

**DIET ANALYSIS OF ADULT BOREAL CHORUS FROGS (*PSEUDACRIS
MACULATA*) AND PLAINS SPADEFOOT TOADS (*SPEA BOMBIFRONS*)
DURING THE BREEDING SEASON**

JORDAN VOS

Bachelor of Ecosystem Management, Lethbridge Polytechnic, 2022

A thesis submitted
in partial fulfilment of the requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGICAL SCIENCES

Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

© Jordan Vos, 2026

DIET ANALYSIS OF BOREAL CHORUS FROGS (*PSEUDACRIS MACULATA*) AND PLAINS
SPADEFOOT TOADS (*SPEA BOMBIFRONS*) DURING THE BREEDING SEASON

Jordan Vos

Date of Defence: April 24, 2026

Dr. Dan Johnson Thesis Supervisor	Professor	Ph.D.
Dr. Andrew Iwaniuk Thesis Examination Committee Member	Professor	Ph.D.
Dr. Everett Hanna Thesis Examination Committee Member Lethbridge Polytechnic Lethbridge, Alberta	Instructor	Ph.D.
Dr. Dmytro Yevtushenko Chair, Thesis Examination Committee Member	Associate Professor	Ph.D.

DEDICATION

For my husband, Jelle, who continues to go frog hunting with me.

ABSTRACT

Amphibians play roles in Canadian prairie ecosystems, contributing to food web dynamics. Despite their ecological importance, the dietary interactions of prairie amphibians remain understudied, creating a knowledge gap. Prairie amphibians face a unique suite of threats, including habitat loss, agricultural intensification, and climate change. Knowledge of their basic ecology is outdated, limiting effective conservation in agricultural landscapes. This thesis provides an update on the dietary ecology and morphology of the Boreal Chorus Frog (*Pseudacris maculata*) and the Plains Spadefoot (*Spea bombifrons*) in southern Alberta. Stomach contents from breeding adults ($n = 50$) were analyzed using the Index of Relative Importance (IRI), volumetric estimation, and inferential models. Results characterize Boreal Chorus Frogs as a resilient terrestrial generalist; while Coleoptera and Diptera were the numerically dominant, Lepidoptera contributed the majority (62.1%) of dietary volume. Diet composition was significantly influenced by local habitat and constrained by predator morphology; gape width limited maximum prey size, and gravid females consumed significantly fewer prey items than non-gravid females, indicating a reproductive trade-off. Breeding male *S. bombifrons* exhibited a complete fasting during calling, consistent with an “explosive” breeding strategy. These findings support holistic wetland and upland management by demonstrating that *P. maculata* relies on terrestrial prey for 73% of its energy. This dependence underscores the need for protected upland buffers. The consumption of crop pests also identifies a potential “ecological trap,” where terrestrial foraging may increase exposure to agrochemicals. This research establishes a modern baseline for amphibian conservation in Alberta.

CONTRIBUTIONS

Jordan Vos: Conceptualization, Field Investigation, Data Curation, Formal Analysis, Writing
Original Draft

Marele Alvarez: Investigation (field assistance), Resources (literature review contributions)

Abbe Pawluk: Taxonomic Invertebrate Identification

Dr. Dan Johnson: Supervision, Methodology, Taxonomic Invertebrate Identification, Field Visit,
Statistical Consultation, Review and Editing

Dr. Greg Pyle: Funding, Initial Guidance, Committee Member

Dr. Andrew Iwaniuk: Editing, Formatting, Committee Member

Dr. Everett Hanna: Editing, Formatting, Committee Member

ETHICS STATEMENT

Work described in this thesis received research ethics approval from the University of Lethbridge Research Ethics Board under the following applications:

Title	Number	Date
University of Lethbridge – Certificate of Animal Welfare	#2315	July 5, 2023, to July 4, 2024
Government of Alberta – Research Permit	#24-2273	April 18 to December 31, 2024

USE OF GENERATIVE AI

Generative AI was used to aid in choice of statistical analysis, coding, and for some template guidance. All ideas are original and my own. All composition of text is my own.

PREFACE

When I was about eleven years old, I would explore the prairies where my family ranches and raises beef cattle. Particularly during the branding season, when we prepared the year's calves for pasture with their mothers, I would explore the sloughs, creeks, and ephemeral wetlands that were close to the branding corrals. I remember the temporary wetlands filled to the brim with tadpoles and would listen for the calls of any frog or toad. My friends and I would try to catch them and observe their beautiful colouration and the unique calls of each species. I remember mass migrations of Tiger Salamanders in high numbers, including the road mortalities, especially on rainy nights. I remember being deafened by the sheer numbers in calling choruses of Boreal Chorus Frogs, Plains Spadefoots, Great Plains Toads, and Northern Leopard Frogs. Consistently, I recall the abundant number of each species. Now, over a decade later, their number is greatly reduced. Finding any amphibian becomes an honoured moment, something to treasure. As I gained experience in the field of environmental science, studying amphibians was an obvious way for me to combine my passions, and to shed some light on the decline of native amphibians in Canada. This passion has fuelled me through hard times when I felt like giving up. I hope this baseline information on the diet of some prairie amphibian species inspires further research and creates other frog, toad, and salamander enthusiasts. This work is far from over.

ACKNOWLEDGEMENTS

A very sincere thank you to my committee members, Dr. Dan Johnson, Dr. Greg Pyle, Dr. Everett Hanna, and Dr. Andrew Iwaniuk. I appreciate every facet of their input, especially Dan for helping to keep me inspired and to persevere through every twist of life.

To my fellow frog-hunting nerd and brainstormer, Marele Alvarez, thank you for the late nights in the field season, the shared passion for amphibians, and challenging me by discussing papers. This project could not have happened without you. Thank you also to the people that helped make my master's experience bearable at the worst times and for sharing in my joy at the high times, especially Abbe Pawluk.

I am grateful for the experts and mentors that have helped make this project a success, including Brad Taylor, Kris Kendall, Andrew Didiuk, and Nick Cairns. I thank the researchers continuing to look at the ground and get their feet wet for our prairie species, including those continuing work at the Alberta Conservation Association: Brad Downey and Phillip Rose.

I am thankful to the organizations and landowners that gave me permission to do my research on their properties, including the Alberta Conservation Association, the Government of Alberta, Paul von Huene, and Linda Fisher. Thank you very much to the Stryker family and the surrounding land owners that welcomed us in the community.

This project could not have happened without the generous funding from the Natural Sciences and Engineering Research Council (NSERC) and scholarships from the University of Lethbridge and the Alberta Chapter of the Wildlife Society.

Thank you to my family, including my mom, Dana Vos, my dad, Bryce Jans, and my siblings Taylor, Riley, Bobbie, and Harlie. Thank you for promoting my passion and letting me go frog hunting even when there was work to be done.

Thank you to my dear friends that have made the process worth it, for proofreading, letting me ramble about frogs, and to encourage a balance in life. This includes Anastasia Hegedus, Josey Robinson, Ashley Halvorson, Jessie Hein, Randi Harty, Sarah Hatt, and Gabby Kirk.

Finally, thank you to my partner, Jelle Hiddink, for cheering me on through my accomplishments, driving during late nights to go look for amphibians, and helping me through the highs and lows. You are the biggest reason I am able to see this through to completion.

TABLE OF CONTENTS

DEDICATION.....	iii
ABSTRACT	iv
CONTRIBUTIONS.....	v
ETHICS STATEMENT	vi
USE OF GENERATIVE AI	vii
PREFACE.....	viii
ACKNOWLEDGEMENTS	ix
TABLE OF CONTENTS	xi
LIST OF TABLES.....	xiii
LIST OF FIGURES.....	xiv
LIST OF ABBREVIATIONS.....	xv
 CHAPTER 1: INTRODUCTION	 1
1.1 Introduction	1
1.2 Previous Studies on Amphibian Diet	3
1.3 Theoretical Framework	6
1.4 Research Questions and Hypotheses.....	8
CHAPTER 2: METHODS	9
2.1 Introduction	9
2.2 Study Areas	9
2.3 Species Sampled.....	11
2.4 Field Sampling	12
2.5 Laboratory Analysis	13
2.6 Data Analysis and Volume Estimation	15
2.7 Statistical Methods	16
CHAPTER 3: RESULTS.....	18
3.1 Species Overview Statistics	18
3.2 Findings for <i>Pseudacris maculata</i>	19

3.3 Breeding Season Baseline for <i>Spea Bombifrons</i>	31
3.4 Summary of Results	31
CHAPTER 4: DISCUSSION	33
4.1 Determinants of Diet Matrix and Habitat Divergence	33
4.2 Morphological and Physiological Foraging Trade-Offs.....	35
4.3 Conservation Implications and the Pesticide Paradox	38
CHAPTER 5: CONCLUSION.....	41
5.1 Historical Baselines and Data Gaps	41
5.2 Methodological and Seasonal Limitations	42
5.3 Future Research and Conservation Horizons	44
5.4 Synthesis and Final Summary	45
REFERENCES.....	48

LIST OF TABLES

Table 1: Summary of Amphibian Captures and Stomach Content Status Across Three Study Sites in southern Alberta (n=50).	18
Table 2: Descriptive Morphology Statistics for All Captured Anurans by Species, Stomach Status, and Sex (n=50).	19
Table 3: Descriptive Morphology Statistics for All Captured <i>Pseudacris maculata</i> by Site (n=45).	20
Table 4: Diet Composition of Boreal Chorus Frogs (<i>Pseudacris maculata</i>) from southern Alberta, with Prey Items Ranked by Index of Relative Importance (IRI)(n=33).	21
Table 5: Prey categories classified by habitat zone (Terrestrial, Aquatic Surface/Emergent, and Aquatic Sub-Surface) for <i>Pseudacris maculata</i> (n=33).	22
Table 6: Taxonomic composition of prey items recovered from non-empty <i>Pseudacris maculata</i> (n = 33) across three study sites in Southern Alberta. Values represent the total count and total volume (mm ³) per order, with the relative percentage of the total site contribution provided in parentheses.	23
Table 7: Descriptive Statistics for Total Prey Volume and Prey Count in <i>Pseudacris maculata</i> Females by Reproductive Status (n=25).	24

LIST OF FIGURES

Figure 1: Map of the three study sites (Chinook, Escape Coulee, and Silver Sage) within the Dry Mixedgrass Natural Subregion of southern Alberta.	10
Figure 2: Diagram of a drift fence and pitfall trap array used for passive amphibian capture at wetland study sites.	12
Figure 3: Example of dissected and identified stomach contents (UNK = Unidentifiable Contents).	14
Figure 4: Relationship between gape width (mm) and maximum prey length (mm) consumed by <i>Pseudacris maculata</i> (n=33). Prey length is presented on a natural logarithmic scale to normalize variance. The solid line illustrates the linear regression trend, with the grey shaded region representing the standard error (SE).	25
Figure 5: Relationship between predator morphology and maximum ingested prey length (mm, natural log scale) for Boreal Chorus Frogs (<i>Pseudacris maculata</i>) (n = 33). Panel A displays the trend for predator gape width (mm); Panel B displays the trend for predator snout-vent length (SVL, mm).	26
Figure 6: Distribution of total prey volume (mm ³) consumed by female (n = 19) and male (n = 14) <i>Pseudacris maculata</i> . Prey volume is presented on a natural logarithmic scale to improve visualization of the data spread. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent individual frogs with non-empty stomachs.	27
Figure 7: Total number of prey items (N) consumed by female (n = 19) and male (n = 14) <i>Pseudacris maculata</i> with non-empty stomachs. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent the exact prey counts for individual frogs.	28
Figure 8: Distribution of total prey volume (mm ³) consumed by gravid (n = 11) and non-gravid (n = 14) female <i>Pseudacris maculata</i> . Prey volume is presented on a natural logarithmic scale to improve visualization of the data spread. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent individual frogs with non-empty stomachs.	29
Figure 9: Total number of prey items consumed by gravid (n = 11) and non-gravid (n = 14) female <i>Pseudacris maculata</i> . The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent the exact prey count for individual frogs with non-empty stomachs.	30

LIST OF ABBREVIATIONS

ACA	Alberta Conservation Association
ANOVA	Analysis of Variance
DNA	Deoxyribonucleic acid
GIS	Geographic Information System
GLM	General Linear Model
GW	Gape Width
IRI	Index of Relative Importance
IRR	Incidence Rate Ratio
IUCN	International Union for Conservation of Nature
MANOVA	Multivariate Analysis of Variance
MULTISAR	Multiple Species at Risk
<i>N</i>	Number (Sample Size or Count)
NSERC	Natural Sciences and Engineering Research Council
OFT	Optimal Foraging Theory
<i>p</i>	Probability value (p-value)
<i>r</i>	Correlation coefficient (Pearson)
<i>rho</i> (ρ)	Spearman's rank correlation coefficient
SD	Standard Deviation
SE	Standard Error
SVL	Snout-Vent Length
UVB	Ultraviolet B
<i>W</i>	Wilcoxon rank sum test statistic
<i>Z</i>	z-statistic (from GLM)

CHAPTER 1: INTRODUCTION

1.1 Introduction

Value of Studying Amphibians

Amphibians are experiencing more severe global population declines than any other class of vertebrate (González-del-Pliego et al., 2019; Luedtke et al., 2023; Stuart et al., 2004; Alroy, 2015; Catenazzi, 2015). In Canada, herpetofauna (reptiles and amphibians) is considered among the most threatened vertebrate groups, with population declines averaging 34% between 1973 and 2014, and with monitoring data that are less comprehensive than that available for classes such as Aves and Mammalia (Currie & Marconi, 2020). Within the Canadian interior, amphibians inhabiting prairie ecosystems face multiple threats, including habitat loss and degradation, climate change, wetland pollution, infectious diseases, and increased UVB (Ultraviolet B) radiation (Collins, 2010; Blaustein et al., 2011). These stressors, along with competition, invasive species, predation, and contaminants, often lead to population declines and extinctions (Blaustein et al., 2011; Collins, 2010). Amphibians select habitats based on their needs for unpolluted water and breeding habitat, as well as connectivity. Consequently, seasonal wetlands located within agricultural land are utilized less frequently than those found on native prairie or protected lands. The disparity exists because wetlands embedded in conservation grasslands provide the essential habitat required to sustain amphibian biodiversity across the Prairie Pothole Region (Balas et al., 2012). Restoration of amphibian habitat has the potential to support population recovery following anthropogenic disturbance. It is not known what role diet plays specifically for prairie amphibians in habitat selection, migration, breeding, life history, overwintering, or especially the effects of uptake of pollutants through prey items.

In prairie ecosystems, amphibians function both as prey for higher trophic levels, and as predators of a wide variety of invertebrates, including species that humans consider pests. As such, they contribute valuable ecosystem services such as natural pest control in agricultural landscapes (Newman, 1999; Pafilis et al., 2019; Valencia-Aguilar et al., 2013). Despite their ecological role, amphibians remain one of the most understudied vertebrate classes, particularly in grassland ecosystems (González-del-Pliego et al., 2019).

Attention has been given to rare or declining species, and common amphibians have often been overlooked in basic life history research. The knowledge gap in common species presents a risk, as early warning signs of population stress may go unnoticed until declines are well underway. Among the least understood aspects of prairie amphibian ecology is diet composition. Diet is a fundamental component of life history, influencing individual fitness, population health, and interactions with the environment. Understanding dietary preferences (i.e., which prey types are most frequently consumed), prey selection (i.e., how amphibians choose among available prey), prey size limitations, and prey habitat use can provide insight into how these animals meet their nutritional needs in variable and often fragmented prairie ecosystems (Gustafson & Newman, 2016). These parameters also help explain broader patterns in amphibian ecology, such as breeding success, movement, and habitat use. For example, if prey items are exposed to pesticides or other agricultural contaminants, they may serve as a route of chemical exposure for amphibians, potentially leading to stress or broader ecological disruptions such as the loss of natural pest regulation (Hopkins, 2007). Therefore, diet may play a previously underestimated role in how amphibians respond to anthropogenic stressors. This thesis seeks to fill critical knowledge gaps and contribute foundational data that may inform conservation strategies, especially for common species whose declines might otherwise go undetected.

