demographic observations include a sex ratio skewed towards females in individuals using ponds and the occurrence of typical (one-season) larval development. One-season larval development was somewhat surprising because larvae western tiger salamanders in cold climates often require multiple years to complete metamorphosis (Wissinger & Whiteman 1992), and populations within the Beaver Hills live at the northern edge of the global tiger salamander distribution where the growing season is short. However, given the inhospitable nature of breeding wetlands over winter, i.e., low oxygen levels and low water depth due to thick and persistent ice cover, rapid larval development is likely a necessity. Like the western tiger salamander, all four anuran species that occur in the Beaver Hills avoid wetlands in winter and are terrestrial hibernators (Russell and Bauer 2000).

Lastly, I demonstrated that canned catfood and glow sticks are ineffective bait for post-metamorphic western tiger salamanders using wetlands, but that glow sticks are effective bait for larval salamanders. Ambystomatid salamanders are notoriously difficult to detect and thus sampling effort is often a trade-off between the number of wetlands sampled or the number of individuals sampled at a wetland. Baiting has the potential to increase detections and sample size with less intensive efforts. Capture success of post-metamorphic individuals among baited and unbaited traps was not significantly different for either bait type. In contrast, capture success of larval salamanders was significantly higher in funnel traps baited with glow sticks. The effect of glow sticks on larval captures echoed the effect observed by Bennet et al. (2012), where larval ambystomatid salamanders (*A. mabeei* Bishop, *A. opacum* Gravenhorst, *A. talpoideum* Holbrook, and *A. tigrinum*) were caught more frequently in baited traps than un-baited traps. To my knowledge, this is the first study that examined the effect of baiting on multiple life stages of any caudate, or on the western tiger salamander. These results suggest that the effect of baiting varies not only among species (as indicated by Baker (2013)), but also among life stages of the same species. Future surveys for western tiger salamanders should consider baiting if trying to establish presence, but baiting is not worthwhile if sampling focuses on post-metamorphic individuals.

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Appendix

Table A.1. Capture history of post-metamorphic western tiger salamanders after 44 sampling events at site GS, site S1, and site S3. Each row is a specific capture history, where '0' = nondetection during a specific capture event (out of 44 total capture events), and '1' = detection. The frequency column denotes the number of individuals that share a specific capture history.

Site	Capture History	Frequency
GS	00000000000000000000000000000000000000000001	1
	00000000000000000000000000000000000000000100	1
	00000000000000000000000000000000000010000000	1
	00000000000000000000000000000001000000000000	1
	00000000000000000000000000000010000010100010	1
	00000000000000000000000100000100000000100000	1
	00000000000000000000000100100000100010100000	1
	00000000000000000000010000000000000000000000	1
	00000000000000000000010000000000100000010000	1
	00000000000000010000000000000000000000100000	1
	00000001010000000000000000000000000000000000	1
	00000100000000000000000000000000000000000000	1
	00000100000100000000000000000000000000000000	1
	01000000000000000000000000000000000000000000	1
	01000000000000000000000000000000000000100000	1
S1	00000000000000000000000000000000000010000000	7
	00000000000000000000000000000000000000010000	4
	00000000000000000000000000001000000000000000	2
	00000000000000000000010000000000000000000000	2
	00000000000000000000100000000000000000000000	2
	00000000000000000001000000000000000000000000	2
	00000000000000000100000000000000000000000000	2
	00000000000000001000000000000000000000000000	2
	00000000000100000000000000000000000000000000	2
	00000000000000000000000000000000000001000000	1
	00000000000000000000000000000000000010010000	1
	00000000000000000000000000000000010000000000	1
	00000000000000000000000000000000100000010000	1
	00000000000000000000000000000001000000000000	1
	00000000000000000000000000000010000000000000	1
	00000000000000000000000000000010100000000000	1
	00000000000000000000000000001010000000000000	1
	00000000000000000000000100000010000000000000	1
	00000000000000010000000000000000000000000000	1
	00000000000000100000000000001000000000000000	1
	00000000000010000001000000000000000000000000	1
	00000000001000000000000000000000000000000000	1

Table A.1 cont’d.

