THE AMPHIBIANS AND REPTILES OF ALBERTA

A Field Guide and Primer of Boreal Herpetology

With colour photographs by
Wayne Lynch and
Illustrations by Irene McKinnon

Anthony P. Russell and
Aaron M. Bauer

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For
Geraldine, Sarah, Helen and James (APR)
and
Monica (AMB)

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SECOND EDITION

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Preface to the First Edition

AMPHIBIANS AND REPTILES ARE a fascinating but poorly understood component of the Alberta fauna. While the herpetofaunas of virtually all Canadian provinces and American states have been reviewed in technical, popular or semi-popular books, that of Alberta has not been so treated. This publication is our attempt to redress this situation. We feel that documenting our herpetofauna has added significance at this time because of the heightened awareness of conservation and associated environmental issues. It is difficult to conserve when the basic raw materials for such efforts have not been assembled into a manageable compendium.

In compiling this book we have attempted to outline the basic features of the natural history of the amphibians and reptiles of Alberta. In so doing we have added what we feel is sufficient background information to enable the interested reader to place our amphibians and reptiles into a comparative context. Thus, while the focus of this volume is Alberta, the significance of the features of our amphibians and reptiles can only be appreciated if the general biology of these types of animal is considered.

While we have referred to a significant body of literature, we have not attempted to be exhaustive in this regard. Representative books and papers have been cited at the end of each chapter and each individual species account, but in the body of the text we have endeavoured to present the pertinent information in an essentially non-technical way. We hope that each chapter can be understood without the need for reference to the cited literature, but those who are interested in pursuing these topics further can follow them up by using the bibliography. Some general references are included in the bibliography but are not cited at the end of any particular chapter. These are included in order to provide a broad array of general sources. Following these are over 980 more specific references that allow the reader to pursue in more depth the information presented in the various chapters and species accounts. Included here are 100 references that relate directly to the herpetology of Alberta. Specific literature that is directed towards descriptive embryology, anatomy and laboratory physiology has normally not been included in the bibliography as such sources do not generally relate directly to aspects of natural history. A glossary is provided to help explain the more technical terms.

We hope that by taking this approach this book will be useful at two levels. The general information contained herein should be appropriately formulated to be directly accessible and comprehensible to the interested layperson, but it should also be able to serve as a source book for the more advanced student of the reptiles and amphibians of Alberta. We trust that this book will contribute to further and broader understanding of our amphibians and reptiles and place into sharper focus this rather neglected component of our vertebrate fauna.

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Preface to the Second Edition

IN THE SEVEN YEARS since the appearance of the first edition of this book, Albertan herpetology has experienced a period of dynamic growth. Much of this has been focussed on the task of gaining basic information on the biology and ecology of amphibians and reptiles in this province, and on determining the status of their populations. Thus, there is now in progress the production of a series of status reports on the wildlife of Alberta, which will include all reptile and amphibian species. Currently eight species have been documented in this way (report numbers placed in parentheses): *Ambystoma macrodactylum* (22), *Bufo cognatus* (14), *Bufo hemiophrys* (12), *Rana luteiventris* (17), *Rana pipiens* (9), *Phrynosoma hernandesi* (5), *Heterodon nasicus* (15), and *Crotalus viridis* (6). This undertaking of Alberta Fish and Wildlife has greatly enhanced our knowledge of the herpetofauna of this province and will provide a baseline for future monitoring and for the addressing of conservation issues, in concert with the activities of the Alberta Conservation Association.

The last seven years have witnessed significant activities in the study and documentation of the herpetofauna of the entire North American continent. Such work has a major impact on the understanding of our more localized fauna. For example, five of the eighteen species of amphibians and reptiles occurring in Alberta have undergone name changes, and another (*Ambystoma tigrinum*) is in a state of flux. This does not indicate mere caprice on behalf of the researchers involved, but rather reflects that with intensified study we are able to refine our understanding of these species, to more adequately circumscribe them, and thus more appropriately develop strategies for issues pertinent to conservation.

The bibliographic reference sections of this book have grown significantly since the previous edition—another sign of the vitality of the work going on. The references pertaining directly to the herpetofauna of Alberta have increased by more than fifty percent, and currently number in excess of 150. All sections of the text have been updated to reflect these new additions of pertinent data and reports.

Despite recent activity, much remains to be done. Certain key areas of the province remain understudied, and it is not yet possible to definitively state that no new species will be added to the list of confirmed reptiles and amphibians of Alberta. Further, although our understanding of the status of many species has improved, the causes of phenomena, such as amphibian decline, remain incompletely known.

The success of the first edition of this book, and the need for a second, and much revised, edition reflects positively on the interest that Albertans have taken in these less conspicuous components of the province's fauna. We hope that this new edition will serve to further catalyze and foster this interest.

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1 Introduction

ALBERTA IS WELL KNOWN for its reptiles, but for those of the past rather than the present. This province is one of the world's focal points for the discovery and study of dinosaurs and their relatives. These animals were spectacular and represent terrestrial life on a scale that no longer exists. Such reptilian giants no longer roam the province, and the present-day reptiles and amphibians (the herpetofauna) appear rather modest in contrast. Why, then, should they be considered of interest?

In the age of the dinosaurs (200 million to 65 million years before present), the climate of what is now Alberta was much different than it is today, being semi-tropical and rather equitable. Since the demise of the dinosaurs, continental movement has brought a very different climatic regime to our province, one that is characterized by long, cold winters and short, but often hot, summers. These conditions offer a great challenge to amphibians and reptiles. In tropical and subtropical regions the number of amphibian and reptile species is relatively large and these animals are often a conspicuous part of the biota. In Alberta, by contrast, there are relatively few species. This, in itself, is of interest, as the species that persist here do so at, or close to, the edges of their range and display some significant solutions to the problems of existence in a rather hostile climate. Alberta amphibians and reptiles are truly northern animals, are adjusted to their circumstances, and play an important role in the overall economy of nature within the province.

The living reptiles and amphibians of Alberta are generally inconspicuous and one is not likely to come across them except by accident. They are dormant throughout the winter. In the spring and summer, the times of their greatest activity, they are relatively secretive. Unlike birds and mammals, most do not have complex social behaviour and thus cannot usually be found at particular sites carrying out specific social interactions. Breeding is generally an exception to this, but for the most part breeding activities are also conducted in an inconspicuous way. The one exception to this is the breeding activities of frogs and toads, which are accompanied by loud and specific vocalizations. Thus, while one is unlikely to encounter amphibians and reptiles in the normal course of events, except accidentally, it is almost certain that frogs and toads will be heard in the spring and summer, unless one stays deep in the heart of cities. But hearing them and locating the source of the sound are two quite different things. When frogs and toads call, they are very sensitive to movements around them and will normally cease if you begin to approach, especially in daylight hours. One gets the feeling that frogs are always somewhere else—they cease calling where you are and start calling where you have just been! Being elusive does not make amphibians and reptiles unapproachable, however, and in Chapter 3 we provide some information that will allow you to focus your search and to have a greater chance of observing these fascinating creatures.

Despite their apparent elusiveness, the reptiles and amphibians of Alberta are both interesting and important for a number of reasons, and are well worth the effort of observation and study for anyone interested in the natural history of our province. Among the vertebrates, the reptiles and amphibians of Alberta are by far the most neglected group. The fishes, birds and mammals all have numerous books wholly or partially devoted to them, and the recently published "Bibliography of Alberta Mammals" indicates just how much information is available for this group. Until now, however, there has not been a single book devoted, even partially, to a survey of the amphibians and reptiles of this province. The current work is therefore an attempt to begin to redress this imbalance.

While there are only eighteen species of amphibian and reptile known to occur in Alberta, this relative paucity hides a wide array of diversity. In terms of biomes (extensive communities of plants and animals whose makeup is determined by soil and climatic conditions), Alberta shows great variations, from the almost desert-like conditions of the southeast to the mountainous conditions of the west. Thus, while amphibians and reptiles are found throughout the province, the mix of species varies from place to place and reflects quite accurately the boundaries between the biomes. The area of greatest richness, in terms of species numbers, is the extreme southeastern corner of the province, a region in which relatively few people live and few visit. The species that live in this zone are especially interesting because they are found at the northern extremity of their ranges. Some of these species barely make it into the province at all, but have much more extensive ranges further south. In Alberta, they are thus at the limit of the conditions that they can tolerate, and studying species in such situations can tell us a great deal about how distributions are determined and limited.