1.2 Previous Studies on Amphibian Diet

Diet Content Methodologies

Historically, there have been several techniques used to investigate amphibian diet, each with advantages and limitations. In early diet studies, stomach contents were obtained from dissections of deceased amphibians (Newman, 1999; Moore & Strickland, 1954, 1955; Jancowski & Orchard, 2013). While dissection was an effective method, it posed ethical and conservation concerns, especially when working with at-risk species, and is now considered questionable in cases outside of museum specimens (Solé & Rödder, 2010). However, lethal sampling remains a common and valuable practice in the study of invasive species. In these instances, dissection provides high-quality, comprehensive dietary data while simultaneously serving as a management tool to remove problematic species from the ecosystem. For example, research on invasive Cane Toads (*Rhinella marina*) and American Bullfrogs (*Lithobates catesbeianus*) utilizes dissection to precisely quantify their impact on native biodiversity while actively reducing their population density in affected regions (Heise-Pavlov & Longway, 2011; Jancowski & Orchard, 2013). Solé et al. (2005) formalized stomach flushing protocols, which was endorsed as a minimally invasive procedure for diet analysis in amphibians. The procedure involves placing the specimen under anaesthetic and gently opening the mouth, inserting a flexible tube attached to a syringe full of water, and flushing water into the stomach to expel the foraged prey items (Solé et al., 2005). Invertebrates can then be identified by an expert, or through DNA analysis (Solé et al., 2005). Solé et al. (2005) explicitly recommend stomach flushing as alternative to lethal sampling of amphibians because of ongoing global declines. Mahan and Johnson (2007) modified the stomach flushing procedure further by negating the use of anaesthetic. Gray Treefrogs (*Hyla versicolor*) could be immobilized by hand, which allowed scientists to recognize signs of distress

sooner. Some researchers have also noted the higher risk of mortality that accompanies the use of anaesthetic during stomach flushing (Mahan & Johnson, 2007; Solé & Rödder, 2010). Many dietary studies followed both versions of stomach flushing protocols, with great success (Ahlm, 2015; Pafilis et al., 2019; Roner et al., 2020; Solé & Rödder, 2010).

More recent research has adopted fecal DNA analysis as a method, which requires holding the specimen for a longer period of time, until they expel their fecal matter (Hodgkison & Hero, 2002; Pereira & Harris, 2021). Hodgkison and Hero (2002) chose this method specifically because it was the least destructive option for the endangered frogs they studied. Pereira and Harris (2021) note that while microscopic assessment of fecal material has limitations, DNA metabarcoding offers more taxonomic clarity. However, the degree to which prey can be identified is limited by the choice of DNA primers. For example, their 16S primers only identified insects, which meant that they missed other groups like mollusks, arachnids, and myriapods (Pereira & Harris, 2021).

Combining stomach flushing and DNA analysis has the potential for more accurate identification of unknown prey, while still leaving the stomach contents mostly whole for visual identification (Ahlm 2015). However, one potential drawback of stomach flushing is bias due to differential digestion rates. Soft-bodied prey like worms (phylum Annelida) and mollusks (phylum Mollusca) digest faster and may be underrepresented in stomach samples, whereas harder, sclerotized prey like ants (Hymenoptera) and beetles (Coleoptera) may be overrepresented (Solé & Rödder, 2010).

Findings and Patterns of Diet Analysis

Generally, most adult amphibians are characterized as opportunistic, generalist predators (Jancowski & Orchard, 2013; Measey et al., 2015). Amphibian diets are dominated by

arthropods, with Coleoptera (beetles) and Hymenoptera (primarily Formicidae, or ants) frequently reported as the most numerous prey items across a wide range of species and ecosystems (Ahlm, 2015; Mahan & Johnson, 2007; Smith, Gray, & Quarles, 2004). However, to consider amphibians as generalists overlooks the other factors that may drive their dietary choices. Foraging is constrained by predator morphology, shaped by behaviour, and influenced by the environment. One of the most critical constraints is predator body size and gape width, which directly determine the maximum size of prey that can be consumed (Hodgkison & Hero, 2002; Newman, 1999). Even though the majority of amphibians are generalist predators, some studies report evidence of dietary specialization and dietary differences among species, even within the same habitat. Research in Borneo by Ahlm (2015) found that while some frog families behaved as generalists, others (Bufonidae and Megophryidae) were dietary specialists. Furthermore, diet can change with age. Ontogenetic shifts are common, where prey size and type change as an animal grows from a juvenile to an adult (Hodgkison & Hero, 2002; Solé & Rödder, 2010). These variations underscore the risk of overgeneralization and highlight the need to understand foraging ecology at the species and population level. To begin explaining these patterns, it is necessary to ground the research in the theoretical principles and sampling design that govern foraging behaviour.

Foundational research on the diet of prairie amphibians is scarce and dated. The only comprehensive amphibian dietary surveys for the prairies were conducted in Alberta seventy years ago by Moore and Strickland (1954; 1955). They established a baseline by examining the stomach contents of several key species, including the Northern Leopard Frog (then *Rana pipiens*, now *Lithobates pipiens*), the Canadian Toad (then *Bufo hemiophrys*, now *Anaxyrus hemiophrys*), and the Boreal Chorus Frog (then identified as *Pseudacris nigrita*, now *Pseudacris*

maculata). Their follow-up study expanded this scope to include the Wood Frog (then *Rana sylvatica*, now *Lithobates sylvaticus*), the Columbia Spotted Frog (then *Rana pretiosa*, now *Rana luteiventris*), and the Western Toad (then *Bufo boreas*, now *Anaxyrus boreas*). Neither the Plains Spadefoot (*Spea bombifrons*) nor the Western Tiger Salamander (*Ambystoma mavortium*) were included in either of these studies, nor described in other sources for the province or the prairies of Canada. Foundational knowledge for Alberta's amphibians relies on data collected seven decades ago, using taxonomic names that have since been updated with stomach content collection protocols that have since been abandoned due to ethical concerns. The dated foundational knowledge highlights a critical gap in our understanding of prairie amphibian diets in Alberta and underscores the urgent need for a modern re-evaluation.

1.3 Theoretical Framework

The ecological study of amphibian diet is grounded in Optimal Foraging Theory (OFT), which assumes that natural selection favours individuals that maximize their net energy intake per unit of time. As established by Pyke et al. (1977), foraging efficiency is determined by a series of hierarchical decisions regarding diet breadth, patch selection, and movement. Within this framework, a “profitable” prey item is one where caloric gain significantly outweighs the time and energy spent on capture and handling.

A foundational concept supporting these energetic goals is the relationship between physical form and function. Work by Emerson (1985) established predictive models linking frog skull morphology to diet type, arguing that anatomy fundamentally dictates the prey a species can consume. Their research demonstrates that frogs consuming small, slow prey tend to have relatively short jaws, while those consuming larger prey possess longer jaws (Emerson, 1985). This establishes a relevant framework: skeletal morphology (specifically gape width) dictates the

physical boundaries of a potential dietary niche. Modern validations in generalist predators confirm that larger individuals target larger or more “profitable” prey to optimize this intake (Meyer et al., 2025).

Building on these anatomical constraints, kinematic studies reveal that frogs are highly adaptive predators that modify their behaviour based on sensory information from their prey. Research on *Lithobates pipiens* by Anderson and Nishikawa (1993; 1996) demonstrated that frogs use distinct motor programs for different prey sizes. For small prey, *L. pipiens* uses rapid tongue protraction, but for large prey, it reverts to a more primitive pattern involving a full-body lunge and jaw prehension (Anderson & Nishikawa, 1993; 1996). This ability to switch between feeding strategies showcases a remarkable behavioural flexibility.

Such flexibility allows amphibians to assess prey profitability and use different foraging tactics. Jaeger and Rubin (1982) demonstrated that terrestrial amphibians are capable of distinguishing between prey based on profitability, a tactical decision-making process that allows generalists like *P. maculata* to operate along a continuum between sedentary “sit-and-wait” strategies and active foraging (Das, 1996). This sedentary mode is often more energetically efficient during periods of high reproductive expenditures, as it maximizes net gains per unit of energy spent (Das, 1996).

In diverse prairie communities, co-existing species often avoid direct competition by partitioning resources along three primary axes: diet, space, and time (Toft, 1985). While sympatric species may overlap in diet, they often select for different microhabitats or foraging areas to minimize competition (Das, 1996). This interplay between mechanical constraints, behavioural flexibility,

and resource partitioning provides the necessary context for evaluating the dietary ecology of prairie amphibians during the breeding season.

1.4 Research Questions and Hypotheses

The current understanding of prairie amphibian ecology is limited by several knowledge gaps: a reliance on seventy-year-old dietary data, a total absence of diet records for Canadian populations of the Plains Spadefoot, and a lack of modern volumetric analysis to quantify the energetic importance of rare prey. To address these deficiencies, this research established a modern baseline for amphibian conservation in southern Alberta by investigating the interplay between habitat, morphology, and reproductive biology.

I first sought to characterize the taxonomic composition and foraging microhabitats of the Boreal Chorus Frog across native and restored grasslands, specifically testing the extent of their reliance on terrestrial versus aquatic habitat subsidies. Building on this environmental context, the study then evaluated the physical constraints of foraging by determining how gape width may limit maximum prey size.

Furthermore, recognizing that diet is not uniform across a population, I analyzed intraspecific variations to see how sexual dimorphism and reproductive status influence foraging. This involved a comparison of energetic intake between males and females, alongside a targeted investigation into the physical and behavioural trade-offs that lead to reduced foraging frequency in gravid females. Finally, this work documented the feeding status of male Plains Spadefoots during explosive breeding events, providing a novel data point for this species at its northern range limit. By synthesizing these diverse ecological parameters, this thesis provides a snapshot of the role of common and at-risk amphibians within the food webs of the Canadian prairies.

CHAPTER 2: METHODS

2.1 Introduction

Understanding the diet of prairie amphibians is an important step in assessing their ecological role and conservation needs, yet the foundational data for species in the Canadian prairies remain scarce; the primary baseline surveys date back seventy years (Moore & Strickland, 1954; 1955). This knowledge gap limits modern conservation planning, as it obscures how native amphibians interact with agricultural environments, altered wetland dynamics, and fluctuating invertebrate communities. To establish a rigorous and repeatable methodological framework, this study developed a field and laboratory sampling design targeting two anuran species: the Boreal Chorus Frog (*Pseudacris maculata*) and the Plains Spadefoot (*Spea bombifrons*).

2.2 Study Areas

Study sites were initially selected using Geographic Information Systems (GIS) analysis to identify suitable, accessible wetlands within the Dry Mixedgrass Natural Subregion of southern Alberta (Alberta Parks, 2015). Final site selection was confirmed on the ground at three locations managed by the Alberta Conservation Association (ACA): Chinook, Silver Sage, and Escape Coulee (Figure 1).

Rather than distributing survey efforts broadly across modified landscapes like irrigation canals, river corridors, or agricultural farm dugouts (which are confounded by routine chemical runoff, artificial hydroperiods, and frequent mechanical disturbance) sampling was intentionally concentrated within these three conservation tracts. This localized, multi-species inventory design was used to maximize the probability of encountering the target species within a geographically constrained area, ensuring rigorous data collection within strict logistical and budgetary boundaries.

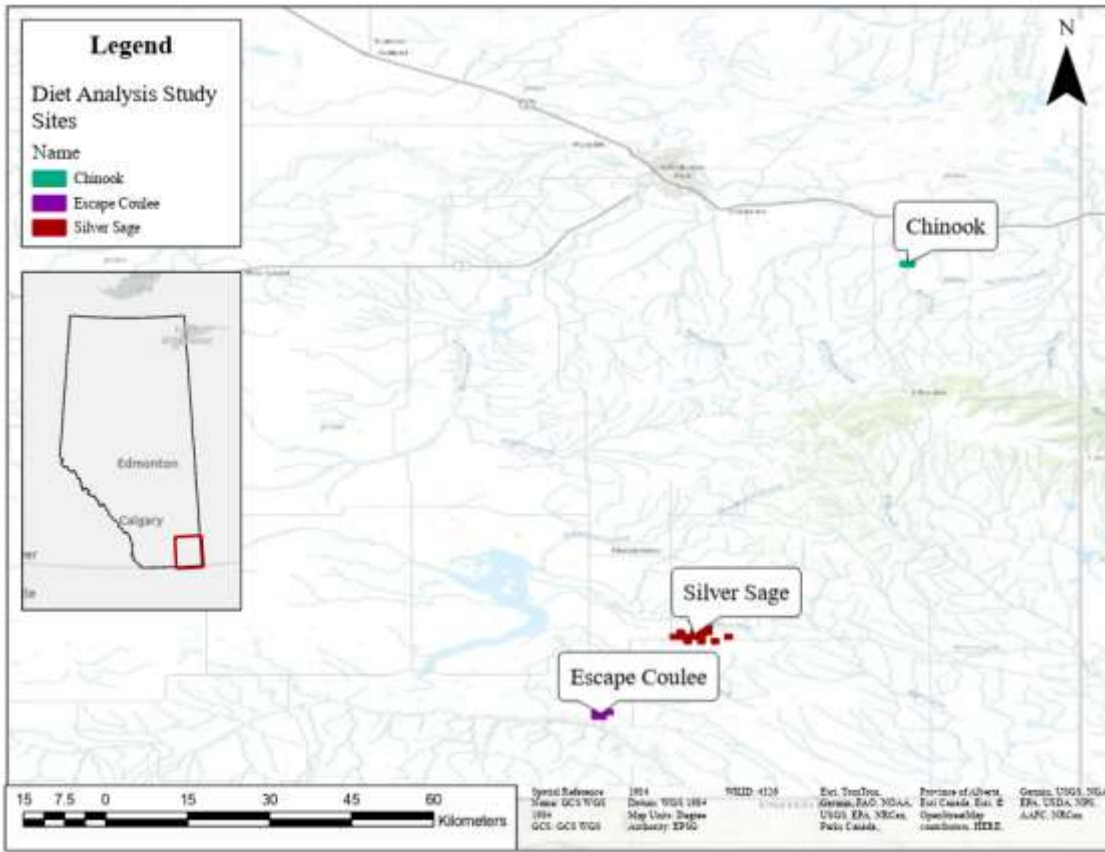


Figure 1: Map of the three study sites (Chinook, Escape Coulee, and Silver Sage) within the Dry Mixedgrass Natural Subregion of southern Alberta.

The choice of these specific locations was guided by a combination of historical records, citizen-science databases (e.g., iNaturalist), direct consultation with ACA regional biologists, and preliminary reconnaissance surveys. Each site was strategically selected to capture a distinct combination of microhabitats and targeted species:

- Chinook: Characterized by a slow-moving lotic creek system modified by beaver (*Castor canadensis*) infrastructure. This site was selected because the deep pools, flooded regular channels, and dense woody debris created by beaver dams provide ideal cover and overwintering refugia for *Lithobates pipiens*, whose breeding activity on the site was confirmed by the presence of tadpoles in preceding seasons. While active adults were

visually confirmed using the deep-water and woody debris escape routes during the survey window, their rapid flight responses restricted successful physical capture, leaving *P. maculata* as the primary sampled anuran at this location.

- Silver Sage: Representing a restored grassland, this site was integrated into the study to assess amphibian habitat use within restored systems and to investigate whether the specialized, fossorial *S. bombifrons* or *Anaxyrus cognatus* use restored grasslands during the breeding window.
- Escape Coulee: Characterized by rugged, undisturbed native prairie coulee topography, this site was chosen specifically because historical records and clustered citizen-science observations identified the location as the highest probability of encountering *S. bombifrons* and *A. cognatus*.