	00000000001000001000000000000000000000000000	1
	00000000001010000000000000000000000000000000	1
	00000000010000000000000000000000000000000000	1
	00000001000000010000000000000000000000000000	1
	00010000000000000000000000000000000000000000	1
	10000000000000000000000000000000000000000000	1
S3	00000000000000000000000000000000000000010000	2
	00000000000000000000000000000000100000000000	2
	00000000000000001000010000000000000000000000	2
	00000000001000000000000000000000000000000000	2
	00000000000000000000000000000000000000000010	1
	00000000000000000000000000000000000000100000	1
	00000000000000000000000000000000000010000000	1
	00000000000000000000000000000000000100100000	1
	00000000000000000000000000000000010000000000	1
	00000000000000000000000000000000100001000000	1
	00000000000000000000000000000001000000001000	1
	00000000000000000000000000000100100000000000	1
	00000000000000000000000000000101000000000000	1
	00000000000000000000000000001010010000000000	1
	00000000000000000000000000010000000000000000	1
	00000000000000000000000000010000100001001001	1
	00000000000000000000000000100000101001000000	1
	00000000000000000000000001000000000000000000	1
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	00000000000000000000100000000000000000010000	1
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	00000000000000000001000000000000000000000000	1
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	00000000000000000100000001000000100001000000	1
	00000000000000000100000100000100000000000000	1
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	00000000000000010000000000000000000000000000	1
	00000000000001000000000000000000000000010010	1
	00000000000001000000000000010000000000000000	1
	00000000000010001000010001000001000000000000	1
	00000000000100000000000000000000000000000000	1
	00000000000100000000000000000000000000010000	1

Table A.1 cont'd.

00000000000100000001010000000000000000000000	1
00000000001000100000000000100000000000000000	1
00000000001001000100100000001000000000000000	1
00000000100000000000000000000000000000000000	1
00000000100000000000000000000000101001010000	1
00000000100000000000000000001001010000000000	1
00000000100000000100100001010010000000000000	1
00000000100010010100000001000100010000010000	1
00000000101000000000000000000000000000000000	1
00000010000000000001000000000000000000000000	1
00001000000000000000000000000000000000000000	1
00001010101000000000000000001000010010100000	1

Table A.2. Summary of size and weight of western tiger salamander sexes and life-stages among three populations (sites GS, S1, and S3) in the Beaver Hills, Alberta in 2014.

Sex/Life-stage	Weight(g)	SVL(cm)	Total length(cm)	Tail:SVL(95% CI)
Males				
mean	43	11	21	0.86(0.83-0.88)
s.d.	11	1	2	0.06
n	25	25	25	22*
Females				
mean	40	11	19	0.81(0.79-0.82)
s.d.	12	0.9	2	0.06
n	58	58	58	52*
Juveniles				
mean	16	8	14	-
s.d.	7	1	2	-
n	36	36	36	-
Metamorphs				
mean	20	9	15	-
s.d.	6	1	2	-
n	6	6	6	-

* Only individuals of known sex were used to analyze tail:SVL.

Sizes and weights rounded to nearest whole unit to avoid false precision.

Table A.3. Coordinates (NAD 1983 UTM zone 12) for study wetlands at each study site in 2013 and 2014. Salamander abundance and detection data for each site are available in Table 2.1.

* Not included with analyses because landowners actively managed for pocket gopher presence, therefore pocket gopher densities were not natural. However, tiger salamanders and pocket gophers both occurred at this site.

** Not included in analyses because this site was not randomly selected. This is the dugout at N. Annich's house. Tiger salamanders and pocket gopher's were both present at this site.

Pond	UTM Easting	UTM Northing
GS2	372593.4344	5952217.934
G28	379017.4912	5950145.542
P2	361079.8914	5944026.984
G19	368781.9409	5940913.728
G42	380465.1023	5952501.63
P4	370897.1165	5939330.208
PT10	381961.9778	5925182.455
G10	382429.9674	5925304.371
G25	381681.4358	5924588.418
S1	384064.751	5929671.624
P6	382649.939	5923513.606
G33	378322.0584	5952960.8
PT13	372664.7142	5900423.158
P10	374385.9894	5900134.883
G46	375650.7562	5902258.853
S3	375754.8621	5903691.98
G22	375673.6884	5900577.545
P7	369275.6936	5944270.64
P8	365927.8442	5945158.731
G15	370178.2769	5904753.37
PT11	376235.807	5904224.863
P11	371641.4009	5909812.297
P12	369313.2305	5914810.671
G48	373467.2647	5925479.871
G43	373292.8699	5931361.855
P13	373920.92	5928517.71
G31	381957.5709	5930324.836
G13	377553.8591	5926819.377
G27	382876.4011	5923965.454
G36	383494.0789	5933436.6
G14	373449.7813	5915541.701
P15	367488.4644	5934287.427
P16	363284.3434	5928162.448
P17*	359453.8255	5943352.869
P18	363280.4037	5940983.544
P19	382240.2102	5944599.143
P20	380321.4505	5937571.249
P21	378130.0846	5937424.592
P22	380094.4112	5915962.826
P23	378085.0668	5914591.964
P24	377330.2338	5945213.543
NP**	328422.2133	5951641.343