Conversely, some species of frogs that occur in Alberta extend great distances north into the Northwest Territories and are close to the southern edges of their ranges in Alberta. Thus, again we can view Alberta as an area of transition and can begin to understand what limits the distribution of amphibians and reptiles by understanding our species. The mountains, to the west too, bring about abrupt changes in the pattern of species representation. The relative inaccessibility of the majority of land in the northern half of our province means that we still know almost nothing about population patterns and structure of amphibians and reptiles in these regions, except where they intersect major waterways and roads. The challenges of Alberta's rigorous climate place limitations on our amphibians and reptiles that we are only just beginning to understand. Our climate is one of extremes, and in this book we will focus on how our amphibians and reptiles are able to respond to these environmental challenges and survive in an area where most amphibians and reptiles cannot.

Another reason why our amphibians and reptiles are of particular interest is because they appear to be rather susceptible to environmental change. They have already withstood the ravages brought about by agricultural practices, industrialization and urbanization and have survived these crises, although often at some cost to population size or populations as a whole. There are now new environmental challenges that are of a more continent-wide and worldwide nature. Issues such as "global warming" and "acid rain" are of prime concern, and there is already considerable evidence that such factors are having an effect on amphibians and reptiles throughout the world (see Chapter 11). Amphibians in particular seem to be rather sensitive to the effects of acid rain because it directly affects their breeding sites. Population declines of amphibians have become dramatic over the last decade or so in various parts of the world, and the same trends are apparent among some of our own species. Amphibians may thus serve as environmental monitors. If we do not know very much about the distribution and population structure of our own species, we will not be able to interpret the messages inherent in any changes in population structure. While many species are not threatened by direct human intervention in Alberta (although others are), they may all be threatened by influences from outside that may have a larger message for us.

Our main aim in this book is to raise the level of awareness about the amphibians and reptiles of this province and to provide a base of information that we hope can be added to as time passes. Following a series of introductory remarks about amphibians and reptiles in general, which are designed to place our own forms in perspective, we have divided the remainder of the book into two parts. The first is a species by species account of the reptiles and amphibians known to occur in Alberta (plus four species that may occur but have not yet been reported from our province). This portion of the book, along with its keys and supplementary information, can be used as a field guide and will assist in identification and observation. The second component of the book consists of a series of chapters that attempt to place our amphibians and reptiles into a biological perspective. In this regard, we have attempted to consider the general biology of amphibians and reptiles and to relate these details to what is known about our native species and how the particular conditions encountered in Alberta influence the lives of our local forms. Alberta is both cold and arid, and these two major factors play a pivotal role in the lives of our indigenous amphibians and reptiles. For a province that rejoices in the glory of its past reptilian populations, it is strange that so little is known of their living relatives that share the province with us.

2 Characterization of Amphibians and Reptiles

AMPHIBIANS AND REPTILES ARE traditionally studied together and form the subject matter for the discipline of herpetology. This clustering is artificial in an evolutionary sense, since these two very different groups have been evolving independently for a very long time. The association of the two groups is based on their shared absence of features, such as feathers or hair, which characterize the other, more conspicuous, tetrapod lineages. Further, while amphibians and reptiles are very distinctive in regard to their genealogy, they do share a number of similar physiological and behavioural traits that are related to their particular modes of existence.

In the Devonian Period (about 400 million years ago) a group of freshwater bony fishes with a well-ossified vertebral column ("backbone") and stout, fleshy limb-like fins gave rise to the stem amphibians, the first truly terrestrial vertebrates (Fig. 2.1). These fishes, the osteolepiform rhipidistians, were somewhat similar in appearance to the living lungfishes and the coelacanth. All are members of a group of vertebrates collectively known as sarcopterygians. The early amphibians were in many ways quite dissimilar in appearance from those of today, but also displayed many common features. Throughout the latter part of the Palaeozoic Era and into the first part of the Mesozoic the amphibians diversified and exhibited a wide array of body forms and sizes. Only two of the many lineages of fossil amphibians gave rise to animals that survived to the present day. One group, the temnospondyls, are believed to have been the ancestors of the Lissamphibia, the group that includes all of the living amphibians. The second group, the anthracosaurs, are thought to have led to the reptiles, and ultimately, through them, to the other amniotes (birds and mammals).

In all, there are about 49,000 living species of vertebrates and these are distributed among the following groups:

Group name	Contents	No. of Species
"Agnatha"	jawless vertebrates (lampreys and hagfishes)	85
Chondrichthyes	sharks, skates and rays	835
Actinopterygii	Ray-finned fishes	23,000
Sarcopterygii	lobe-finned fishes (lung fishes, coelacanth)	7
Amphibia	frogs, toads, salamanders, caecilians	4855
Reptilia	snakes, lizards, amphisbaenians, turtles, crocodiles	6970
Aves	birds	8710
Mammalia	mammals	4550

The term "Lissamphibia" combines the essential features of these living animals, referring to their typical biphasic lifestyle (living both in water and on land = amphibia) and their generally smooth (liss-) skin. Neither of these features, taken literally, characterize all members of the group, however, as among the almost 5,000 species currently recognized a great deal of variation in body form and lifestyle is seen. The features that were shared by the ancestor of all the living amphibians, and therefore serve to unite the group, are rather more subtle. Chief among these are characteristics of the teeth, skull, vertebrae, ribs, hearing apparatus, skin, eyes and musculature.

Some characteristics of amphibians are adaptations to life on land, others to life in the water. Their eggs are laid in water or in moist surroundings, and they are covered by several gelatinous envelopes but do not possess a shell or embryonic membranes other than the yolk sac (see Fig. 2.6).

Extant amphibians retain a larval stage in their life history (Fig. 2.2). Thus, in most cases, the eggs give rise to a free-living "tadpole" stage that somewhat later metamorphoses to produce the definitive adult. In some species, the free-living larval stage is reduced or almost eliminated from the life cycle, but such instances are rare. The tadpole or larva is essentially an aquatic feeding machine and makes effective use of seasonally abundant plant life or prey items, depending upon the species, and thus permits a rapid

Figure 2.1 Relationships of the major groups of vertebrates.

increase in the biomass of the population. The food resources used by the larvae may be much different from those consumed by the adults, and at metamorphosis there may be marked changes in the gut system, as well as in external appearance, as the shift in diet takes place. The fact that amphibians have a larval stage has led to the belief that they are "chained to the water." This view, however, results largely from study of northern temperate amphibians, and many tropical forms show adaptations that enable them to develop, either partially or completely, in the absence of water.

The living members of the Amphibia are divided into three major subgroups, two of which occur in Alberta. The least known and smallest group are the caecilians (Gymnophiona) (Fig. 2.3). These approximately 160 species of elongate, limbless animals are limited in their distribution to the tropical regions of the Americas, Africa and Asia. The caecilians are primarily burrowers, but some species are aquatic. They feed primarily on insects, annelids (segmented worms) and other invertebrates. Although the eyes are usually reduced and often covered with skin or even bone, caecilians are able to perceive their external environment through a number of other sense organs including the tentacle, a small chemoreceptive device unique to the Gymnophiona. Caecilian eggs are usually few in number and heavily yolked, and in many forms the embryos are retained in the mother's oviduct for the entire embryonic period.