While all three locations featured active breeding assemblages of *P. maculata* and evidence of *A. mavortium*, they offered an ideal structural mosaic: Chinook and Escape Coulee served as historical native prairie baselines, while Silver Sage provided an active look at a restored grassland interface. This design allowed for a targeted assessment of prairie amphibian foraging across varying conditions while maintaining high logistical efficiency.

2.3 Species Sampled

Based on their presence at the study sites and the objectives of this research, this study focused on two anuran species: the Boreal Chorus Frog and the Plains Spadefoot. While the Western Tiger Salamander was observed, they were not captured in sufficient numbers and were excluded from analysis.

2.4 Field Sampling

Field sampling was conducted between April 15 and June 30, 2024. All animal handling and sampling procedures were approved by the University of Lethbridge Animal Welfare Committee (Permit #2315) and conducted under authority of a Government of Alberta Research Collection Permit (Permit #24-2273). Amphibians were captured using three methods: passive capture in drift fence arrays with pitfall traps (Figure 2), active hand-capture during diurnal and nocturnal auditory surveys at wetland edges, and opportunistic hand-captures. Upon capture, each specimen was placed in an individual, ventilated plastic container with a small amount of water from the source wetland and processed immediately in the field. Total handling time before the recovery period was one to five minutes, with an average handling time of two minutes.

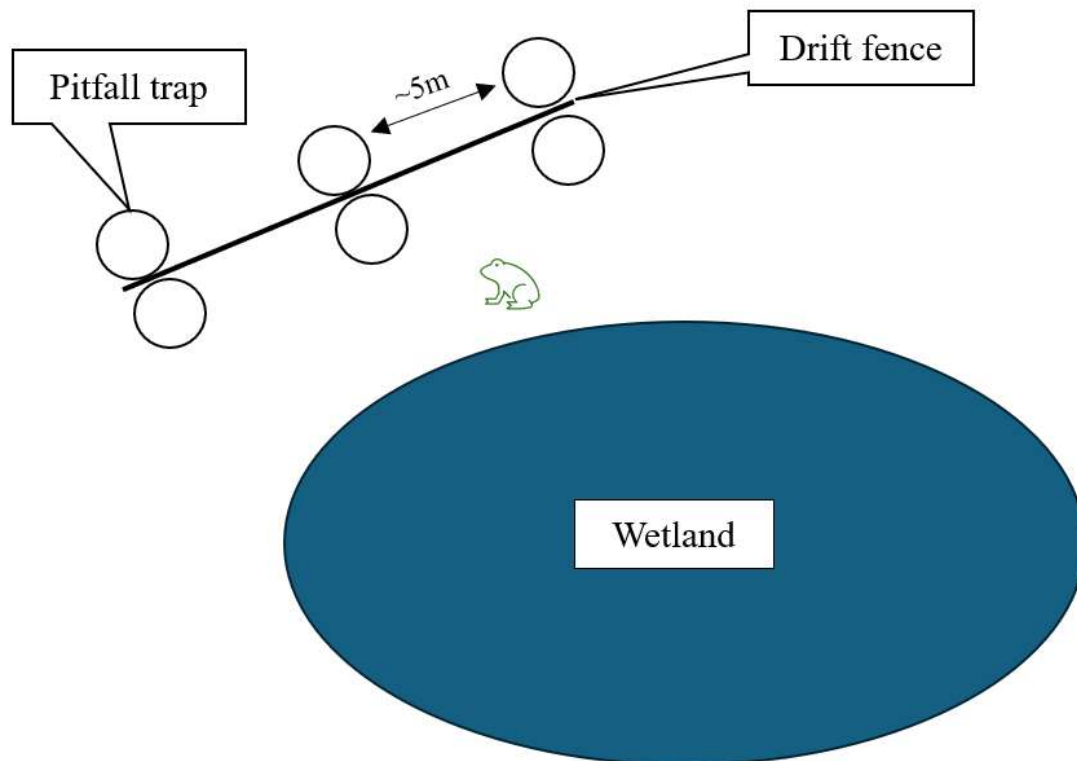


Figure 2: Diagram of a drift fence and pitfall trap array used for passive amphibian capture at wetland study sites.

Snout-vent length (SVL) and gape width (GW) of each frog were measured to the nearest millimeter using a ruler. Stomach contents were obtained non-lethally using the stomach flushing technique adapted from Solé et al. (2005). Due to small size in Boreal Chorus Frogs, we used appropriately sized tubing [e.g., 1.7 mm diameter flexible tubing for *Pseudacris maculata*] and a smaller volume of water [10-20 ml]. Each frog was gently restrained without anesthetic to allow for constant monitoring of its condition, should complications arise during the procedure. Following the procedure, frogs were held for five to ten minutes before release directly into source water bodies. Regurgitated prey items were preserved in 70% ethanol for later analysis.

2.5 Laboratory Analysis

In the lab, preserved stomach contents were sorted and identified to the lowest possible taxonomic level, typically Order or Family, using a dissecting microscope and seeking the knowledge of entomological experts (Figure 3). To quantify prey items, a minimum diagnostic part, such as a head capsule or pair of elytra, was required to count as a single individual. This ensured that fragmented remains of a single prey item were not counted multiple times.

The total length of each intact prey item was measured from the rostral to the caudal end to the nearest 0.1 of a millimeter using a reticle. For partially digested items, original length was estimated by comparing key, sclerotized body parts (e.g., Coleoptera elytra) to intact reference specimens found in the samples. This allowed for the standardization of prey size to reflect its state at the time of consumption.

Following taxonomic identification, all quantifiable prey items were categorized by their expected foraging microhabitat to better understand the amphibian foraging location. Prey were assigned to one of three habitat zones: Terrestrial (prey living on land or soil, e.g., spiders, ants),

Aquatic Sub-Surface (true aquatic larval stage or organisms found below the water's surface), and Aquatic Surface/Emergent (invertebrates utilizing the air-water interface or recently emerged adults, e.g., mosquitoes, flea beetles). The specific classification was determined through a combination of expert consultation and direct field observation of invertebrate behaviour during the sampling period. For instance, flea beetles (Family: Chrysomelidae) while primarily terrestrial, were frequently observed bouncing on the water surface and were therefore classified as Aquatic Surface/Emergent prey, reflecting their accessibility to the frogs. Prey items with habitats unidentified, or too broad to categorize a specific habitat, were excluded from habitat-specific analysis.

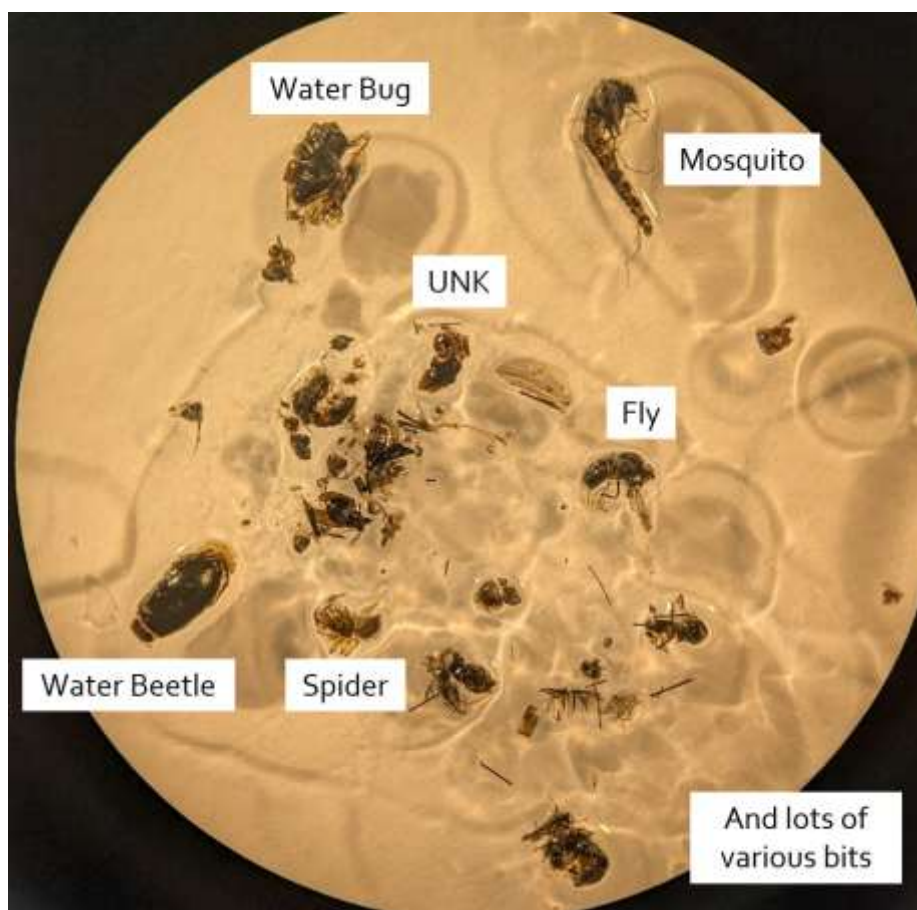


Figure 3: Example of dissected and identified stomach contents (UNK = Unidentifiable Contents).

2.6 Data Analysis and Volume Estimation

The biomass (dry mass in mg) of each identifiable item was estimated from its measured or estimated length (mm) using published length-mass regression equations in the form of $\text{Mass} = a * \text{Length}^b$, excluding the digested pieces that could neither be measured nor identified. This approach is a standard and widely accepted practice for non-destructively estimating invertebrate biomass and volume from linear measurements (Johnston & Cunjak, 1999).

To ensure the highest possible accuracy, taxon-specific regression coefficients (a and b) were sourced from comprehensive and regionally relevant studies. Equations were primarily drawn from the comprehensive review of North American aquatic invertebrates by Benke et al. (1999) and supplemented with data from Canadian studies to provide more geographically appropriate estimates (Johnston & Cunjak, 1999). For terrestrial taxa, coefficients were sourced from foundational work on terrestrial arthropods (Rogers et al., 1976; Sample et al., 1993; Sage, 1982). Estimated dry mass was then converted to wet mass by multiplying by a standard conversion factor of 5 (Benke et al., 1999). Finally, volume (mm^3) was assumed to represent wet mass (mg), based on the assumption that fresh invertebrate tissue has a density of approximately 1 mg/mm^3 .

Prey items that were too digested to allow for reliable length estimation were included in frequency and numeric counts but were excluded from volumetric and Index of Relative Importance (IRI) analyses (Solé & Rödder, 2010). To describe the diet, three standard metrics were calculated for each prey category: Percent Frequency of Occurrence (%F), Percent Numeric Abundance (%N), and Percent Volume (%V). The Index of Relative Importance (IRI) was then calculated using the formula: $\text{IRI} = (\%N + \%V) * \%F$ (Pinkas et al., 1971).

2.7 Statistical Methods

All statistical analysis were performed using the R statistical computing environment (R Core Team, 2024). Data cleaning, manipulation, and visualization were conducted using the tidyverse (Wickham et al., 2019), ggpubr (Kassambara, 2023) packages. Prior to model implementation, continuous environmental and morphological datasets were evaluated for normality and homogeneity of variance using Shapiro-Wilk tests and Levene's tests, respectively. Because prey count data consisted of discrete, non-negative integers and continuous dietary volumes exhibited severe right-skewness that violated parametric assumptions, non-parametric equivalents and generalized linear frameworks were used (Sullivan, 2017). Statistical significance across all operations was assessed at an alpha level of $\alpha = 0.05$.

To compare diet composition between study sites, a Fisher's Exact Test was employed. This exact test was selected over the Chi-Square test to account for small sample sizes at the Chinook ($n = 4$) and Escape Coulee ($n = 5$) sites. Sites were analyzed by pooling the Chinook and Escape Coulee "Native Prairie" sites against the Silver Sage "Restored Grassland" site to test for broad habitat-based differences in prey frequency.

To evaluate sexual dimorphism regarding total ingested prey volume (V), a two-tailed Wilcoxon Rank Sum Test (Mann-Whitney U Test) was conducted to compare male and female cohorts. To evaluate the physiological and behavioural foraging trade-offs experienced by female anurans during the breeding season, numeric prey counts (N) per individual were modeled against reproductive status (gravid vs. non-gravid) using a Generalized Linear Model (GLM). The model was fitted using a log-link function and a Poisson error distribution to explicitly account for the discrete, bound nature of the count data. To validate these findings using a classic parametric framework, a parallel one-way Analysis of Variance (ANOVA) was also performed. Because raw

prey counts violated assumptions of normality and homoscedasticity, data were log-transformed ($\log(x + 1)$) prior to linear modelling to satisfy parametric assumptions, where x represents the total numeric prey count per individual.

The relationship between predator morphology and maximum prey size was assessed using Spearman's Rank Correlation (ρ or ρ). This non-parametric correlation method was chosen to minimize the influence of outliers (e.g., rare, high-volume prey items) and to test for monotonic relationships. Discrete, independent correlation models were run to contrast maximum prey length against both SVL and GW.

CHAPTER 3: RESULTS

3.1 Species Overview Statistics

A total of forty-five Boreal Chorus Frogs and five Plains Spadefoots were captured across the three study sites between April 15 and June 30, 2024 (Table 1). Of the Boreal Chorus Frogs, thirty-three (nineteen females, fourteen males) had non-empty stomachs and were used for diet analysis, the remaining 12 individuals exhibited empty stomachs. All five Plains Spadefoots captured were males and all had empty stomachs; this finding prevented further trophic analyses.

Table 1: Summary of Amphibian Captures and Stomach Content Status Across Three Study Sites in southern Alberta (n=50).

Site	<i>Pseudacris maculata</i>					<i>Spea bombifrons</i>				
	Non-Empty		Empty		Total	Non-Empty		Empty		Total
	Female	Male	Female	Male		Female	Male	Female	Male	
Chinook	1	3	0	0	4	0	0	0	0	0
Escape Coulee	0	5	0	0	5	0	0	0	5	5
Silver Sage	18	6	9	3	36	0	0	0	0	0
Total	19	14	9	3	45	0	0	0	5	5

Note: Sample size (n = 50) represents individuals captured across three study sites. “Non-Empty” denotes individuals from which identifiable stomach contents were recovered via stomach flushing, while “Empty” denotes individuals with no recoverable prey items.

In all captured individuals the baseline physical dimensions were evaluated to establish structural context before testing for selective feeding behaviours. The morphological parameters of the sampled populations are presented below (Table 2). Within *P. maculata*, there was no notable size difference between empty and non-empty individuals. Males in the non-empty sample (Mean SVL = 24.7 mm, Mean GW = 5.8 mm) were, on average, slightly larger than females (Mean SVL = 24.2 mm, Mean GW = 5.4 mm).

Table 2: Descriptive Morphology Statistics for All Captured Anurans by Species, Stomach Status, and Sex (n=50).

Variable	Species	Stomach Status	Sex	n	Mean (mm)	SD (mm)	SE (mm)	Min (mm)	Max (mm)
Snout-Vent Length (SVL)	<i>P. maculata</i>	Non-Empty	Female	19	24.1	1.4	0.3	21.0	27.0
			Male	14	24.6	1.7	0.5	22.0	29.0
		Empty	Female	9	24.2	1.8	0.6	20.0	26.0
			Male	3	24.7	1.2	0.7	24.0	26.0
	<i>S. bombifrons</i>	Empty	Male	5	50.6	6.2	2.8	44.0	60.0
Gape Width (GW)	<i>P. maculata</i>	Non-Empty	Female	19	5.5	0.6	0.1	5.0	7.0
			Male	14	5.4	0.5	0.1	5.0	6.0
		Empty	Female	9	5.9	0.6	0.2	5.0	7.0
			Male	3	5.7	0.6	0.3	5.0	6.0
	<i>S. bombifrons</i>	Empty	Male	5	19.2	1.3	0.6	18.0	21.0

Note. SD = Standard Deviation; SE = Standard Error of the Mean; Min = Minimum; Max = Maximum.