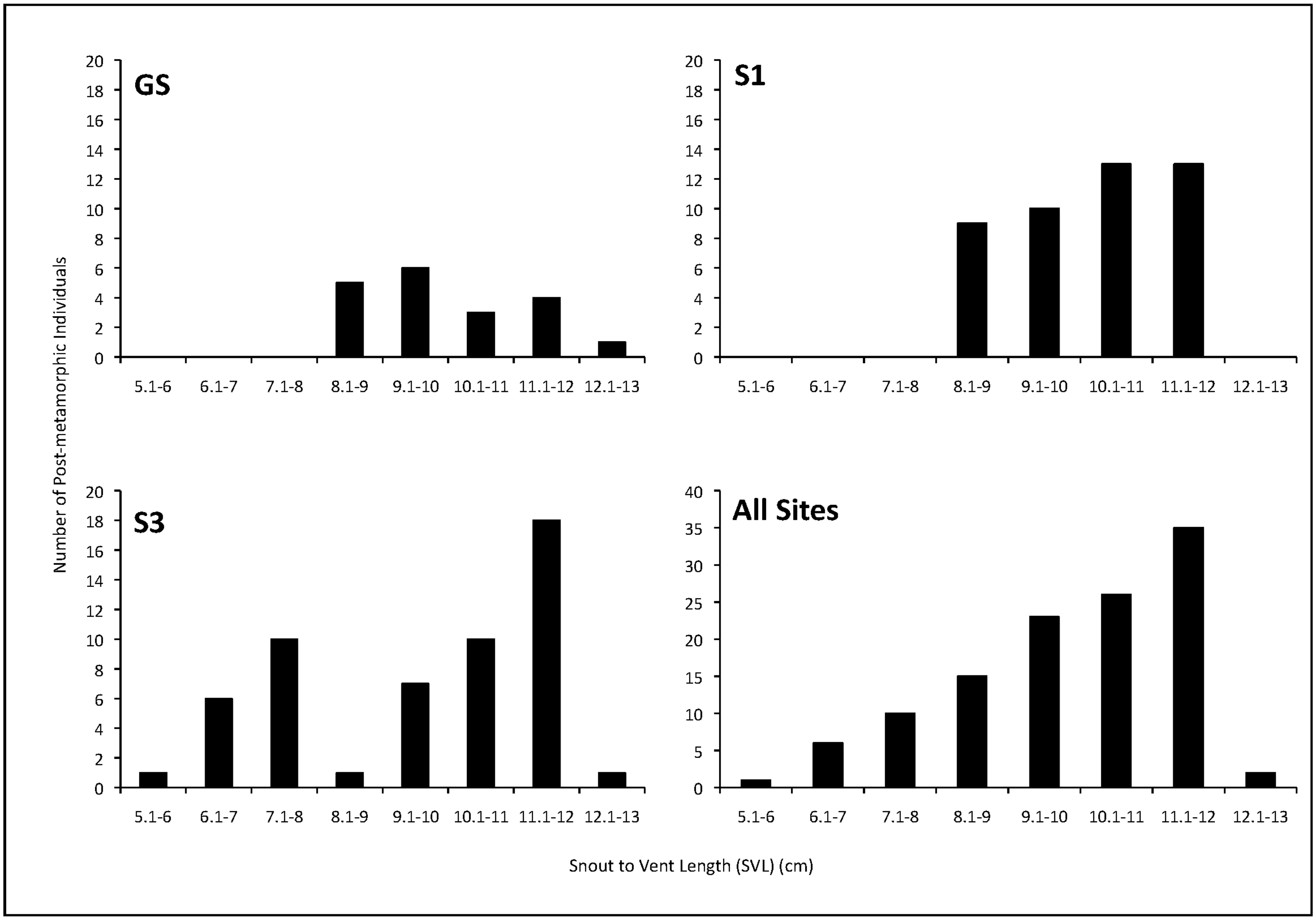

Figure A.1. Size (SVL) distribution of post-metamorphic individuals at all sites in 2014. Size at first capture was used for individuals that were captured multiple times. Note that panel 4 has a different y-axis.