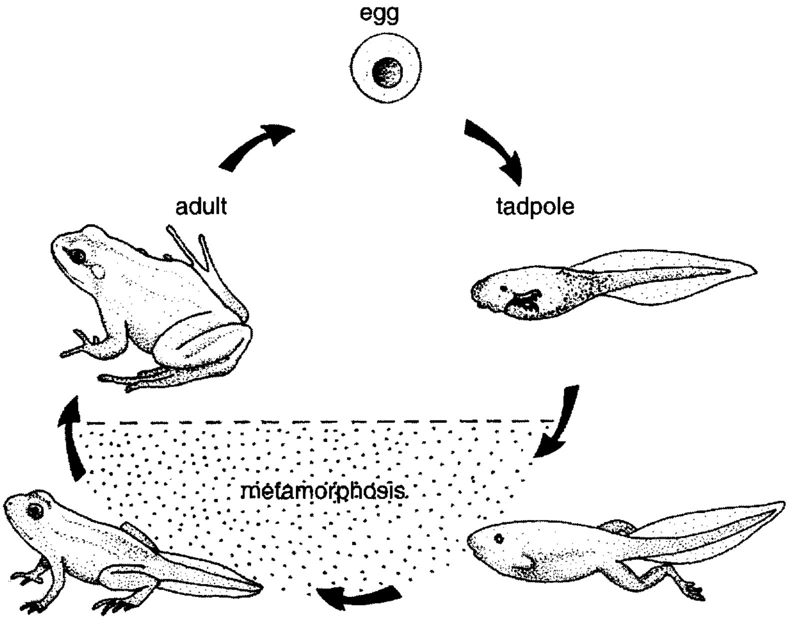


Figure 2.2 *The life cycle of an anuran amphibian.*

The remaining two groups of amphibians constitute the more familiar salamanders (Caudata) and frogs (Anura). The first of these is largely restricted to the Northern Hemisphere and achieves its greatest diversity in North America, where eight of the nine families are represented. Salamanders (Fig. 2.4) are characterized by: their generalized tetrapod body form, usually with four-toed fore feet and five-toed (pentadactyl) hind feet; metamorphosis from a well-limbed larva with external gills; long tail; teeth in both jaws; internal fertilization; and absence of external ears. There are approximately 390 species of living salamanders, ranging in size from the tiny neotropical *Thorius* (30 mm total length) to the giant aquatic salamanders of China and Japan, *Andrias*, which reach lengths of 1.8 m and may weigh more than 60 kg.

Although most are terrestrial as adults, many salamanders retain the features of the larval stage and are unable to metamorphose, maturing sexually and breeding as apparent juveniles—a phenomenon known as paedomorphosis (= childlike form). Some of these salamanders, such as members of the families Amphiumidae and Sirenidae, not only retain larval features, such as gills, but also show reduction of the limbs. Some other salamanders may utilize

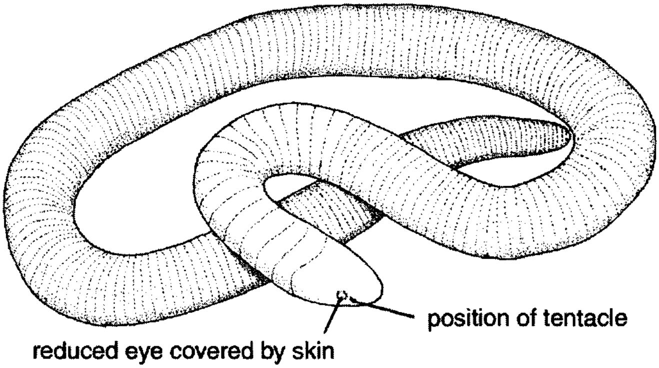


Figure 2.3 A Gymnophione.

paedomorphosis as an option to overcome unfavourable conditions, but will metamorphose if and when conditions are appropriate and will reproduce as typical, terrestrial adults. The best examples of facultative paedomorphs are shown by members of the family Ambystomatidae, which is the only group of salamanders found in Alberta. It is possible that this option is exercised by northern populations of the tiger salamander (*Ambystoma tigrinum*) in Alberta. As in certain other groups of salamanders, ambystomatids have the ability to regenerate lost limbs or portions thereof, although this capacity is related to size, and larger individuals may lose this potential.

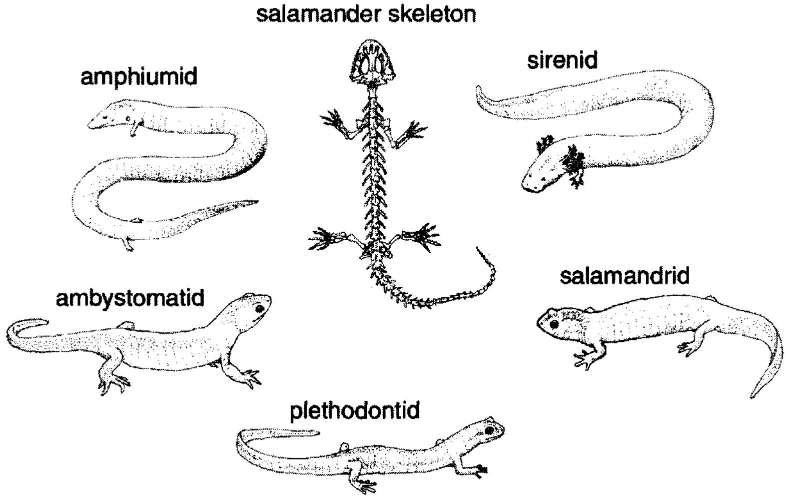


Figure 2.4 Salamander Diversity.

Another salamander family, the Salamandridae or newts, undergo normal metamorphosis. After spending a period as terrestrial efts, they return to the water to breed, undergoing a second major change in form (although larval features are not regained). During all life stages, newts are protected by potent skin toxins, which make them unpalatable to all but a few potential predators. Newts, which occur as close as British Columbia, often have elaborate underwater courtship displays. Males deposit packages of sperm (spermatophores) on the substrate and entice females to pick them up with the lips of their cloaca. Fertilization is thus internal, as it is in most salamanders, although copulation is not involved.

The most speciose family of salamanders is the Plethodontidae. These are remarkable in that they lack lungs and exchange almost all of their respiratory gases through the skin. The tongue skeleton, which in most salamanders helps to force air back into the lungs, no longer has a dual function and is devoted entirely to assisting in prey capture. In some plethodontids, the tongue may be rapidly extended to distances almost as great as the length of the body, allowing the salamanders to capture insect prey at a considerable range. Plethodontids are also unusual in that most species do not exhibit a free larval stage. The eggs are laid in terrestrial nests and the embryos undergo direct development, hatching as miniature versions of the adults.

The frogs and toads (Fig. 2.5) constitute by far the largest group of amphibians. The more than 4,300 species are divided into about twenty-four families. Frogs and toads occur throughout the world, except for Antarctica and many remote oceanic islands. Anurans are immediately recognizable by: their short and compact bodies; elongate hind limbs; relatively short fore limbs; lack of tail; prominent eyes; lightly built skull; urostyle (fused and compacted caudal vertebrae); absence of free ribs; prominent tympanum (ear drum); external fertilization preceded by amplexus (male grasps female from dorsal surface); voice; and morphologically distinct tadpole larvae. Anurans are generally small, with some *Eleutherodactylus* being less than 12 mm in body length. There are, however, some relative giants such as *Conraua goliath,* a ranid frog from Africa, which attains a body length of 350 mm and a weight of three kilograms or more.

Unlike some salamanders, all anurans must undergo metamorphosis before they are able to breed. Many, however, undergo some or all of their premetamorphic development in the egg, often away from the water in specially constructed nests, but sometimes in the reproductive tract of the female. In some groups, the eggs or larvae are brooded in special pouches on the dorsal or lateral surfaces of

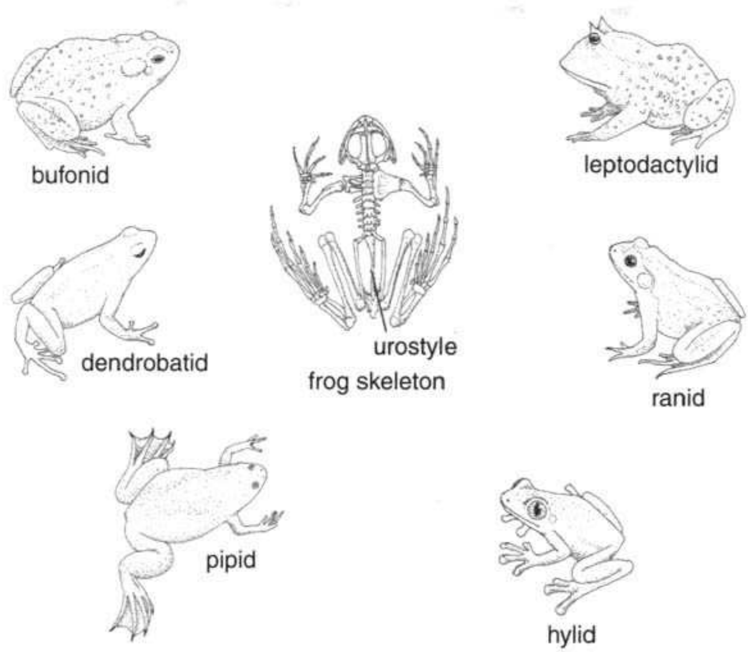


Figure 2.5 Frog Diversity.

the body, in the vocal sacs of males, or even in the stomach, as in the gastric brooding frog, *Rheobatrachus silus* of Australia. Typical free-living tadpoles are radically different in appearance from adults, much more so than are the larvae of salamanders when compared to their adults. Many organ systems are not expressed for much of the larval period, and metamorphosis is rapid and drastic. The diet, habitat and general ecology of the larvae are all forsaken for those typical of the adults.