3.2 Findings for *Pseudacris maculata*

To assess whether frog size was a confounding variable for site-based diet comparisons, the morphology of all forty-five captured *P. maculata* was compared across sites (Table 3). Mean SVL and GW were consistent across all three locations. For example, mean SVL was 24.5 mm (n=4) at Chinook, 25.2 mm (n=5) at Escape Coulee, and 24.1 mm (n=36) at Silver Sage. A Kruskal-Wallis rank sum test confirmed that these spatial variations were not statistically significant for either SVL ($X^2 = 3.37$, $df=2$, $p = 0.185$) or GW ($X^2 = 2.41$, $df=2$, $p = 0.299$). These results statistically verify that localized differences in frog morphology were not a confounding factor in subsequent site-based dietary comparisons.

Table 3: Descriptive Morphology Statistics for All Captured *Pseudacris maculata* by Site (n=45).

Variable	Site	n	Mean (mm)	SD (mm)	SE (mm)	Min (mm)	Max (mm)
Snout-Vent Length (SVL)	Chinook	4	23.0	0.8	0.4	22.0	24.0
	Escape Coulee	5	25.2	1.3	0.6	24.0	27.0
	Silver Sage	36	24.3	1.6	0.3	20.0	29.0
Gape Width (GW)	Chinook	4	5.3	0.5	0.3	5.0	6.0
	Escape Coulee	5	5.8	0.4	0.2	5.0	6.0
	Silver Sage	36	5.6	0.6	0.1	5.0	7.0

Note. SD = Standard Deviation; SE = Standard Error of the Mean; Min = Minimum; Max = Maximum.

The diet composition of the thirty-three non-empty *P. maculata* is detailed below (Table 4). A total of two hundred two prey items, representing at least nine invertebrate orders, were identified. Based on the Index of Relative Importance (IRI), Coleoptera (beetles) were the most important prey item (IRI = 2566.7), ranking highest in both volume (20.8%) and frequency (57.6%). The second most important category was “Unidentified Arthropod” (IRI = 2173.7). This abundance was attributed to its high numeric abundance (31.2% and its presence in 69.7% of all non-empty stomachs), highlighting the prevalence of heavily digested prey.

Diptera (flies; IRI = 1550.8) and Lepidoptera (moths/butterflies; IRI = 777.2) were also key components of the diet of Boreal Chorus Frogs. While numerically rare (2.0% of items), Lepidoptera was the single largest contributor by volume (62.1%).

Table 4: Diet Composition of Boreal Chorus Frogs (*Pseudacris maculata*) from southern Alberta, with

Prey Items Ranked by Index of Relative Importance (IRI)(n=33).

Prey Order	N	V (mm³)	F	%N	%V	%F	IRI
Coleoptera	48	87.1	19	23.8	20.8	57.6	2566.7
Unidentified Arthropod	63	0	23	31.2	0.0	69.7	2173.7
Diptera	44	27.8	18	21.8	6.6	54.5	1550.8
Lepidoptera	4	259.9	4	2.0	62.1	12.1	777.2
Hemiptera	15	24.7	12	7.4	5.9	36.4	484.7
Hymenoptera	7	10.4	6	3.5	2.5	18.2	108.3
Trombidiformes	9	0.8	7	4.5	0.2	21.2	98.6
Araneae	6	7.0	6	3.0	1.7	18.2	84.3
Sarcoptiformes	4	0.5	4	2.0	0.1	12.1	25.4
Thysanoptera	2	0.1	2	1.0	0.0	6.1	6.2
Grand Total	202	418.3	33				

Note. Diet composition based on the stomach contents of 33 non-empty Boreal Chorus Frogs (*Pseudacris maculata*). F = raw frequency of occurrence (number of stomachs containing the prey taxon); N = total number of individual prey items; V = total volume of prey items. %F = percent frequency of occurrence; %N = percent numeric abundance; %V = percent volume. The Index of Relative Importance (IRI) = (%N + %V) * %F. Totals for N and V are based on the full prey count (202 items) and total volume (418.3 mm³).

To further characterize foraging behaviour, prey items were classified by habitat zone (Table 5). The analysis of identifiable prey volume indicates that *P. maculata* primarily foraged on land, or at least terrestrial invertebrate families that may fall in the wetland and be foraged upon. However, aquatic resources were also utilized, with Aquatic Surface/Emergent prey contributing 22% and Aquatic Sub-Surface prey contributing 5%. This observation corroborates the field observations that Boreal Chorus Frogs would opportunistically forage at the air-water interface, where individuals were observed striking at prey in response to visual movement cues.

Table 5: Prey categories classified by habitat zone (Terrestrial, Aquatic Surface/Emergent, and Aquatic Sub-Surface) for *Pseudacris maculata* ($n=33$).

Prey Habitat	Sum Prey Volume (mm ³)	Prey Volume %	Sum Prey Count	Prey Count %
Aquatic Sub-Surface	21.9	5.2	16.0	15.2
Aquatic Surface/Emergent	92.9	22.2	61.0	58.1
Terrestrial	303.5	72.6	28.0	26.7
Total	418.3		105.0	

Note. Analysis excludes the 63 unidentified arthropod items that were too heavily digested to accurately assign a specific microhabitat category, preventing spatial bias.

The diet composition was further explored by shifting focus to a structural matrix sorted by study site, based on the proportional volume of each prey order (Table 6). The primary source of dietary volume varied by site; Diptera (flies, mosquitoes) contributed the most volume to the Escape Coulee site, compared to the higher volume of Lepidoptera at both the Chinook and Silver Sage sites. To test for differences in diet composition between habitat types, the numeric frequency of prey orders was compared between the restored grassland (Silver Sage) and the pooled native prairie sites (Chinook and Escape Coulee). A Fisher's Exact Test indicated that the overall diet composition differed significantly between site types ($p < 0.001$). The numeric frequency of prey orders was significantly different between restored grassland (Silver Sage) and the pooled native prairie sites (Chinook and Escape Coulee) ($p < 0.001$). This structural divergence was driven by a distinct taxonomic shift between landscapes: the diet of individuals in the restored grassland was heavily characterised by Coleoptera, which accounted for 29.1% of the site's total numeric count (Table 6). In contrast, the pooled native prairie baseline sites exhibited different dominant profiles, notably at Escape Coulee where Diptera formed the primary volumetric contribution at 71.0%. To quantify the magnitude of this habitat-driven variance, a post-hoc Cramer's V analysis

was performed, revealing a moderately strong association ($V = 0.42$) between landscape matrix type and prey taxonomic frequency.

Table 6: Taxonomic composition of prey items recovered from non-empty Pseudacris maculata ($n = 33$) across three study sites in Southern Alberta. Values represent the total count and total volume (mm^3) per order, with the relative percentage of the total site contribution provided in parentheses.

Study Site	Prey Order	Count (N) (%of site)	Volume mm3 (% of site)
Chinook	Lepidoptera	1 (3.3%)	5.6 (54.0%)
	Coleoptera	4 (13.3%)	2.3 (26.4%)
	Trombidiformes	3 (10.0%)	0.6 (6.8%)
	Sarcoptiformes	1 (3.3%)	0.2 (2.7%)
	Unidentified*	19 (63.3%)	0.0 (0.0%)
	Araneae	1 (3.3%)	0.0 (0.0%)
	Diptera	1 (3.3%)	0.0 (0.0%)
Escape Coulee	Diptera	7 (22.6%)	7.1 (71.0%)
	Coleoptera	3 (9.7%)	2.4 (23.9%)
	Hemiptera	3 (9.7%)	0.5 (5.1%)
	Unidentified*	15 (48.4%)	0.0 (0.0%)
	Hymenoptera	2 (6.5%)	0.0 (0.0%)
	Lepidoptera	1 (3.2%)	0.0 (0.0%)
Silver Sage	Lepidoptera	2 (1.4%)	254.3 (63.7%)
	Coleoptera	41 (29.1%)	82.4 (20.6%)
	Hemiptera	12 (8.5%)	24.2 (6.1%)
	Diptera	36 (25.5%)	20.7 (5.2%)
	Hymenoptera	5 (3.5%)	10.4 (2.6%)
	Araneae	5 (3.5%)	7.0 (1.7%)
	Sarcoptiformes	3 (2.1%)	0.2 (0.1%)
	Trombidiformes	6 (4.3%)	0.2 (0.1%)
	Thysanoptera	2 (1.4%)	0.1 (0.3%)
	Unidentified*	29 (20.6%)	0.0 (0.0%)

Note: Unidentified* includes prey items that could not be taxonomically identified. All sites had some degree of Unidentified prey items due to digestion.

To explore the diet of the female cohort in more detail, stomach contents were compared by reproductive status of the female Boreal Chorus Frogs (Table 7). The data supports field observations that gravid females forage less. Gravid females (n=11) consumed, on average, three times fewer prey items (Mean N = 2.2, SE = 0.8) than non-gravid females (n=14, Mean N = 6.6, SE = 1.7).

Table 7: Descriptive Statistics for Total Prey Volume and Prey Count in Pseudacris maculata Females by Reproductive Status (n=25).

Variable	Reproductive Status	n	Mean	SD	SE	Min	Max
Total Prey Volume (mm³)	Gravid	11	9.4	21.9	6.6	0.0	74.1
	Non-Gravid	14	5.2	7.4	2.0	0.0	22.9
Total Prey Count (N)	Gravid	11	2.2	2.7	0.8	0.0	8.0
	Non-Gravid	14	6.6	6.5	1.7	0.0	20.0

Note. This table compares the total volume and number of prey items for all captured females with known reproductive status (n=25). SD = Standard Deviation; SE = Standard Error of the Mean; Min = Minimum; Max = Maximum.

The relationship between frog gape width and maximum prey size is presented below (Figure 4). For the thirty-three non-empty frogs, the data suggest a positive trend. This is driven by the largest prey items (15 mm and 21 mm), which were consumed by frogs with gape widths of 5.0 mm and 6.0 mm respectively. However, the majority of prey items consumed by all frogs were smaller than 8.0 mm.

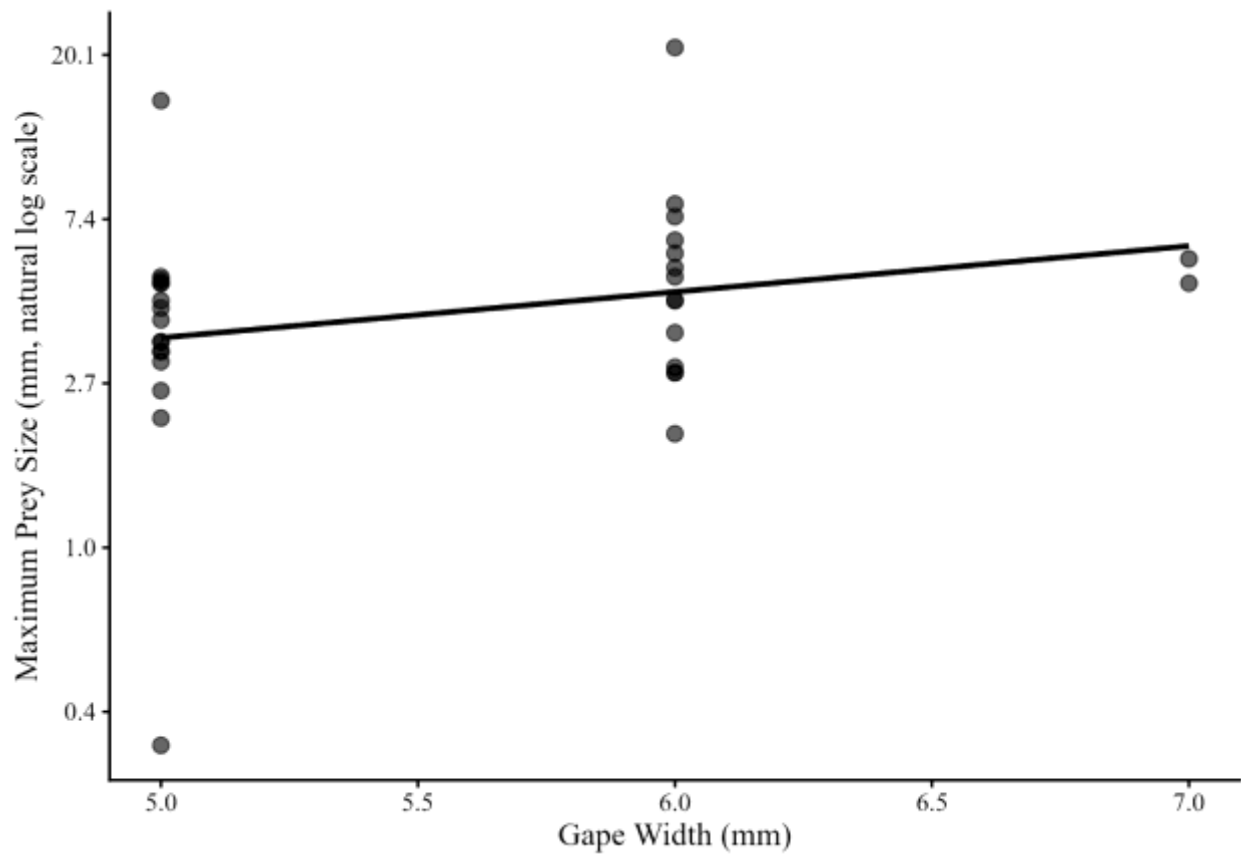


Figure 4: Relationship between gape width (mm) and maximum prey length (mm) consumed by Pseudacris maculata (n=33). Prey length is presented on a natural logarithmic scale to normalize variance. The solid line illustrates the linear regression trend, with the grey shaded region representing the standard error (SE).

There was no significant correlation between SVL and maximum prey size ($\rho = 0.258$, $p = 0.154$). However, there was a positive trend between gape width and maximum prey size ($\rho = 0.312$, $p = 0.082$) (Figure 5).

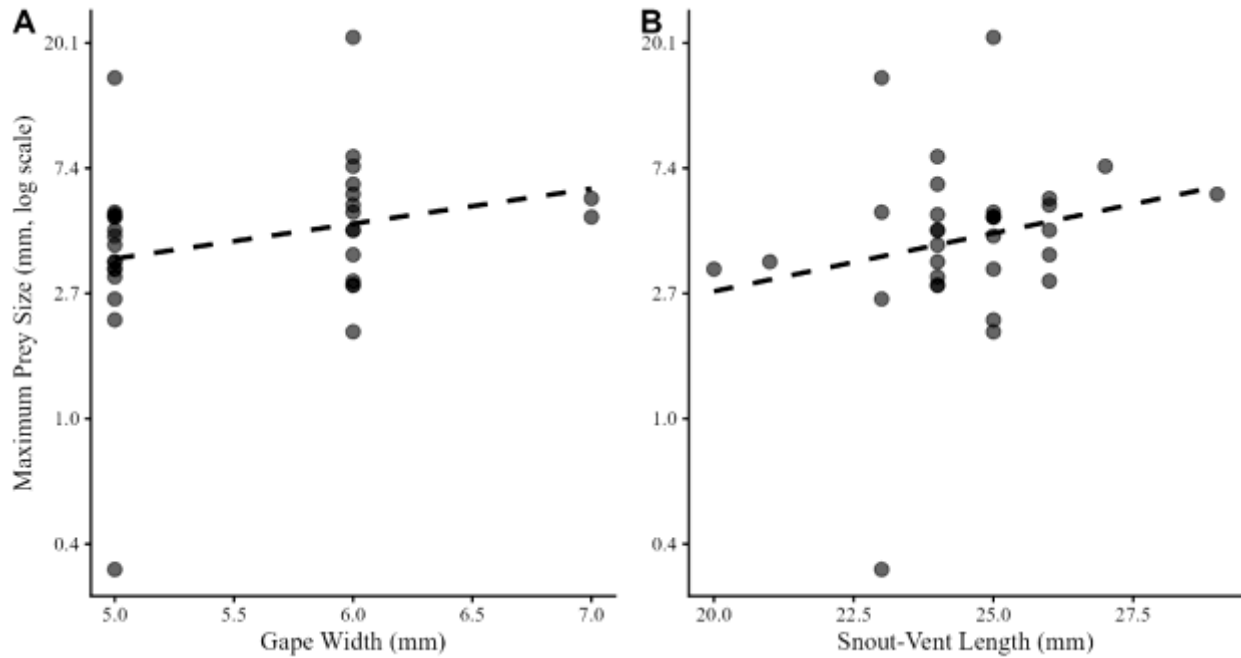


Figure 5: Relationship between predator morphology and maximum ingested prey length (mm, natural log scale) for Boreal Chorus Frogs (*Pseudacris maculata*) ($n = 33$). Panel A displays the trend for predator gape width (mm); Panel B displays the trend for predator snout-vent length (SVL, mm).

There was no significant difference in the total volume of prey consumed between males and females ($W = 361$, $p = 0.291$; Figure 6). Foraging females exhibited a median prey volume of 11.2 mm^3 (range: $0.1\text{-}74.1 \text{ mm}^3$) which was statistically indistinguishable from the male median intake of 10.8 mm^3 (range: $0.2\text{-}23.9 \text{ mm}^3$).

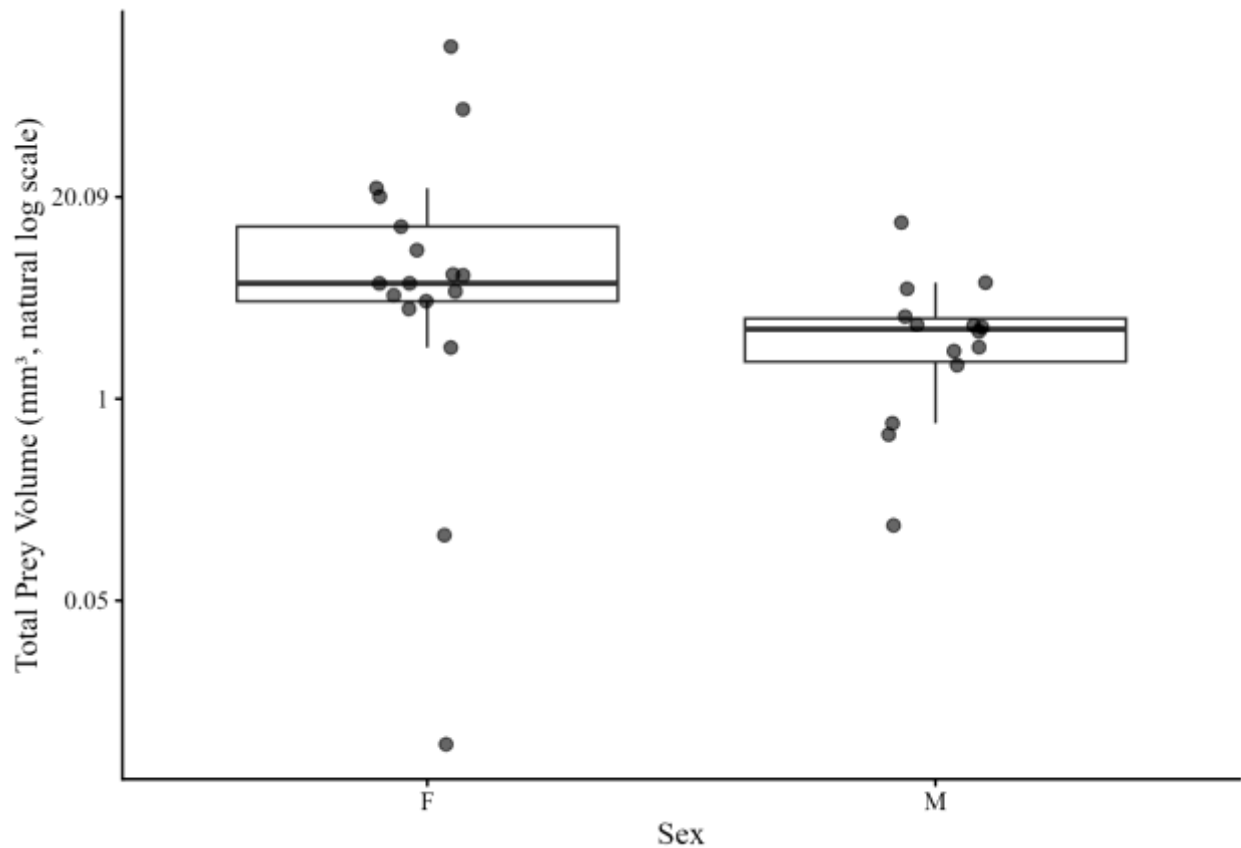


Figure 6: Distribution of total prey volume (mm^3) consumed by female ($n = 19$) and male ($n = 14$) *Pseudacris maculata*. Prey volume is presented on a natural logarithmic scale to improve visualization of the data spread. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent individual frogs with non-empty stomachs.

Similarly, no significant difference was detected in the absolute number of prey items consumed between sexes ($W = 137.5$, $p = 0.883$; Figure 7). However, the underlying structural distribution of prey counts revealed distinct foraging patterns between the cohorts. The female cohort exhibited a highly skewed foraging strategy, the median feeding output was low at three items per stomach, yet individual variation was high, impacted by heavy-feeding outliers consuming up to 14 and 20 items. In contrast, the male cohort demonstrated a more uniform, consistent foraging output, centred around a higher median of six items per stomach with a compressed overall variance.

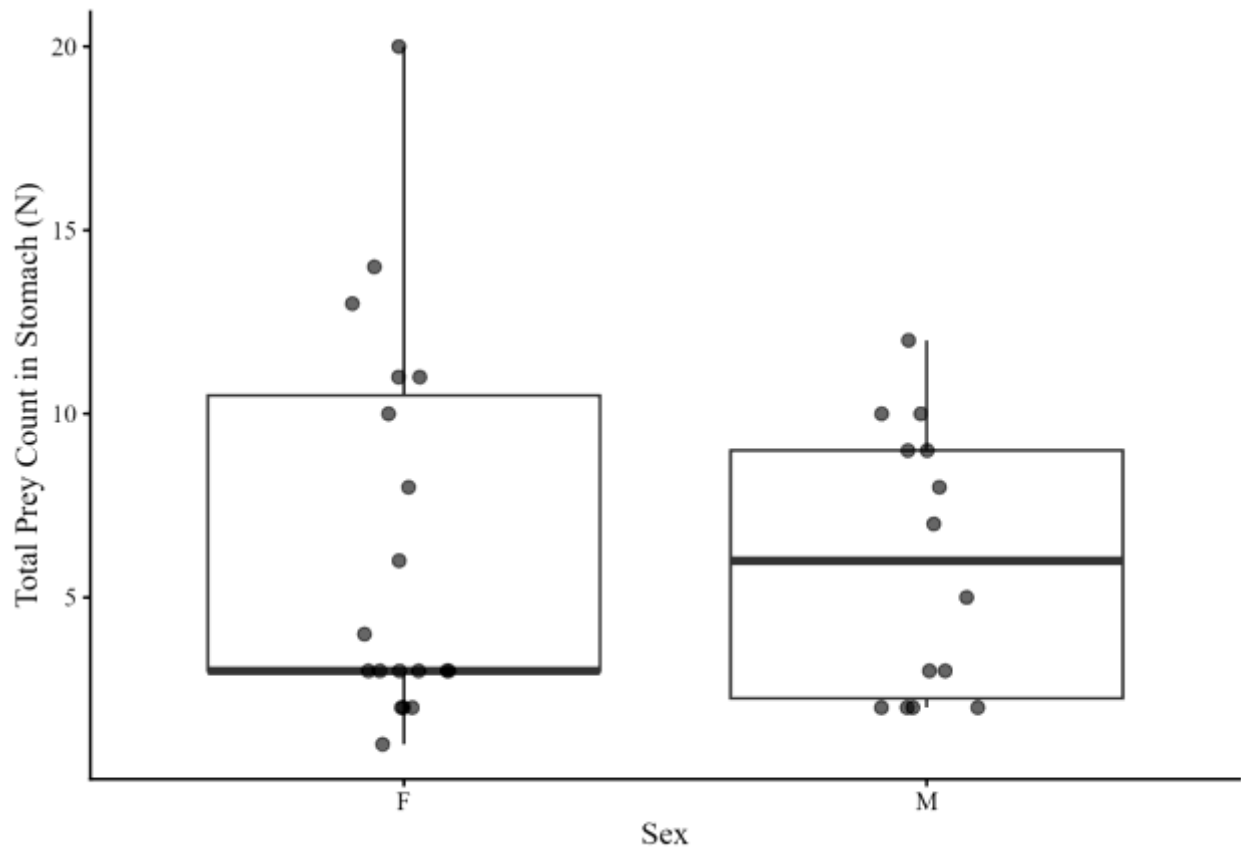


Figure 7: Total number of prey items (N) consumed by female ($n = 19$) and male ($n = 14$) *Pseudacris maculata* with non-empty stomachs. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent the exact prey counts for individual frogs.

To evaluate the energetic trade-offs of reproduction, foraging success was compared between gravid ($n = 11$) and non-gravid ($n = 14$) females (Figure 8). While reproductive status constrains how often females forage, it does not necessarily reduce their maximum volumetric intake. Gravid females exhibited a higher mean total prey volume (9.4 ± 6.6 SE mm^3) compared to non-gravid females (5.2 ± 2.0 SE mm^3). This distribution is highly skewed; while the medians remain visually comparable, the gravid cohort's volume is driven by opportunistic consumption of exceptionally large prey items, creating a massive upper variance (maximum volume: 74.1 mm^3) compared to the more constrained intake of the non-gravid cohort.

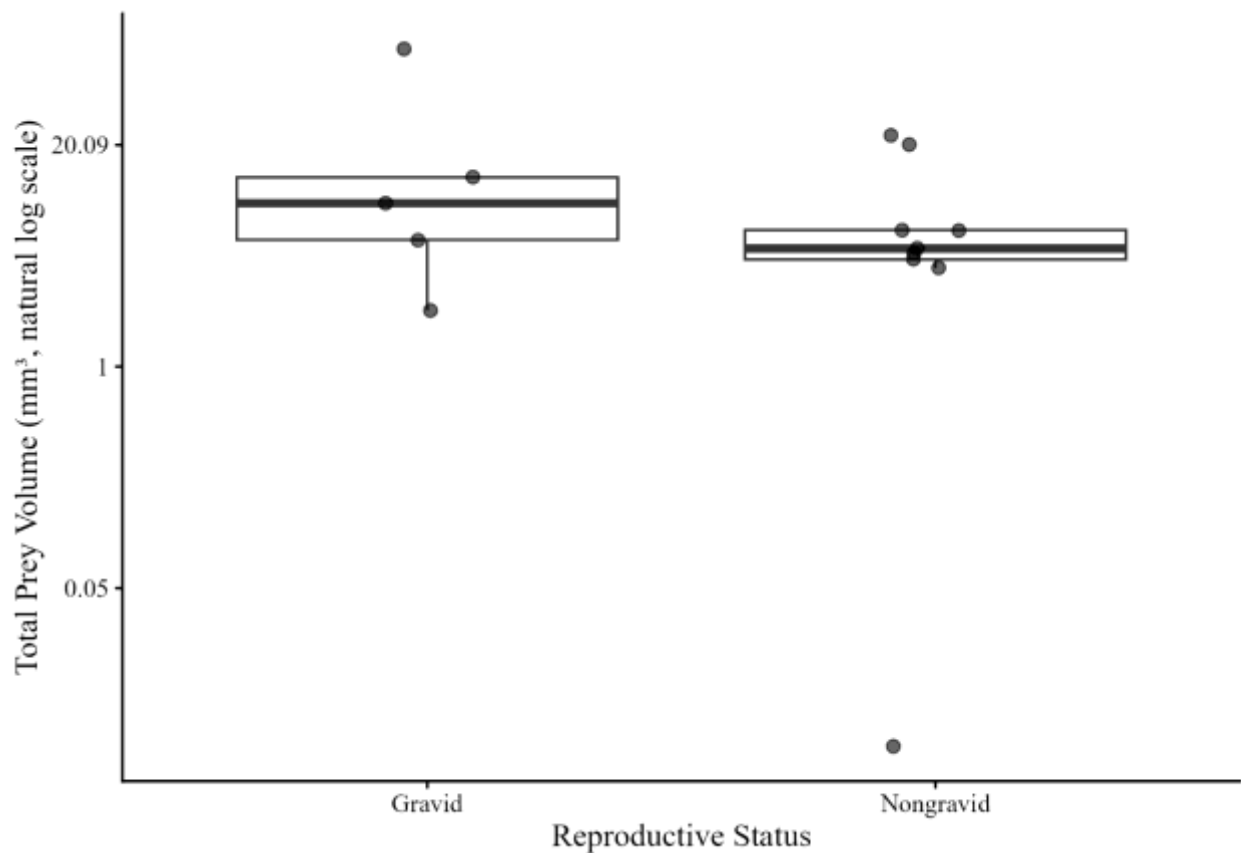


Figure 8: Distribution of total prey volume (mm^3) consumed by gravid ($n = 11$) and non-gravid ($n = 14$) female *Pseudacris maculata*. Prey volume is presented on a natural logarithmic scale to improve visualization of the data spread. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent individual frogs with non-empty stomachs.

The GLM indicated that reproductive status was a significant predictor of prey count ($z = 4.811$, $p < 0.001$). To quantify the magnitude of this biological constraint, an Incidence Rate Ratio (IRR) was calculated as a measure of effect size, revealing that non-gravid females consumed prey at a rate 3.01 times higher than gravid females. To ensure robustness, a parallel one-way Analysis of Variance (ANOVA) on log-transformed counts was performed, which yielded a similar biological trend, though it was marginally non-significant under a linear framework ($F_{(1,23)} = 2.94$, $p = 0.100$). Consequently, the primary count model confirms that non-gravid females consumed significantly more prey items than gravid females (Figure 9).