One of the most notable traits of frogs in general is their ability to vocalize. The Amphibia is the first of the vertebrate groups to have a larynx (voice box). This is formed from the modified anterior end of the trachea (windpipe). With its associated cartilages and vocal cords, the larynx enables sounds to be produced. Tightening or relaxing of the vocal cords causes variations in pitch. Male frogs usually possess vocal sacs which act as resonators to help broadcast species-specific advertisement calls to females. Vocalization is chiefly associated with mating, and the calls of frogs are as characteristic as those of birds. Most frogs do not have elaborate courtship rituals like those of many salamanders. Rather, males grasp females in amplexus, and gametes of both sexes are shed into the water. Amplexus may persist for long periods of time. External fertilization is the rule in all frogs except a few representatives of the large families Bufonidae and Leptodactylidae, and in *Ascaphus truei*, the tailed frog (which may enter Alberta in the region of Waterton Lakes National Park).

Some frogs have toxins similar to those of salamanders. These include the tropical American dendrobatids, or arrow-poison frogs, as well as the true toads (Family Bufonidae), which are represented by three species in Alberta. In the genus *Bufo*, the poison is largely concentrated in large parotoid glands behind the eyes and is often more noxious than deadly. The secretion of certain arrow-poison frogs, however, is the most powerful animal-derived toxin known. The skin of a single arrow-poison frog may contain enough toxin to kill 10-20,000 mice. Many frogs, nonetheless, rely on their agility as a means of escape. Most features of frog anatomy are in some way related to modifications of the body for jumping or swimming. The hind limbs are powerfully built and provide the thrust for both of these activities. The forelimbs and shoulder girdles of most terrestrial frogs are likewise modified as shock absorbers that receive the weight of the animal upon landing. Some frogs are capable of jumps exceeding five metres. Certain frog groups are characterized as being permanently aquatic. These include the pipids, of which *Xenopus*, a common laboratory animal, is an example. None of the Alberta species is exclusively aquatic, although *Rana luteiventris* spends much of its time submerged. Many more frogs have abandoned the water for the trees and are modified for an arboreal existence. Hylid frogs, in particular, have adhesive toe pads which help them cling to vegetation. In spite of the difficulties of obtaining water, frogs have also invaded desert regions, where burrowing and nocturnality protect them from excessive dehydration. In some frogs, water loss is also slowed by keratinization of the skin, or the secretion of a protective waxy layer over the exposed surfaces of the body.

Frogs are typically insectivores, although other prey may be taken. Most frogs obtain their prey by flipping out their tongue, which attaches at the front of the mouth. Tadpoles feed primarily on vegetation or detritus and may themselves be food for aquatic insects, fish and other tadpoles.

Despite the many differences between caecilians, salamanders and frogs, all share certain problems in dealing with their environments. Amphibian skin is typically highly permeable, and amphibians are prone to desiccation if exposed to a drying environment. Ultimately, most amphibians rely on a source of water for reproduction and larval existence. Such constraints have circumscribed the habitats and ecological niches available to amphibians. The strategies employed by amphibians to deal with the problems posed by the environment will form the basis for portions of the second part of this book.

Reptiles, which arose from an amphibian stock (Fig. 2.1), have escaped from many of the constraints acting upon living lissamphibians by way of two major innovations: a desiccation-resistant keratinized skin, and a shelled egg that permits direct development on land. Reptiles are therefore much more terrestrial than amphibians, and their distribution is not so closely related to the availability of free water.

Reptiles first appeared in the Carboniferous Period (about 330 million years ago) and radiated in the Permian period and throughout the Mesozoic Era. The latter is commonly known as the "Age of Reptiles" and is testimony to their apparent dominance in terrestrial situations during this time. Most conspicuous were the various groups collectively known as the dinosaurs. Until their sudden demise at the end of the Cretaceous Period (about 65 million years ago), the dinosaurs were the major large herbivores and carnivores throughout most of the world. The dinosaurs were representatives of a large group of reptiles known as the archosauromorphs. Other members of this lineage include the crocodylians, which still survive, and the flying pterosaurs. Birds too are archosauromorphs and, in fact, are the living legacy of the dinosaurs, current orthodoxy suggesting that they are their direct descendants.

The archosauromorphs are one major branch of a group of reptiles known as diapsids (= two arches) because of the configuration of bones on the side of the skull, behind the eye. The other major diapsid lineage is the Lepidosauromorpha. This group contains less spectacular animals, but includes the most successful of the living reptiles, the squamates (lizards and snakes), and their close relatives, the tuataras. Mesozoic reptiles also invaded the marine environment, a feat never achieved by the amphibians. The most well-known of these were the plesiosaurs and ichthyosaurs, which have no living relatives.

Another reptile group with some marine forms are the turtles. These animals established their particular body plan during the "Age of Reptiles" and have persisted relatively unchanged since that time. Synapsid reptiles, on the other hand, were also established early, but their history led them to one of the major transitions among tetrapods, resulting in the origin of mammals in the Triassic. Not surprisingly the synapsids are also known as the mammal-like reptiles.

From the foregoing, it is evident that both birds and mammals have evolved from the group that we refer to as reptiles. Thus, the Class Reptilia, excluding birds and mammals, is not a real evolutionary unit since it incorporates elements that are more closely related to groups that are not regarded as reptiles than they are to other nominal reptiles (Fig. 2.1). Even at the level of living "reptiles," this problem applies. For example, the crocodylians are more closely allied to birds than they are to lizards and snakes, yet birds are not usually regarded as reptiles. The currently accepted pattern of relationships among all of these forms is represented as a cladogram (a type of genealogical tree) in Fig. 2.1. In this book, we will also exclude birds from our consideration. This poses some problems from the point of view of generalizing about living reptiles or comparing them to one another. These problems do not apply to the living lissamphibians as evidence points to their common ancestry, independent of other fossil and living groups.

The living reptiles have in common: a scaly, keratinized integument; true claws; a cleidoic egg; extraembryonic membranes; modified wrist and ankle joints; full complement of cranial nerves; internal fertilization following copulation; and excretion of uric acid as the primary nitrogenous waste product. One of the most crucial developments in reptilian phylogeny was the evolution of the cleidoic egg (Fig. 2.6). Cleidoic eggs, for example chicken eggs, have controlled exchanges with the environment, allowing for the diffusion of respiratory gases while protecting the developing embryo from desiccation and mechanical shock. Such eggs are able to develop terrestrially, but can only do so if deposited in situations with particular environmental characteristics. Typically, reptiles do not incubate their eggs, and thus selection of the nest site is critical. This is even more apparent for those reptiles that have parchment-shelled (pliable and porous) rather than calcareous-shelled (hard, as in chickens) eggs. There are three extraembryonic membranes typical of reptiles, birds and mammals (the amniotes), and these play critical roles in development: the amnion provides a fluid-filled sac around the embryo; the allantois serves as a site of storage of waste products and, along with the chorion, provides a surface for respiratory gas exchange.

The second reptilian "innovation" was a less permeable integument. This, however, reduced the potential for gas exchange through the skin, but permitted the reptiles to fully exploit the terrestrial realm. Crucial in this transition was an effective waterproofing of the outer layers of the skin that greatly reduced the osmotic flux potential, more effectively isolating the internal environment

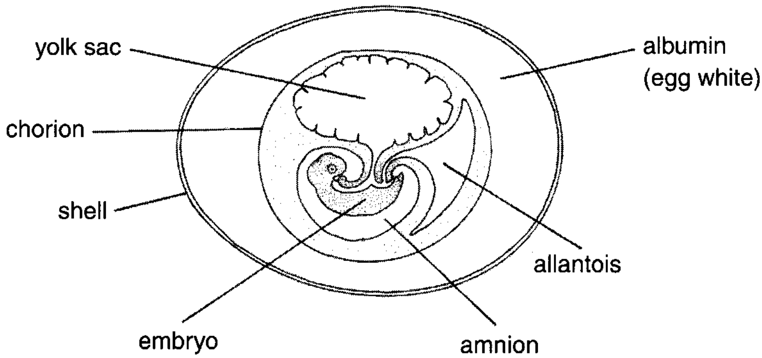


Figure 2.6 The Cleidoic Egg.

of the body from the external environment. This same modification was inherited from the reptiles by both birds and mammals.

The reptiles, like the amphibians, are ectothermic (obtaining their body heat from external sources) and poikilothermic (having a fluctuant body temperature). They are thus unable to fully regulate their body temperature physiologically. They do, however, thermoregulate by behavioural means (Fig. 2.7). Those which gain heat directly from the sun's rays are known as heliotherms, and those that gain it from the ground upon which they rest are known as thigmotherms. While reptiles in general may require a fairly high environmental temperature to maintain them in an active state, they are very susceptible to overheating. They may be killed when the body temperature rises to a level only a few degrees above that to which they will normally expose themselves. Body temperatures of about 46°C may be potentially lethal to certain desert lizards, whilst temperatures of about 40° may be tolerated without stress. The germ cells (those associated with reproduction), however, may have a higher sensitivity than the body in general, and males of some lizards become sterile at temperatures which apparently cause no physical discomfort. Susceptibility to heat is probably in large part due to the fact that reptiles have no rapid cooling device comparable to the sweat glands of mammals. Many species do pant, but this is a drastic solution and rapidly depletes body water. Postural thermoregulation is also possible, and many forms stand high on their legs in order to radiate heat. Behavioural thermoregulation ensures that body temperatures remain within a certain tolerable range, known as the preferred temperature. This is basically higher in diurnal (day active) than it is in nocturnal (night active) and burrowing forms.

Some physiological modifications to control temperature also exist. In large active lizards, such as monitors, the rate of heat loss or absorption is influenced by changes in distribution of circulating blood. This distribution is between the superficial and deep tissues of the body. Colour change is another method of temperature control, and the amount of heat absorbed by an object depends to some extent upon its coloration. Thus, some species tend to grow darker when they are first exposed to the sun, in order to increase heat absorption, and then become lighter, in order to retard further temperature rise.

Reptiles are more resistant to extremes of cold than they are to extremes of heat. Prolonged exposure to sub-zero temperatures is probably lethal, but above this level many species can exist for long periods in a state of torpor. In temperate zones, such torpor is always a feature of reptile life, as it is of amphibian life. These organisms thus become adapted to a seasonal climate in which certain parts of the year provide too little warmth for them to remain active. Many forms of both amphibians and reptiles in cold regions tend to burrow beneath the permanent frost line in the winter to avoid extreme temperatures.

As a rule, reptiles breathe atmospheric air and utilize lungs. Gills are never present. The pulse pump seen in the frog, in which air is forced into the lungs from the buccal cavity, is replaced in reptiles by the suction pump. This involves an interaction between the ribs, the viscera and many muscles to enable the thorax to expand and contract. This suction pump has advantages over the force pump. The lungs are filled or emptied in a single pass, independent of the size of the buccal cavity. In frogs, only as much air as can be housed in the buccal cavity can be taken into the lungs at any one time. The flow of air in reptiles thus becomes more or less continuous and the buccal cavity, freed from its role in ventilation, can be designed more effectively for food capture and processing. It also enables the skin to become armoured as a protective device and keratinized to prevent water loss, as the skin is no longer used as an organ of gas exchange.

The 6,970 species of living reptiles are divided into five major groups, each characterized by a different body form and different biological characteristics. The relationships of these groups to each other are indicated in Fig. 2.1.

There are more than 250 species of living turtles (Fig. 2.8). This number includes both fresh-water and marine turtles, as well as partially and wholly terrestrial forms. Turtles, the Testudinata (or Chelonia), are of course immediately identified by their "shells,"

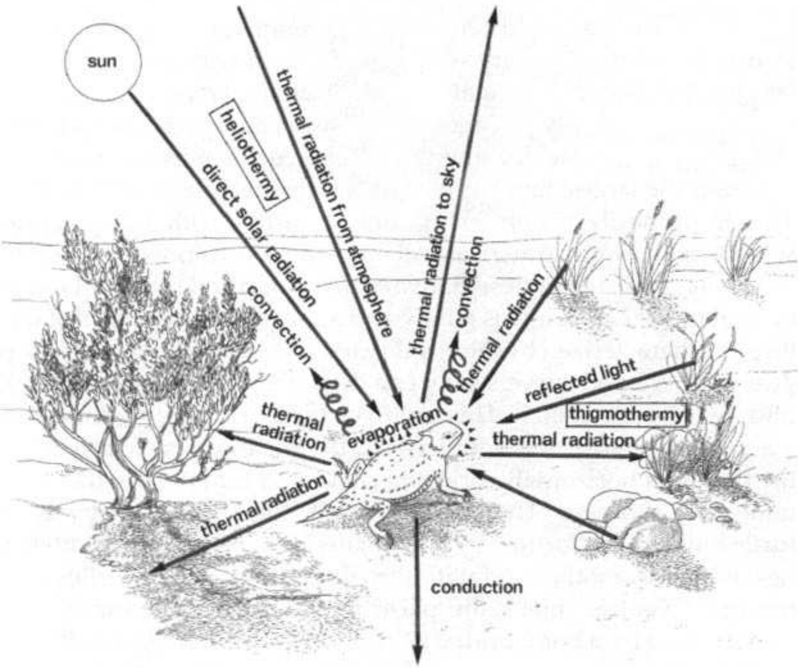


Figure 2.7 The ways in which a reptile interacts with its thermal environment.

consisting of a dorsal carapace and a ventral plastron. In addition, turtles exhibit the loss of teeth; the absence of temporal fenestrae; the placement of the shoulder girdle inside the rib cage; the modification of the neck vertebrae for packaging inside the shell as the head is withdrawn; the presence of a single copulatory organ in males; and modification of ventilatory motions in association with the presence of a rigid shell. Turtles range in size from less than ten centimetres in carapace length for some testudinids to more than 2.0 metres in length and 800 kg in weight for *Dermochelys coracea*, the leatherback sea turtle. As a group, turtles occur worldwide, except for high latitudes and some remote oceanic islands.

All turtles lay eggs which, even in sea turtles, are buried on land. In some turtles, the choice of egg-laying site is especially important as it may influence the sex ratio of the offspring in the clutch. In these turtles, sex determination is temperature-dependent rather than genetically programmed. The depth of individual eggs within the nest exposes them to different temperatures along a temperature gradient. Eggs deeper in the nest, where temperatures are cooler, will form males, while eggs incubated at warmer temperatures, nearer the surface, yield females. The temperature at which this transition occurs may vary with latitude, both within and between species. If they survive to maturity, individuals of most turtle species may live to relatively old ages. In at least some species of tortoises (Family Testudinidae), longevity may exceed one hundred years.

One of the largest families of turtles is the fresh-water Emydidae. This is primarily a northern group of turtles with many representatives in North America. Alberta's only confirmed chelonian, *Chrysemys picta*, is a representative of this group and is rather typical in its general features. This family and all of the northern turtle families are characterized by their ability to bend the neck in a vertically directed *S*-shaped curve. Many can draw the entire head and neck into the protective shell. This group of turtles, the cryptodires, has a southern hemisphere counterpart, the pleurodires, which bend the neck in a horizontally oriented curve and cannot hide the head under the carapace. The carapace itself influences all aspects of turtle biology. It is formed by bony plates derived from the skin that fuse with one another and with the ribs and vertebrae. Turtles also possess a ventral shield, the plastron, which may be attached to the carapace by a bony bridge between the fore and hind limbs. In some forms, such as box turtles, the plastron may be hinged to allow it to be closed against the carapace when the head, limbs and tail are withdrawn. The shell may be reduced in some species, such as *Chelydra serpentina*, the snapping turtle, which has a reduced plastron, sea turtles (Families Cheloniidae and Dermochelyidae), which have reduced carapaces, and soft-shelled turtles (Family Trionychidae), which have both components reduced and exhibit a rather fleshy shell.