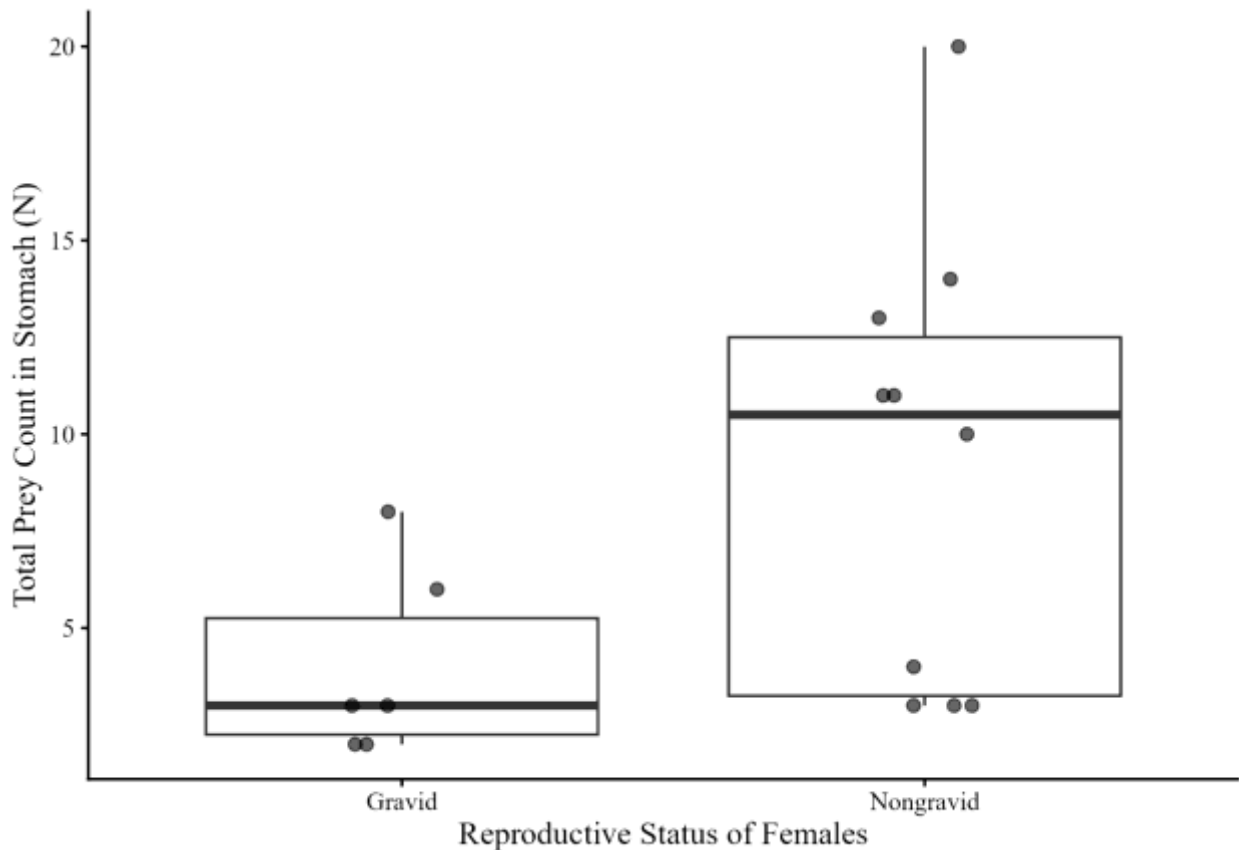


Figure 9: Total number of prey items consumed by gravid ($n = 11$) and non-gravid ($n = 14$) female *Pseudacris maculata*. The thick horizontal line represents the median, the box represents the interquartile range (IQR), and individual points represent the exact prey count for individual frogs with non-empty stomachs.

3.3 Breeding Season Baseline for *Spea Bombifrons*

While targeted sampling efforts successfully captured five adult male Plains Spadefoots at the Escape Coulee native prairie site, 100% of the recovered individuals exhibited entirely empty stomachs. This uniform lack of stomach contents prevented further taxonomic or volumetric trophic modeling for the species. However, this finding establishes an important morphological and behavioral baseline for Canadian populations at the northern limit of their range. The physical parameters of the captured *S. bombifrons* cohort were highly uniform, exhibiting a mean SVL of 50.6 ± 6.2 mm (range: 44.0-60.0 mm) and a mean gape width of 19.2 ± 1.3 mm (range: 18.0-21.0 mm). This complete cessation of foraging activity aligns with the specialized, explosive breeding strategy characteristic of fossorial anurans in semi-arid environments (Dimmitt & Ruibal, 1980). Because these amphibians rely on ephemeral wetlands that can desiccate within weeks of formation, males must prioritize 100% of their time and energy into vocalization and mating displays, completely suspending foraging behavior to maximize reproductive success before the water resource disappears.

3.4 Summary of Results

In summary, the statistical analyses of this regional assemblage revealed that while broad morphological dimensions do not structurally vary by locality, anuran foraging outcomes are intensely shaped by a combination of external landscape matrices and internal physiological states. For *Pseudacris maculata*, local habitat type acted as a primary driver of taxonomic and volumetric diet composition, distinguishing the Coleoptera-heavy profiles of restored uplands from the Diptera-dominated baselines of native prairie. Furthermore, while absolute sex-based differences in energetic uptake were absent, female foraging dynamics were profoundly constrained by reproductive state, with gravid females experiencing a significant reduction in

prey count frequency. While a 100% empty stomach rate among captured *Spea bombifrons* prevented further trophic modelling for the species, it establishes an important baseline regarding breeding season capture states.

CHAPTER 4: DISCUSSION

The trophic profiles and foraging dynamic observed in this study reveal four distinct ecological and physiological patterns that underpin the community role of *Pseudacris maculata* within the grassland and native prairie landscapes of southern Alberta. First, *P. maculata* exhibited a broad, generalist diet dominated by terrestrial arthropods. Coleoptera and Diptera were the most significant prey items based on the Index of Relative Importance (IRI), consistent with the opportunistic foraging strategy typical of hylids (Ethier et al., 2021; Toft, 1981). However, while numerically rare, Lepidoptera contributed the majority of the dietary volume, suggesting they represent a high-value energetic resource that drives a distinct optimal foraging strategy. While the data did not support hypotheses regarding sexual dimorphism or a linear relationship between body length (SVL) and prey size, they confirmed that diet composition is significantly influenced by site and that female foraging frequency is constrained by reproductive status. Collectively, these statistical results show how both the local environment and the anuran biology shape their feeding habits, setting up a clear framework to discuss their foraging behaviour and conservation in changing prairie ecosystems.

4.1 Determinants of Diet Matrix and Habitat Divergence

Statistical testing confirmed that local habitat was a significant factor of diet composition. The Fisher's Exact Test ($p < 0.001$) indicated that the dietary profile of *P. maculata* differs significantly between the restored grassland and native prairie sites. This confirms the differences observed (such as the prevalence of Diptera at Escape Coulee versus Coleoptera at Silver Sage) are not artifacts of sampling design but represent a genuine ecological response to local invertebrate availability. For instance, the statistical dominance of Diptera at the native prairie site (Escape Coulee) likely reflects a high local abundance of wetland-associated mosquitoes

(Culicidae), whereas the Coleoptera-dominated diet at the restored grassland (Silver Sage) was composed primarily of flea beetles (Chrysomelidae), a known agricultural pest of canola crops (Li et al., 2024). This dominance aligns with previous research on chorus frogs and other amphibians, which consistently characterizes them as opportunistic generalists (Ethier et al., 2021; Toft, 1981). Notably, taxonomic identification revealed that these broad categories were represented by a high number of specific pest species: Coleoptera were primarily represented by flea beetles (Chrysomelidae), a known agricultural pest, while Diptera were dominated by mosquitoes and midges (Culicidae) (Li et al., 2024). These prey orders are typically abundant in prairie wetlands (Semlitsch et al., 2015), suggesting that *P. maculata* consumes prey largely in proportion to availability and operates as a true generalist capable of thriving on diverse invertebrate communities.

Furthermore, the high prevalence of these specific insect groups highlights the potential role of *P. maculata* in providing ecosystem services through the biological control of both crop pests in restored upland habitats and disease vectors in wetland systems. The classification of prey by habitat zone further supports this, indicating that *P. maculata* acts primarily as a terrestrial forager within the wetland complex. With 73% of identifiable prey volume originating from terrestrial sources (or perhaps terrestrial species that fall in the water), these frogs appear to forage extensively on wetland banks and in upland grasses, rather than strictly in the water column during the breeding season. This reliance on terrestrial prey highlights the importance of the riparian and upland habitat immediately surrounding the wetland for maintaining amphibian populations (Hopkins, 2007).

4.2 Morphological and Physiological Foraging Trade-Offs

When examining predator morphology, the data suggest that physical constraints on foraging are primarily driven by specific mouth dimensions rather than overall body length. While neither GW nor SVL showed a statistically significant linear correlation with maximum prey size, gape width exhibited a positive trend ($p = 0.08$) and a stronger correlation coefficient ($\rho = 0.31$) than SVL ($\rho = 0.26$). This lends weight to the biological prediction that mouth width, rather than total body length, acts as the primary physical constraint on the ingestion of large prey items. This gape limitation has been documented in metamorphosed spadefoot toads, where larger individuals are more successful at capturing larger prey (Newman, 1999). The lack of statistical significance may be attributed to the limited sample size ($n = 33$) and the high proportion of small prey consumed by all frogs regardless of size, which effectively reduces the signal of the maximum limit.

However, the volumetric importance of Lepidoptera reveals a nuance. Although numerically rare (2.0%), Lepidoptera contributed over 62% of the total dietary volume. This suggests that while *P. maculata* frequently consumes small, abundant prey like beetles and flies, the opportunistic capture of large, high-energy prey like caterpillars likely plays a disproportionate role in their overall energetic intake. This strategy of relying on frequent small meals supplemented by rare, high-value items is an efficient foraging mode for small ectotherms in variable environments (Roner et al., 2020; Toft, 1981). This ability to exploit large, high-energy prey appears to be morphologically constrained; the positive trend between gape width and maximum prey size (Figure 6) suggests that larger frogs have a wider dietary niche breadth, granting them access to the largest, most calorie-dense prey items (Newman, 1999; Emerson, 1985).

In addition to these structural mouth constraints, the dataset revealed an unexpected descriptive pattern regarding overall body size dimensions. Contrary to the expected pattern of female-biased

sexual size dimorphism typical for *Pseudacris maculata* across its range (Ethier et al., 2021), males within this non-empty sample exhibited a slightly larger mean snout-vent length (SVL) than females. This subtle variation in body size, however, did not translate into a divergence on actual resource consumption between the sexes. The analysis of sexual dimorphism revealed no significant variation between the sexes. The Wilcoxon Rank Sum Test revealed no significant difference in total prey between males and females ($p = 0.29$). Descriptive outliers suggested that females were capable of consuming exceptionally large meals; however, the statistical result clarifies that while females can achieve higher maximum volumes, the typical (median) energetic intake for males and females is statistically indistinguishable during the breeding season.

In contrast, a highly significant physiological trade-off was identified within the female cohort based on reproductive condition. The GLM confirmed that reproductive status is a strong predictor of foraging frequency ($p < 0.001$), confirming that gravid females consumed significantly fewer prey items than non-gravid females (mean counts of 2.2 vs. 6.6 respectively). This descriptive pattern aligns with field observations of smaller stomach plugs in gravid individuals and reflects a behavioural trade-off documented in other anuran species (Garcia et al., 2015). The reproductive condition of females in this study aligns with recent phenological observations of *P. maculata* in Colorado, USA (Goldberg, 2021), suggesting this behaviour is tied to specific breeding windows.

This reduction in prey count was accompanied by a large standard error in prey volume for the gravid group ($SE = 6.6 \text{ mm}^3$), reflecting highly variable individual intake driven by a few exceptionally large items. For example, one gravid female consumed a single caterpillar with a volume of 73.8 mm^3 . This example suggests that while gravid females may reduce their

movement and foraging frequency to save energy, they remain capable of capitalizing on high-value prey items when encountered.

This unique foraging pattern is likely influenced by a combination of physical and physiological constraints. Physically, the abdominal cavity of a gravid female is distended with eggs, compressing the stomach and mechanically limiting the volume of food that can be ingested or held (Nunes-de-Almeida & Haddad, 2019). Physiologically, this reduction may be mediated by hormonal signals, similar to the leptin-induced appetite suppression observed in female Spadefoot Toads (Garcia et al., 2015). By reducing foraging activity, gravid female Boreal Chorus Frogs may also minimize their exposure to predation during a life stage where locomotor performance is compromised by mass (Garcia et al., 2015).

The distinct morphometric and reproductive adjustments observed in this study provide strong empirical support for core tenets of Optimal Foraging Theory (OFT) within a prairie context. Classic foraging models dictate that generalist predators optimize their energy economics by balancing handling time against a prey item's nutritional profitability (Pyke et al., 1977). This is clearly demonstrated by the disproportionate volumetric contribution of Lepidoptera larvae; despite being numerically rare, these large prey items represent a high-profitability resource that justifies the energetic investment of capture for an opportunistic forager (Toft, 1981). This energetic optimization, however, is mechanically moderated by functional morphology. The positive trend observed between gape width and maximum prey size aligns with established constraints where cranial dimensions set the upper boundary on an individual's dietary niche breadth (Emerson, 1985; Newman, 1999). Furthermore, the distinct behavioural rules observed in reproductive females fit cleanly within Jaeger and Rubin's (1982) tactical selectivity framework. The significant reduction in foraging frequency among gravid Boreal Chorus Frogs suggests a

strategic shift in decision priorities, where individuals actively minimize movement to mitigate heightened predation risks and conserve energy, while selectively capitalizing on highly profitable, large prey items when an immediate opportunity arises.

4.3 Conservation Implications and the Pesticide Paradox

The findings of this study support a holistic conservation strategy that encompasses both wetlands and their surrounding uplands. The dietary analysis revealed that 73% of the identifiable prey volume consumed by *P. maculata* was terrestrial in origin, indicating that these amphibians are energetically dependent on the upland habitat surrounding wetlands, rather than strictly the aquatic column itself. This reliance on terrestrial subsidies reinforces the need to protect “buffer zones” of native vegetation around breeding ponds. Research on *Pseudacris* life history confirms that adults migrate from upland overwintering sites to breed and then return to terrestrial habitats shortly after spawning (Ethier et al., 2021; Lee & Randall, 2022). Consequently, management practices that cultivate crops directly up to the wetland edge sever the landscape link between wetland breeding habitat and the terrestrial foraging grounds required for survival.

This study provides empirical evidence that prairie amphibians contribute to regulating ecosystem services by consuming agricultural pests (Hocking & Babbitt, 2014). The identification of mosquitoes (Culicidae) and flea beetles (Chrysomelidae) in the diet of *P. maculata* assigns a tangible economic value to these species as consumers of known pests to humans (Li et al., 2024). While naturalists and non-government organizations have traditionally driven conservation efforts, framing amphibians as indicators of productive, sustainably managed land may resonate more effectively with agricultural producers. Interactions with nearby landowners, including ranchers and producers, during this study revealed a growing interest in stewardship, particularly among younger generations concerned with their ecological footprint

(Hartel et al., 2019). Promoting amphibians not just as fragile species at risk, but as signs of a healthy, functioning landscape (ACA, 2019), may be the most effective strategy for securing amphibian habitat on private lands.

This economic service, however, introduces a complex ecotoxicological trade-off. *Pseudacris maculata* remains widespread and abundant across Alberta, persisting in landscapes where other species have declined. This resilience is likely underpinned by their small body size, which allows them to use micro-habitats for overwintering, and their dietary plasticity. Their predominantly terrestrial foraging strategy (73% of prey volume) shapes their ecotoxicological risk profile in modified landscapes. Recent ecotoxicological research indicates that while aquatic runoff heavily impacts breeding pools (Anderson, 2005), upland terrestrial habitats can be subject to significant pesticide accumulation via spray drift, dust from treated seeds, and direct soil deposition (Van Meter & Glinski, 2021). Consequently, foraging on land does not shield *P. maculata* from agrochemicals; rather, it shifts their exposure from aquatic pathways to the terrestrial routes.

This terrestrial presence creates a unique, compounded vulnerability. In addition to direct dermal contact with contaminated upland soils and vegetation, their diet of agricultural pests (e.g., flea beetles) opens a direct dietary pathway for further contaminant exposure. Because flea beetles are the primary target of neonicotinoid seed treatments (Sekulic & Rempel, 2016) and regularly come in contact with other agrochemicals, *P. maculata* may be ingesting concentrated toxins directly from their prey. This finding complicates the narrative of the “resilient generalist” and suggests that the combination habitat exposure and dietary intake may be an underestimated threat for this species in high-intensity agricultural zones (de Oliveira et al., 2025). This link is particularly relevant in restored grasslands like Silver Sage, where historical cultivation may have

established persistent pest populations, forcing individuals to interact directly with the agricultural food web.

CHAPTER 5: CONCLUSION

5.1 Historical Baselines and Data Gaps

Prior to this study, the only comprehensive assessment of *Pseudacris maculata* diet in Alberta was conducted by Moore and Strickland (1954; 1955), who examined the stomach contents of 37 adults from southern Alberta. They identified Coleoptera and Diptera as the “main sources of food” for *P. maculata*, a finding that has been mirrored by the current study where these two orders ranked highest in Index of Relative Importance (Moore & Strickland, 1954). The historical study noted a prevalence of families such as Carabidae (ground beetles) and Curculionidae (weevils), as well as Tipulidae and Culicidae (mosquitoes) among the Diptera (Moore and Strickland, 1954). The persistence of this broad diet composition suggests that *P. maculata* has maintained its role as a terrestrial generalist despite seven decades of significant landscape conversion and agricultural intensification in southern Alberta.