Despite their relatively small number of species, turtles play an important economic role in many human societies. The outer covering of the carapace of sea turtles, "tortoise shell," is valued for its decorative properties. Sea turtles are also hunted for their meat and eggs. Snapping turtles and many other species are also sought after for their flesh. Turtles are popular in the pet trade. In the case of some species, these various human pressures on populations have resulted in a drastic decline in numbers, and even extinction.

Crocodylians (Fig. 2.9) are a group of twenty-three species of archosauromorph reptiles that today occur mostly in the tropics and subtropics. They are quadrupedal and generally largely aquatic. Some species occur in salt water and may travel great distances at sea. Crocodylians, which include alligators, caimans and gavials, as well as crocodiles proper, are characterized by a diapsid skull; elongate, well-toothed jaws; a secondary palate; lack of clavicles

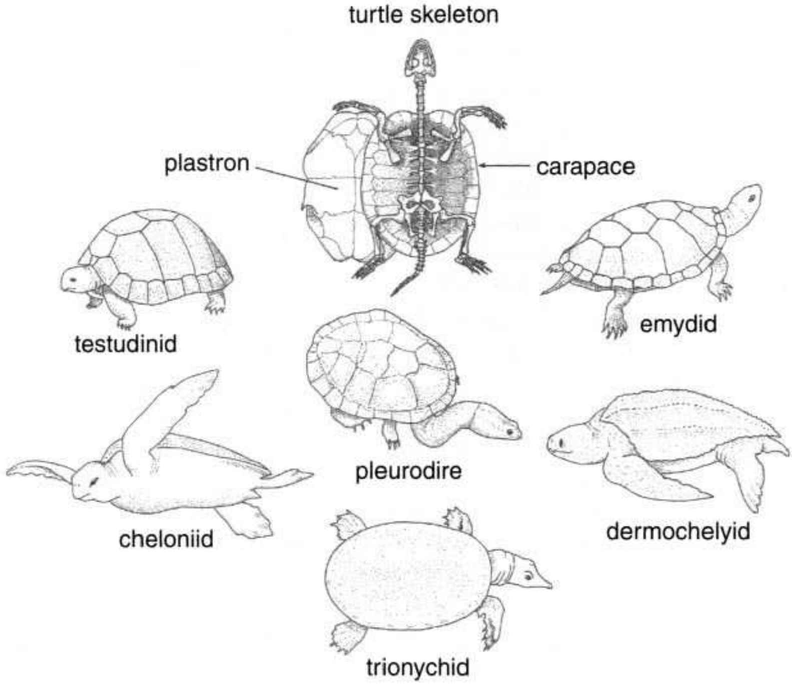


Figure 2.8 Turtle Diversity.

(collar bones); abdominal ribs (gastralia); a specialized ankle joint; osteoderms (bony plates) in the skin; a four-chambered heart; presence of an unpaired penis; and a laterally compressed tail, often with a single or paired dorsal ridge. All crocodylians are large, with several species exceeding six metres in total length.

Only two crocodylians are native to North America. *Crocodylus acutus* is found in southern Florida and *Alligator mississippiensis* is widespread in the southeastern United States. Like turtles, crocodylians are hunted, primarily for their skins which are used in the manufacture of leather goods. This activity was responsible for a great decline in alligator populations earlier in the century, but with government protection alligators have returned to many areas of their former range. In many areas of the world, crocodylians are farmed for their hides and meat. Crocodylians may also interact with humans in another way. Because of their large size, they may be dangerous, especially during the period of reproduction and brooding, and have been responsible for human deaths.

Crocodylians rely exclusively on animal prey. Smaller individuals may take insects and small vertebrates while larger animals eat fish, reptiles and mammals. Crocodiles have a complex social behaviour, and the adults provide parental care to the young. As in turtles, nest sites are chosen carefully as sex is determined by temperature. In the American alligator, intermediate temperatures produce males, whereas low or very high temperatures produce females.

The tuatara (Fig. 2.10), *Sphenodon punctatus*, is placed in a group of its own, the Sphenodontia. A second species has recently been recognized on the basis of genetic differentiation. Tuataras are the sole survivors of a major radiation of lepidosauromorph reptiles. The tuatara, which is lizard-like in appearance, occurs only on about thirty small islands off the coasts of the main islands of New Zealand. It may be distinguished from its nearest living relatives, the squamates (lizards and snakes) by its possession of an unmodified diapsid skull; overlapping processes on the ribs (uncinate processes); gastralia (abdominal "ribs"); absence of a tympanum; and absence of a copulatory organ in males. Tuataras reach sixty centimetres in total length and over one kilogram in weight. Males are larger than females.

Sphenodon is extremely long-lived, reaching confirmed ages in excess of sixty years. Sexual maturity is not attained until an age of approximately twenty. This longevity is related to the low temperatures in the animal's environment (for reptiles, which are ectothermic, age is perhaps most meaningfully measured in terms of metabolic rate rather than absolute time). Tuataras are generally active at night and frequently tolerate temperatures below 10°C. By day, they occupy burrows which may be those of seabirds (with which they may cohabit) or of their own construction. Although they are probably primarily insectivorous, tuataras may also eat lizards and the seabirds that share their daytime retreats. Fertilization by way of copulation occurs about nine months before females lay eggs in burrows excavated for that purpose. Incubation lasts about twelve to fifteen months, the longest period known for any living reptile. The eggs and juveniles are especially sensitive to predation, and the introduction of non-native mammals, especially rats, has wreaked havoc on some tuatara populations. Before the advent of man (and with him, other mammals), *Sphenodon* was widespread on the larger islands of New Zealand.

The vast majority of living reptiles belong to the Squamata. The two groups included in this order are the lizards and snakes. Snakes, however, arose from within lizards. Lizards can, therefore, only be defined as squamates that lack the special features of snakes. Squamates are characterized by a streptostylic (moveable) quadrate bone in the skull; a reduction in the original diapsid skull arches;

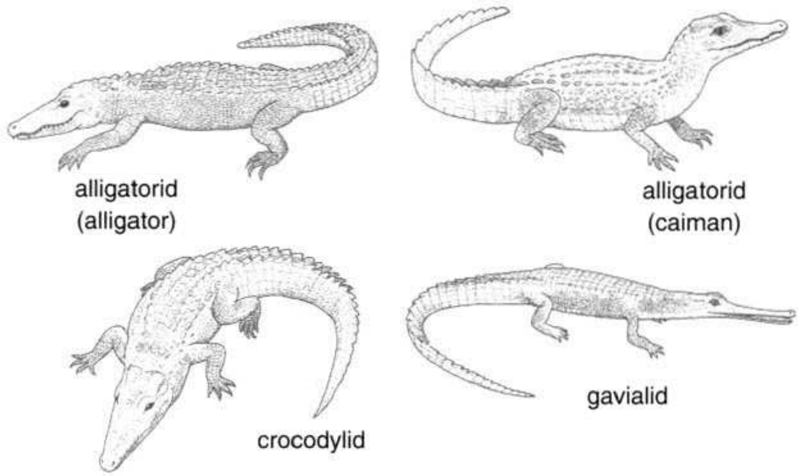


Figure 2.9 Crocodylian Diversity.

paired copulatory hemipenes in males; and absence of gastralia. In addition, lizards possess the following features that have been evolutionarily lost in snakes: specialized wrist and ankle joints; gracile limbs; and a "heel" formed by the hooked metatarsal bone of the fifth digit. There is a great deal of variation among the more than 4,000 species of lizards (Fig. 2.11). They range throughout the world except for very high latitudes. In size, they range from geckos (Family Gekkonidae) less than forty millimetres in total length to Komodo dragons (*Varanus komodoensis*, Family Varanidae) occasionally reaching three metres in length. Fossil varanids were even larger, and the closely related aquatic mosasaurs were the largest lizards ever to have existed, reaching lengths of more than ten metres.

Most lizards are insectivorous, but some larger species are carnivorous and others are largely or entirely herbivorous. The beaded lizards (Family Helodermatidae) employ venom in subduing prey and are the only lizards to do so. For most lizards, prey capture involves the use of the jaws, but in some forms, exemplified by chamaeleons (Family Chamaeleonidae), the tongue is used as a prehensile tool to capture small prey items. Like some plethodontid salamanders, chamaeleons are able to very rapidly project the tongue to a great distance. The mechanism used by these animals, however, is rather different from that of the lungless salamanders.

Chamaeleons also differ in their style of locomotion from most other lizards. Typical lizards (such as those of the families Iguanidae, Lacertidae, Agamidae and Teiidae) have a sprawling posture and move by a combination of lateral undulations of the body and

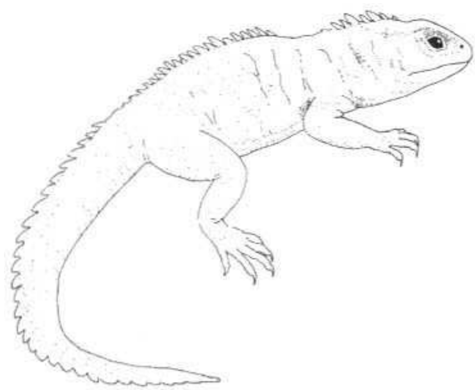


Figure 2.10 The Tuatara.

powerful strokes of the limbs. Chamaeleons, on the other hand, have compressed bodies, erect posture and move slowly and deliberately with little involvement of body motions. Climbing is common in lizards but has reached its extreme in the family Gekkonidae. Many geckos possess a complex adhesive mechanism that allows them to adhere to smooth surfaces and even to ascend vertical faces and hang upside down. Representatives of many other lizard families, on the other hand, have partially or wholly forsaken limbs, usually in association with a burrowing lifestyle. Such forms move in a serpentine fashion, sending waves down the length of the body and pushing against the substrate with their ventral and lateral scales. Examples of these types can be found in the families Pygopodidae, Dibamidae, Anniellidae, Scincidae, Gymnophthalmidae, Anguidae and the gerrhosaurs among the Cordylidae.

Another group, the amphisbaenians, are also chiefly limbless. These animals, which are sometimes placed as a separate branch of the squamates, are exceptionally specialized for a burrowing existence and use their strongly braced skulls to wedge into the substrata as they tunnel.

Although most lizards lay eggs (oviparity), representatives of many families have independently evolved viviparity (the bringing forth of live young). At least one skink (Family Scincidae) has a mammalian type of placental association between mother and young. Incubation period, clutch size and frequency of breeding vary by family, habitat, age and body size.

While lizard behaviour is generally stereotypical, it may be quite elaborate. For example, males of many iguanid lizards have complex courtship behaviour patterns associated with brightly marked

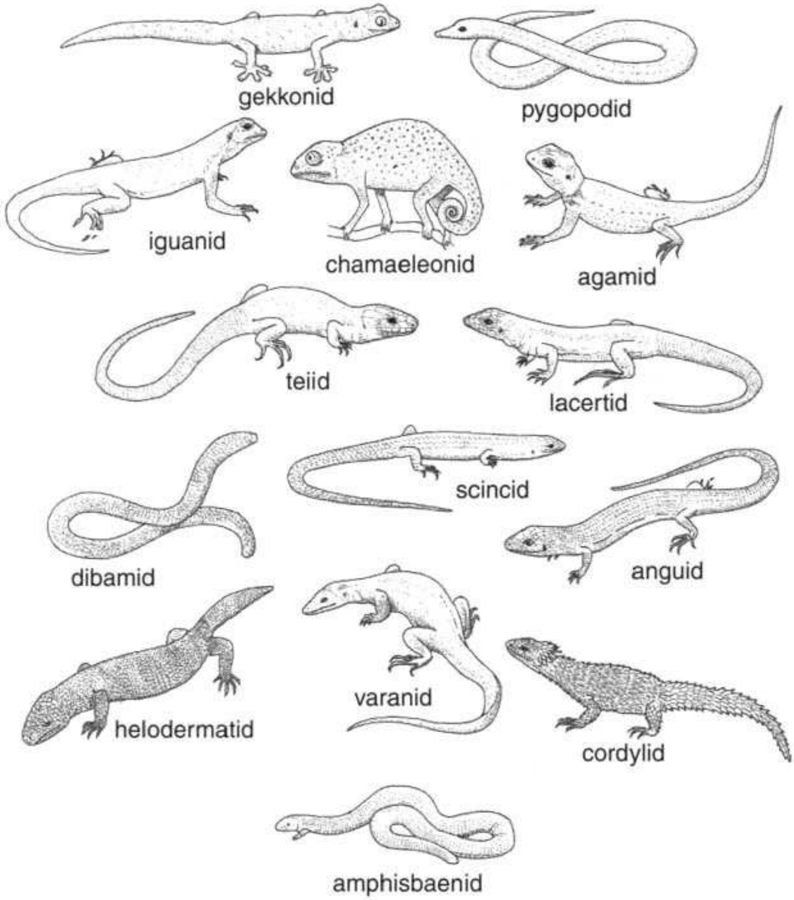


Figure 2.11 Lizard Diversity.

body parts that are prominently displayed to conspecifics. A very few lizards, such as the gecko *Ptenopus,* have calls similar to those of frogs. Chamaeleons and certain other lizards are sexually dimorphic, with males possessing crests, horns and other display organs that may function to attract mates or deter rivals. Displays may also be used as anti-predator defences. However, if bluffs fail, many species are able as a last resort to autotomize (cast off) parts of the tail in order to buy time to escape.

Snakes have approximately the same distribution as lizards, being found throughout the world except for the Arctic and Antarctic regions and a number of moderate-sized to small oceanic islands. There are about 2,600 species, distributed among eleven families (herpetologists differ in their opinions about the subdivisions of snakes, with some recognizing more than eleven families). Although generally similar in body form (Fig. 2.12), important anatomical, reproductive and ecological characters distinguish the major groups of snakes. In size, they range from very small, with an overall length of eleven centimetres (some members of the Family Anomalepididae, the dawn blind snakes), to very large, with an overall length of over eleven metres (the green anaconda, Family Boidae). Characteristically snakes lack legs (although members of the families Pythonidae, Tropidophiidae and Boidae have hook-like remnants of the hind limbs), eyelids and external ears. They have long flexible bodies with large numbers of vertebrae that are very precisely articulated with each other by way of large numbers of accessory processes. Many of the paired internal organs are either reduced to a single representative or staggered so that one of the pair lies in advance of the other within the long, slender body cavity. All snakes are either insectivorous or carnivorous and the head skeleton is modified in such a way that the jaws can be "dislocated" and spread apart to enable large prey items to be consumed.

Boids and pythons feed mainly on mammals and kill them by constriction. Members of the families Elapidae and Viperidae subdue prey with venom, injected by way of fangs and produced in modified salivary glands. These families include snakes that are dangerous to man and are thus regarded as being truly venomous. Many members of the Family Colubridae, however, that are normally regarded as harmless do, in fact, produce venom, although this is not usually powerful enough to be dangerous to humans. Thus, snakes such as garter snakes (genus *Thamnophis*) employ relatively mild venom to assist them in killing prey. This venom is not powerful enough to enable the snake to bite and then retreat until the victim is dead, which is the strategy adopted by elapids and viperids. The venoms of snakes contain proteins that may act either as neurotoxins (that act by blocking the transmission of nerve impulses) or as haemolytic agents (promoting the breakdown of the circulatory system). Some venoms combine both actions. Blocking of nerve transmission results in paralysis, and the enzymes that promote tissue breakdown affect such things as heart and kidney function. More than fifty species have been reported to have envenomated humans, their effects ranging from mild to fatal. Annually as many as 40,000 deaths occur worldwide as the result of snake bite.