However, the current study expands significantly upon this historical snapshot by incorporating volumetric analysis alongside traditional frequency metrics. Moore and Strickland (1954) noted the presence of Lepidoptera (moths and caterpillars) but, relying on numeric counts, did not identify the order as a major dietary component. In contrast, the current volumetric analysis revealed that while Lepidoptera remain numerically rare (consistent with the 1954 baseline), they constitute the absolute majority of the total prey biomass consumed. This discrepancy highlights a critical vulnerability in historical methodologies; relying solely on numeric abundance overemphasises the tiny, highly frequent prey items while completely obscuring the caloric contributions of larger taxa. By employing indices like the Index of Relative Importance, this

study reveals the cryptic energetic importance of rare, large prey items that traditional numeric surveys may underestimate.

Beyond *P. maculata*, these findings reveal a profound, long-term data deficiency for other prairie amphibians across the province. Despite targeted survey efforts, Northern Leopard Frogs (*Lithobates pipiens*), Great Plains Toads (*Anaxyrus cognatus*), and Western Tiger Salamanders (*Ambystoma mavortium*) were not captured in sufficient numbers to permit meaningful dietary analysis. This is a critical gap; the Northern Leopard Frog is legally designated as “Threatened” under the “Wildlife Act”, while the Great Plains Toad and Plains Spadefoot are listed as “May Be At Risk” in Alberta (Government of Alberta, 2025).

The last comprehensive dietary analysis for these species in the province dates back to the original 1950s surveys (Moore & Strickland, 1954; 1955). Given the agricultural intensification that has occurred since then, updated dietary baselines are urgently needed to determine if these declining species face nutritional constraints or heightened pesticide exposure risks similar to those identified here for *P. maculata*. Future research should prioritize these “missing” species, employing targeted capture techniques or fecal DNA collection to build a complete picture of the contemporary prairie amphibian food web.

5.2 Methodological and Seasonal Limitations

The primary analytical limitation was the high proportion of “Unidentified Arthropod” material (IRI = 2173.7), which occurred in nearly 70% of all non-empty stomachs, accounted for a substantial portion of the total dietary volume. This finding points to a systematic underrepresentation of soft-bodied prey due to rapid digestion, a known limitation of stomach flushing techniques (Solé & Rödder, 2010). While stomach flushing is an invaluable, non-lethal

method for dietary analysis, it inherently biases results in favour of heavily sclerotized taxa like beetles (Solé et al., 2005). The capture of soft-bodied prey is facilitated by the non-Newtonian, viscoelastic properties of frog saliva, which adheres tightly to prey during the initial strike (Noel et al., 2017). This adhesion, combined with the mechanical action of ingestion and subsequent flushing, likely accelerates the maceration of soft invertebrates (e.g., Dipteran larvae, aphids), rendering them unidentifiable faster than hard-bodied prey. Given this high contribution of unidentifiable material, the true dietary diversity of *P. maculata* is likely greater than the taxonomic list suggests. Future studies could overcome this limitation by employing DNA metabarcoding on stomach contents to further identify soft tissues that are visually unidentifiable.

A secondary limitation was the unevenness of sample size across sites. While the Silver Sage site yielded a robust cohort (n=36), significantly fewer individuals were recovered at Chinook (n=4) and Escape Coulee (n=5). Because individual morphometric models pooled all collected frogs into a single continuous dataset (n=33 non-empty stomachs), this localized scarcity did not weaken the overall statistical power of the regression analyses. However, this high variance in localized capture rates does restrict the reliability of localized, site-to-site descriptive comparisons, reducing the statistical power needed to run multi-site tests of differences in regional morphology or diet composition. Furthermore, the absence of concurrent invertebrate sampling limits the interpretation of prey selection versus availability. While the diet appears generalist, future studies should incorporate simultaneous invertebrate surveys to definitively determine whether *P. maculata* is consuming prey in proportion to their environmental abundance or exhibiting selectivity.

Finally, this study was restricted to the spring breeding season (April to June). While this captures the critical period of reproductive energy expenditure, high activity of breeding vocalization, and

the assembly of populations in a smaller area, it misses the foraging period for lipid reserves which occurs in late summer prior to winter dormancy. For fossorial species like *S. bombifrons*, which rely on lipid reserves to survive up to 10 months of dormancy (Dimmit & Ruibal, 1980), the foraging in July and August is likely more intense and potentially different in composition than what was observed in spring. Similarly, *P. maculata* individuals must gain significant energy stores to produce glucose cryoprotectants for freeze tolerance during winter (Ethier et al., 2021). Therefore, the dietary profiles described here should be viewed as a “breeding season snapshot” rather than a comprehensive annual diet. Ultimately, this temporal limitation, coupled with the small sample sizes at secondary sites, demands careful consideration when drawing broad regional inferences or making management decisions across the prairies.

5.3 Future Research and Conservation Horizons

The upland-wetland connection identified in this study highlights a need to expand conservation frameworks from localized wetland monitoring to broader terrestrial landscape management. This upland connection is likely even more important for fossorial specialists like the Plains Spadefoot. This species requires sandy, well-drained soils in native grassland habitats to construct the deep burrows necessary for brumation and estivation (Lauzon, 1999; Taylor, 2004). The observation of 100% empty stomachs in breeding males during this study strongly suggests that their energy acquisition occurs almost entirely in these upland habitats prior to or after the explosive breeding window (Dimmit & Ruibal, 1980). While their association with sandy soils is well-documented in Alberta (Lauzon, 1999), specific data on their movement corridors and brumation depths in Canada remain limited. Consequently, this species’ seasonal reliance on terrestrial landscapes represents a significant knowledge gap that underscores the need for future tracking studies, and expanded dietary analyses conducted outside of the breeding season.

Future ecological assessments must transition from descriptive dietary catalogs to active models of foraging preference. A key limitation of this study was the absence of concurrent invertebrate surveys, which prevents the calculation of standard electivity indices to establish selection parameters (i.e., are frogs choosing beetles, or just eating them because they are everywhere?). Future dietary assessments should incorporate simultaneous field collection methods, such as pitfall or sweep-net surveys of local invertebrates to definitively determine whether *P. maculata* exhibits taxonomic preference or simply reflects environmental availability across different habitat types (Grant et al., 2013).

Perhaps the most urgent avenue for future research lies at the intersection of diet and toxicology. This study confirmed that *P. maculata* consumes flea beetles (Chrysomelidae), which are the primary target of neonicotinoid seed treatments in canola production (Sekulic & Rempel, 2016). This dietary link creates a potential pathway for the bioaccumulation of neurotoxins within the upland food web. While amphibians are frequently cited as “canaries in the coal mine,” their sensitivity to specific agricultural contaminants varies significantly by species and life-history stage (Kerby et al., 2010). Given that *P. maculata* in the Canadian prairies has already been shown to bioaccumulate contaminants like mercury (Boczulak et al., 2017), future research should explicitly quantify agrochemical levels in amphibian tissues and prey items. Such toxicological monitoring is essential to determine if their role as “pest control agents” is exposing them to lethal or sublethal chemical loads on agricultural landscapes (de Oliveira et al., 2025).

5.4 Synthesis and Final Summary

The dietary patterns observed in *Pseudacris maculata* and *Spea bombifrons* provide empirical support for several core tenets of Optimal Foraging Theory (OFT) within a seasonal prairie context. As established by Pyke et al. (1977), predators prioritize prey that maximizes net energy

intake relative to handling time. This optimization is shown in this study by the disproportionate volumetric contribution of Lepidoptera (62.1%); despite being numerically rare, these large prey items represent a highly profitable resource that justifies the energetic costs of capture for a generalist forager (Toft, 1981). This energetic optimization is physically moderated by functional morphology. The positive trend between gape width and maximum prey size aligns with Emerson's (1985) models, confirming that cranial dimensions act as the primary mechanical constraint on a species' dietary niche.

Furthermore, the tactical selectivity identified by Jaeger and Rubin (1982) provides a framework for the behavioral trade-offs observed in reproductive females. The significant reduction in foraging frequency among gravid Boreal Chorus Frogs suggests a shift in "decision rules," where individuals may minimize movement to reduce heightened predation risk and conserve physical energy while selectively capitalizing on high-value prey when encountered.

At the community level, the dietary overlap and spatial separation between species support the principles of resource partitioning. The high reliance on terrestrial prey (73%) during an aquatic breeding event demonstrates spatial partitioning that likely reduces direct competition with other sympatric amphibians (Toft, 1985; Das, 1996). Modern ecological frameworks by Meyer et al. (2025) suggest that such generalist predators can exert effective top-down pressure on specific prey, such as agricultural pests, without destabilizing the broader invertebrate community.

However, this "resilient generalist" strategy may create a direct dietary pathway for contaminant exposure if targeted prey items, such as flea beetles, are associated with systemic agrochemicals (de Oliveira et al., 2025). By integrating these theoretical frameworks, the results of this study clarify the complex energetic and environmental factors that sustain amphibian populations across modified landscapes.

In conclusion, this thesis provides the first update on the dietary ecology of prairie amphibians in Alberta since the 1950s. The findings characterize *Pseudacris maculata* as a resilient terrestrial generalist that provides ecosystem services within the working landscapes of the Dry Mixedgrass Natural Subregion, including consuming invertebrates considered pests to humans. However, this resilience is not absolute; it is constrained by morphological limits, reproductive energy trade-offs, and the availability of diverse terrestrial prey. Furthermore, the precarious status of *Spea bombifrons*, highlighted here by the observation of reproductive failure during drought, underscores the vulnerability of specialized species to a changing climate and landscape. By identifying these biological patterns and habitat dependencies, this research offers a scientifically grounded baseline for the proactive management of common and at-risk amphibians in an increasingly modified world (Sterrett et al., 2019; González-del-Pliego et al., 2019).

REFERENCES

- Ab Azid, M. A. (2018). *Diet habits of frogs (Family: Megophryidae) in Kubah National Park* [Unpublished manuscript]. Department of Zoology, Universiti Malaysia Sarawak.
<https://doi.org/10.13140/RG.2.2.28317.61927>
- ACA. (2019). *Amphibians on my land: Habitat stewardship in agricultural landscapes*. Alberta Conservation Association.
- Ahlm, K. (2015). *Prey specialization and diet of frogs in Borneo* [Bachelor's thesis, University of Gothenburg].
- Alberta Parks. (2015). *Natural Regions and Subregions of Alberta: A Framework for Alberta's Parks*. Alberta Tourism, Parks and Recreation.
- Alroy, J. (2015). Current extinction rates of reptiles and amphibians. *Proceedings of the National Academy of Sciences*, 112(42), 13003-13008.
- Anderson, A. M. (2005). *Overview of pesticide data in Alberta surface waters since 1995*. Alberta Environment.
- Anderson, C. W., & Nishikawa, K. C. (1993). A prey-type dependent hypoglossal feedback system in the frog *Rana pipiens*. *Brain, Behavior and Evolution*, 42(4-5), 189–196.
<https://doi.org/10.1159/000114213>
- Anderson, C. W., & Nishikawa, K. C. (1996). The roles of visual and proprioceptive information during motor program choice in frogs. *Journal of Comparative Physiology A*, 179(6), 753–762. <https://doi.org/10.1007/BF00227318>

- Awkerman, J., Raimondo, S., Schmolke, A., Galic, N., Rueda-Cediel, P., Kapo, K., Accolla, C., Vaugeois, M., & Forbes, V. (2020). Guidance for developing amphibian population models for ecological risk assessment. *Integrated Environmental Assessment and Management*, 16(2), 223–233. <https://doi.org/10.1002/ieam.4215>
- Balas, C. J., Euliss Jr., N. H., & Mushet, D. M. (2012). Influence of conservation programs on amphibians using seasonal wetlands in the Prairie Pothole Region. *Wetlands*, 32(2), 333–345. <https://doi.org/10.1007/s13157-012-0269-9>
- Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18(3), 308–343. <https://doi.org/10.2307/1468447>
- Blaustein, A. R., Han, B. A., Relyea, R. A., Johnson, P. T. J., Buck, J. C., Gervasi, S. S., & Kats, L. B. (2011). The complexity of amphibian population declines: understanding the role of cofactors in driving amphibian losses. *Annals of the New York Academy of Sciences*, 1223(1), 108–119. <https://doi.org/10.1111/j.1749-6632.2010.05909.x>
- Boczulak, S. A., Vanderwel, M. C., & Hall, B. D. (2017). Survey of mercury in boreal chorus frog (*Pseudacris maculata*) and wood frog (*Rana sylvatica*) tadpoles from wetland ponds in the Prairie Pothole Region of Canada. *FACETS*, 2(1), 315–329. <https://doi.org/10.1139/facets-2016-0041>

- Bovo, R. P., Gouveia, S. F., Ribeiro, G. M., Valença, S. V., & Gomes, F. R. (2018). Ecophysiological information for better mechanistic models for amphibians. *Diversity*, 10(4), 118. <https://doi.org/10.3390/d10040118>
- Brenes-Soto, A., Dierenfeld, E. S., & Janssens, G. P. J. (2018). The interplay between voluntary food intake, dietary carbohydrate-lipid ratio and nutrient metabolism in an amphibian (*Xenopus laevis*). *PLoS ONE*, 13(12), e0208445. <https://doi.org/10.1371/journal.pone.0208445>
- Brinley Buckley, E. M., et al. (2021). Assessing ecological and environmental influences on boreal chorus frog (*Pseudacris maculata*) spring calling phenology using multimodal passive monitoring technologies. *Ecological Indicators*, 121, 107171.
- Catenazzi, A. (2015). State of the world's amphibians. *Annual Review of Environment and Resources*, 40, 91–119. <https://doi.org/10.1146/annurev-environ-102014-021358>
- Cogalniceanu, D., Aioanei, F., Ciubuc, C., & Vadineanu, A. (1998). Food and feeding habits in a population of common spadefoot toads (*Pelobates fuscus*) from an island in the lower Danube floodplain. *Alytes*, 15(4), 145–157.
- Collins, J. P. (2010). Amphibian decline and extinction: What we know and what we need to learn. *Diseases of Aquatic Organisms*, 92(2-3), 93–99. <https://doi.org/10.3354/dao02246>
- Crovetto, F., Romano, A., & Salvidio, S. (2012). Comparison of two non-lethal methods of dietary studies in terrestrial salamanders. *Wildlife Research*, 39(3), 266–270. <https://doi.org/10.1071/WR11103>

- Currie, D. J., & Marconi, R. (2020). An analysis of threats and factors that predict trends in Canadian vertebrates designated as at-risk. *FACETS*, 5(1), 49–66.
<https://doi.org/10.1139/facets-2019-0023>
- Das, I. (1996). Resource use and foraging tactics in a south Indian amphibian community. *Journal of South Asian Natural History*, 2(1), 1–30.
[https://ir.unimas.my/id/eprint/24036/1/91-%20Das%20\(Resource%20use%20%26%20foraging%20tactics\).pdf](https://ir.unimas.my/id/eprint/24036/1/91-%20Das%20(Resource%20use%20%26%20foraging%20tactics).pdf)
- de Oliveira, A. A., Benvindo-Souza, M., dos Santos, H. V. R., Barradas, M. C., Marques, L. P., Costa, A. G., Sarmiento, R. A., e Silva, D. d. M., & Saraiva, A. d. S. (2025). The impact of neonicotinoid insecticides on amphibians: A comprehensive review and future research challenges. *Environmental Research*, 267, 120595.
<https://doi.org/10.1016/j.envres.2024.120595>
- Dimmitt, M. A., & Ruibal, R. (1980). Exploitation of food resources by spadefoot toads (*Scaphiopus*). *Copeia*, 1980(4), 854–862.
- Emerson, S. B. (1985). Skull shape in frogs: Correlations with diet. *Herpetologica*, 41(2), 177–188.
- Ethier, J. P., Fayard, A., Soroye, P., Choi, D., Mazerolle, M. J., & Trudeau, V. L. (2021). Life history traits and reproductive ecology of North American chorus frogs of the genus *Pseudacris* (Hylidae). *Frontiers in Zoology*, 18, 40. <https://doi.org/10.1186/s12983-021-00425-w>

- Garcia, N. W., Pfennig, K. S., & Burmeister, S. S. (2015). Leptin manipulation reduces appetite and causes a switch in mating preference in the Plains Spadefoot Toad (*Spea bombifrons*). *PLoS ONE*, 10(4), e0125981. <https://doi.org/10.1371/journal.pone.0125981>
- Gherghel, I., & Martin, R. A. (2020). Postglacial recolonization of North America by spadefoot toads: Integrating niche and corridor modeling to study species' range dynamics over geologic time. *Ecography*, 43(1), 119–130. <https://doi.org/10.1111/ecog.04576>
- Goldberg, S. R. (2021). Notes on reproduction of the Boreal Chorus Frog, *Pseudacris maculata* (Anura: Hylidae), from Colorado. *Sonoran Herpetologist*, 34(3), 56–58.
- González-del-Piiego, P., Freckleton, R. P., Edwards, D. P., Koo, M. S., Scheffers, B. R., Pylon, R. A., & Jetz, W. (2019). Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Current Biology*, 29(9), 1557–1563. <https://doi.org/10.1016/j.cub.2019.04.005>
- Government of Alberta. (2025). *Amphibian species at risk*. <https://www.alberta.ca/amphibian-species-at-risk>
- Grant, E. H. C., Zipkin, E. F., Nichols, J. D., & Campbell, J. P. (2013). A strategy for monitoring and managing declines in an amphibian community. *Conservation Biology*, 27(6), 1245–1254.
- Gustafson, K. D., & Newman, R. A. (2016). Multiscale occupancy patterns of anurans in prairie wetlands. *Herpetologica*, 72(4), 283–291. <https://doi.org/10.1655/HERPETOLOGICA-D-15-00030>

- Hartel, T., Nemes, S., Cogălniceanu, D., Öllerer, K., Schweiger, O., Moga, C.-I., & Demeter, L. (2007). The effect of fish and aquatic habitat complexity on amphibians. *Hydrobiologia*, 583, 173–182. <https://doi.org/10.1007/s10750-006-0490-8>
- Hartel, T., Scheele, B. C., Rozyłowicz, L., Horcea-Milcu, A., & Cogălniceanu, D. (2019). The social context for conservation: Amphibians in human shaped landscapes with high nature values. *Journal for Nature Conservation*, 53, 125762. <https://doi.org/10.1016/j.jnc.2019.125762>
- Heise-Pavlov, S. R., & Longway, L. J. (2011). Diet and dietary selectivity of Cane Toads (*Rhinella marina*) in restoration sites: A case study in Far North Queensland, Australia. *Ecological Management & Restoration*, 12(3), 230–233. <https://doi.org/10.1111/j.1442-8903.2011.00603.x>
- Hocking, D. J., & Babbitt, K. J. (2014). Amphibian contributions to ecosystem services. *Herpetological Conservation and Biology*, 9(1), 1–17.
- Hodgkison, S., & Hero, J. M. (2003). Seasonal, sexual and ontogenetic variations in the diet of the ‘declining’ frogs *Litoria nannotis*, *Litoria rheocola* and *Nyctimystes dayi*. *Wildlife Research*, 30(4), 345–354. <https://doi.org/10.1071/WR01008>
- Hopkins, W. A. (2007). Amphibians as models for studying environmental change. *ILAR Journal*, 48(3), 270–277. <https://doi.org/10.1093/ilar.48.3.270>
- Jaeger, R. G., & Rubin, A. M. (1982). Foraging tactics of a terrestrial salamander: Judging prey profitability. *Journal of Animal Ecology*, 51(1), 167–176. <https://doi.org/10.2307/4332>

- Jancowski, K., & Orchard, S. A. (2013). Stomach contents from invasive American bullfrogs *Rana catesbeiana* (= *Lithobates catesbeianus*) on southern Vancouver Island, British Columbia, Canada. *NeoBiota*, 16, 17–37. <https://doi.org/10.3897/neobiota.16.3806>
- Johnston, T. A., & Cunjak, R. A. (1999). Dry mass-length relationships for benthic insects: A review with new data from Catamaran Brook, New Brunswick, Canada. *Freshwater Biology*, 41(4), 653–674. <https://doi.org/10.1046/j.1365-2427.1999.00400.x>
- Kassambara, A. (2023). ggpubr: 'ggplot2' based publication ready plots (Version 0.6.0) [Computer software]. <https://CRAN.R-project.org/package=ggpubr>
- Kerby, J. L., Richards-Hrdlicka, K. L., Storfer, A., & Skelly, D. K. (2010). An examination of amphibian sensitivity to environmental contaminants: Are amphibians poor canaries? *Ecology Letters*, 13, 60–67. <https://doi.org/10.1111/j.1461-0248.2009.01399.x>
- Larsen, J. H., Jr., & Guthrie, D. J. (1975). The feeding system of terrestrial tiger salamanders (*Ambystoma tigrinum melanostictum* Baird). *Journal of Morphology*, 147(2), 137–153. <https://doi.org/10.1002/jmor.1051470203>
- Lauzon, R. D. (1999). *Status of the Plains Spadefoot (Spea bombifrons) in Alberta*. Alberta Wildlife Status Report No. 25. Alberta Environment, Fisheries and Wildlife Management Division, and Alberta Conservation Association.
- Lee, T. S., & Randall, L. A. (2022). A framework to identify priority wetland habitats and movement corridors for urban amphibian conservation. *Ecological Solutions and Evidence*, 3, e12139. <https://doi.org/10.1002/2688-8319.12139>

- Li, Z., Costamagna, A. C., Beran, F., & You, M. (2024). Biology, ecology, and management of flea beetles in *Brassica* crops. *Annual Review of Entomology*, 69, 199–217.
<https://doi.org/10.1146/annurev-ento-033023-015753>
- Luedtke, J. A., Chanson, J., Neam, K., Hobin, L., IUCN SSC Amphibian Specialist Group, & et al. (2023). Ongoing declines for the world’s amphibians in the face of emerging threats. *Nature*, 622(7983), 308–314. <https://doi.org/10.1038/s41586-023-06578-4>
- Mahan, R. D., & Johnson, J. R. (2007). Diet of the Gray Treefrog (*Hyla versicolor*) in relation to foraging site location. *Journal of Herpetology*, 41(1), 16–23. [https://doi.org/10.1670/0022-1511\(2007\)41\[16:DOTGTH\]2.0.CO;2](https://doi.org/10.1670/0022-1511(2007)41[16:DOTGTH]2.0.CO;2)
- Marty, J. T. (2005). Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology*, 19(5), 1626–1632.
- McWilliams, D. A. (2008). *Amphibian nutrition: A report for the Canadian Association of Zoos and Aquariums (CAZA) Amphibian Taxon Advisory Group (TAG)*.
- Measey, G. J., Vimercati, G., de Villiers, F. A., Mokhatla, M. M., Davies, S. J., Edwards, S., & Altwegg, R. (2015). Frog eat frog: Exploring variables influencing anurophagy. *PeerJ*, 3, e1204. <https://doi.org/10.7717/peerj.1204>
- Meyer, A., Grac, C., Labat, F., Meka, J., van der Zon, K. A. E., Theissinger, K., & Georges, J.-Y. (2025). Testing the optimal foraging theory in a generalist feeder: The case of reintroduced European pond turtles and its impact on macroinvertebrates communities. *Ecology and Evolution*, 15(8), Article e71823. <https://doi.org/10.1002/ece3.71823>

- Monroy, J. A., & Nishikawa, K. C. (2011). Prey capture in frogs: Alternative strategies, biomechanical trade-offs, and hierarchical decision making. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 315(2), 61–71.
<https://doi.org/10.1002/jez.601>
- Moore, J. E., & Strickland, E. H. (1954). Notes on the food of three species of Alberta amphibians. *The American Midland Naturalist*, 52(1), 221–224.
- Moore, J. E., & Strickland, E. H. (1955). Further notes on the food of Alberta amphibians. *The American Midland Naturalist*, 54(1), 253–256.
- Newman, R. A. (1999). Body size and diet of recently metamorphosed spadefoot toads (*Scaphiopus couchii*). *Herpetologica*, 55(4), 507–515.
- Nishikawa, K. C. (1999). Neuromuscular control of prey capture in frogs. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 354(1385), 941–954. <https://doi.org/10.1098/rstb.1999.0445>
- Noel, A. C., Guo, H. Y., Mandica, M., & Hu, D. L. (2017). Frogs use a viscoelastic tongue and non-Newtonian saliva to catch prey. *Journal of the Royal Society Interface*, 14(127), 20160764. <https://doi.org/10.1098/rsif.2016.0764>
- Pafilis, P., Kapsalas, G., Lymberakis, P., Protopappas, D., & Sotiropoulos, K. (2019). Diet composition of the Karpathos marsh frog (*Pelophylax cerigensis*): What does the most endangered frog in Europe eat? *Animal Biodiversity and Conservation*, 42(1), 1–8.
<https://doi.org/10.32800/abc.2019.42.0001>

- Pereira, A., Samlali, M. L., S'khifa, A., Slimani, T., & Harris, D. J. (2021). A pilot study on the use of DNA metabarcoding for diet analysis in a montane amphibian population from North Africa. *African Journal of Herpetology*, 70(1), 68–74.
<https://doi.org/10.1080/21564574.2021.1921058>
- Pinkas, L., Oliphant, M. S., & Iverson, I. L. K. (1971). Food habits of albacore, bluefin tuna, and bonito in California waters. *California Department of Fish and Game Fish Bulletin*, 152, 1–105.
http://content.cdlib.org/view?docId=kt8290062w&brand=calisphere&doc.view=entire_text
- Pyke, G. H. (1984). Optimal foraging theory: A critical review. *Annual Review of Ecology and Systematics*, 15, 523–575. <https://doi.org/10.1146/annurev.es.15.110184.002515>
- R Core Team. (2024). *R: A language and environment for statistical computing*.
- Randall, L. A., Smith, D. H. V., Jones, B. L., Prescott, D. R. C., & Moehrensclager, A. (2015). Seasonal differences in extinction and colonization drive occupancy dynamics of an imperilled amphibian. *PLoS ONE*, 10(5), e0127059.
<https://doi.org/10.1371/journal.pone.0127059>
- Randall, L., Lloyd, N., & Moehrensclager, A. (2018). *Guidelines for mitigation translocations of amphibians: Applications for Canada's prairie provinces (Version 1.0)*. Centre for Conservation Research, Calgary Zoological Society.
- Rogers, L. E., Hinds, W. T., & Buschbom, R. L. (1976). A general weight vs. length relationship for insects. *Annals of the Entomological Society of America*, 69(2), 387–389.
<https://doi.org/10.1093/aesa/69.2.387>

- Romano, A., Salvidio, S., Palozzi, R., & Sbordoni, V. (2012). Diet of the newt, *Triturus carnifex* (Laurenti, 1768), in the flooded karst sinkhole Pozzo Del Merro, Central Italy. *Journal of Cave and Karst Studies*, 74(3), 271–277. <https://doi.org/10.4311/2011JCKS0208>
- Roner, M., Costa, A., Pedrini, P., Matteucci, G., Leonardi, S., & Romano, A. (2020). A midsummer night's diet: Snapshot on trophic strategy of Alpine salamander, *Salamandra atra*. *Diversity*, 12(5), 202. <https://doi.org/10.3390/d12050202>
- Sage, R. D. (1982). Wet and dry-weight estimates of insects and spiders based on length. *The American Midland Naturalist*, 108(2), 407–411. <https://doi.org/10.2307/2425505>
- Sample, B. E., Cooper, R. J., Greer, R. D., & Whitmore, R. C. (1993). Estimation of insect biomass by length and width. *The American Midland Naturalist*, 129(2), 234–240. <https://doi.org/10.2307/2426503>
- Sekulic, G., & Rempel, C. B. (2016). Evaluating the role of seed treatments in canola/oilseed rape production: Integrated pest management, pollinator health, and biodiversity. *Plants*, 5, 14. <https://doi.org/10.3390/plants5030033>
- Semlitsch, R. D., et al. (2015). Intermediate pond sizes contain the highest density, richness, and diversity of pond-breeding amphibians. *PLoS ONE*, 10(4), e0123055.
- Smith, L. M., Gray, M. J., & Quarles, A. (2004). Diets of newly metamorphosed amphibians in the West Texas playas. *The Southwestern Naturalist*, 49(2), 257–263.
- Solé, M., & Rödder, D. (2010). Dietary assessments of adult amphibians. In C. K. Dodd, Jr. (Ed.), *Amphibian Ecology and Conservation: A Handbook of Techniques* (pp. 167–184). Oxford University Press.

- Solé, M., Beckmann, O., Pelz, B., Kwet, A., & Engels, W. (2005). Stomach-flushing for diet analysis in anurans: An improved protocol evaluated in a case study in Araucaria forests, southern Brazil. *Studies on Neotropical Fauna and Environment*, 40(1), 23–28.
<https://doi.org/10.1080/01650520400025704>
- Sterrett, S. C., Katz, R. A., Brand, A. B., Fields, W. R., Dietrich, A. E., Hocking, D. J., Foreman, T. M., Wiewel, A. N. M., & Grant, E. H. C. (2019). Proactive management of amphibians: Challenges and opportunities. *Biological Conservation*, 236, 404–410.
<https://doi.org/10.1016/j.biocon.2019.05.047>
- Stiles, R. M., Hawkins, M., Mitchell, W. A., & Lannoo, M. J. (2016). Amphibian response to a large-scale habitat restoration in the Prairie Pothole Region. *Journal of North American Herpetology*, 2016(1), 70–79. <https://doi.org/10.17161/jnah.v2016i1.11926>
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306(5702), 1783–1786. <https://doi.org/10.1126/science.1103538>
- Sullivan, M., III. (2017). *Statistics: Informed decisions using data* (5th ed.). Pearson.
- Taylor, B. N. (2004). Plains Spadefoot (*Spea bombifrons*). In B. A. Downey, B. L. Downey, R. W. Quinlan, O. Castelli, V. J. Remesz, & P. F. Jones (Eds.), *MULTISAR: The Milk River Basin Habitat Suitability Models for Selected Wildlife Management Species* (Alberta Species at Risk Report No. 86, pp. 106–111). Alberta Sustainable Resource Management, Fish and Wildlife Division.

- Toft, C. A. (1981). Feeding ecology of Panamanian litter anurans: Patterns in diet and foraging mode. *Journal of Herpetology*, 15(2), 139-144.
- Toft, C. A. (1985). Resource partitioning in amphibians and reptiles. *Copeia*, 1985(1), 1–21.
<https://doi.org/10.2307/1444785>
- Valencia-Aguilar, A., et al. (2013). Ecosystem services provided by amphibians and reptiles in Neotropical ecosystems. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 9(3), 257-272.
- Van Meter, R. J., & Glinski, D. A. (2021). Route of exposure influences pesticide body burden and the hepatic metabolome in post-metamorphic leopard frogs. *Science of the Total Environment*, 779, 146358. <https://doi.org/10.1016/j.scitotenv.2021.146358>
- Wickham, H., Averick, M., Bryan, J., Chang, W., D'Agostino McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., . . . Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4(43), 1686.
<https://doi.org/10.21105/joss.01686>
- Winter, M., Fiedler, W., Hochachka, W. M., Koehncke, A., Meiri, S., & De la Riva, I. (2016). Patterns and biases in climate change research on amphibians and reptiles: A systematic review. *Royal Society Open Science*, 3(11), 160158. <https://doi.org/10.1098/rsos.160158>