Venoms, while primarily associated with prey capture, also become important as defensive materials. In order to warn potential aggressors, many venomous snakes have elaborate vocalization

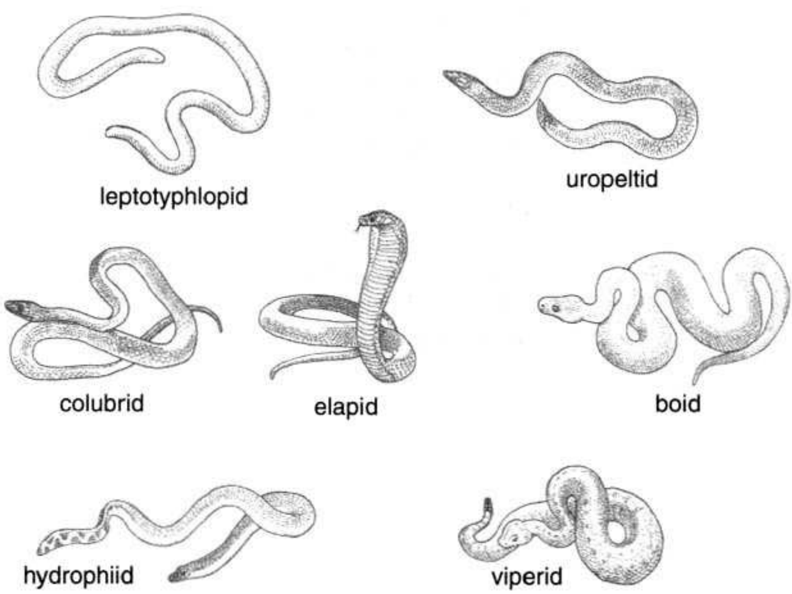


Figure 2.12 Snake Diversity.

patterns, warning colours or other ways of advertising the presence of venom, such as the rattle of rattlesnakes. Not surprisingly, some non-venomous snakes have also adopted these mechanisms, as well as taking on the appearance of venomous species, and thus mimic their venomous look-alikes. In this way, protection is afforded them by association with the venomous species they copy.

The tongue of snakes is highly protrusible and is frequently flicked out as the snake explores its environment. This tongue flicking is important in picking up chemical signals that are transferred to the paired pockets of Jacobson's organ in the roof of the mouth. Some snakes, including the pit vipers (Family Viperidae) and most boids and pythons also have a sensory system for detecting infrared heat. This is accomplished by way of pits on the side of the face or lips and enables these snakes to detect prey items by the heat they radiate, even in total darkness.

There are a variety of ways in which snakes move. Some are able to move the ventral scales and to use these to contact irregularities in the surfaces on which they are travelling. Each scute is attached to two or more pairs of ribs by muscles that allow it to be tilted and to be pushed back and forth. As these scutes overlap they are able to establish contact with surface irregularities and enable the snake to be pulled forward. Such locomotion, is known as rectilinear and is often used by heavy-bodied snakes when they are moving relatively slowly. For faster locomotion snakes employ lateral undulation, using S-shaped curves and pushing against irregularities of the surface. There are a variety of ways in which these lateral undulations are used, including sidewinding and slide-pushing, as well as simple lateral undulation. Climbing is achieved by modifications of rectilinear or lateral undulatory methods, or by a concertina type of locomotion in which the body coils around the support, such as a tree trunk, holds on with the tail and hind end of the body, reaches up with the head and front end of the body and hooks around the trunk higher up. The hind end of the body then releases and is drawn up by the body muscles.

Many snakes lay eggs and deposit them in an appropriate nest site, after which they leave them. Some species, however, such as certain pythons, remain with the eggs and incubate them in coils of the body, using their muscles to generate metabolic heat to assist in incubation. Garter snakes, pit vipers and others retain the eggs in the female reproductive tracts until they hatch. In some of these live-bearers, the female provides nutrients to the developing young by way of a placental relationship.

Significant references: Angelini and Ghiara 1984; Barrett et al. 1970; Bogert 1960; Bruns and Gross 1970; Burghardt 1980; Carpenter 1980, 1986a, 1986b; Clark, G.W. and Bradford 1969; Cuellar 1966; de Jongh and Gans 1969; Dial and Fitzpatrick 1983; Duellman 1979; Duellman and Trueb 1986; Dunn 1926; Emerson 1976, 1984; Ewert et al. 1994; Fitch 1970, 1981, 1985; Gans 1973; Gardiner 1983; Gibbons 1969b, 1987; Goin 1960; Green 1979, 1981; Greene 1983; Guttman 1985; Himstedt et al. 1982; Holtzman and Halpern 1990; Houck and Schwenk 1984; Hutchinson et al. 1968; Jayne 1986; Miller and Larson 1989; Noble and Brady 1930; Salthe 1967; Salthe and Mecham 1974; Sprules 1974; Tihen 1958, 1969.

3 The Amphibians and Reptiles of Alberta: A Brief Introduction

THE HERPETOFAUNA OF ALBERTA is not extensive (Table 3.1), but there remains much to be learned about our native amphibians and reptiles. Even in the short time that has elapsed since the publication of the first edition of this book significant new information has been gained about the biology and conservation status of several species. Moreover, the specific and even generic allocations of several of our native forms have been changed as a result of further research on geographic variation and phylogenetic relationships.

The Albertan herpetofauna includes an interesting mixture of forms with southern and eastern affinities. The greatest concentration of amphibians and reptiles occurs in the arid southeastern corner of the province, but interesting correlations of species distributions with other biotic regions exist. Eight species of reptiles and ten of amphibians are known to occur in the province. (See colour plates for photographs of all taxa known to occur in the province.)

The salamanders of Alberta belong to the family Ambystomatidae and can be distinguished from all other western species by their teeth, which form a continuous or broken row across the roof of the mouth. Typically (Fig. 3.1), they have a broad head, small eyes, prominent costal grooves and a tail flattened from side to side. Males usually have a bulbous vent and a longer tail than that of females. These forms are rarely seen, except during their brief breeding season. They crawl over land to ponds, lakes and streams and sometimes stumble into cellars and light wells. Migrations usually occur at night, during or after rains, and generally take the animals back to the parental pond. Breeding may start early, soon after the ice melts from lakes and ponds, but at high altitudes and in the north it may be delayed until summer. Throughout the rest of the year, except occasionally during rains, these salamanders stay

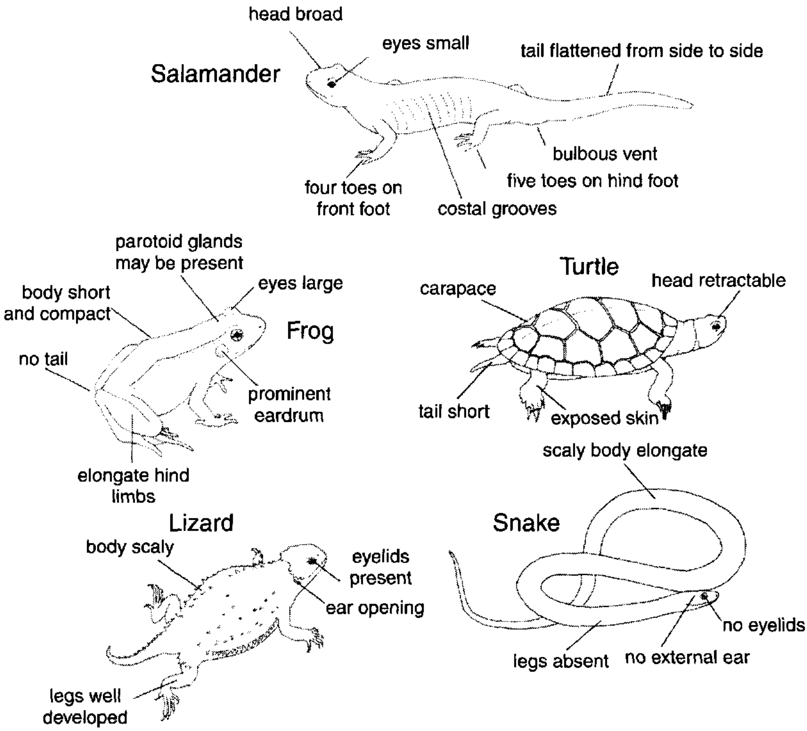


Figure 3.1 The body forms of amphibians and reptiles found in Alberta and their major distinguishing characteristics.

inside rotting logs and animal burrows, or in other moist places underground. Larvae may be found throughout the year. At high elevations and in the north, where temperatures are low and the growing season short, they may not transform until their second season. Some larvae may fail to transform and may breed without metamorphosing. The family ranges from Alaska and Labrador in the north, south to the southern part of the Mexican plateau.

In Alberta, four families of anurans are represented—the Bufonidae, Pelobatidae, Hylidae and Ranidae. The bufonids are the true toads and are worldwide in their distribution, except for extremely cold or dry areas, remote oceanic islands and Australia (where, however, the marine or cane toad has been introduced by man). Toads are able to live under adverse conditions and range from below sea level in Death Valley, California, to above 5,000 metres in the Himalayas; and from the tropics almost to the Arctic Circle.

Typical toads of the genus *Bufo* are chunky, short-legged, warty and have parotoid glands that distinguish them from all other tailless amphibians. The parotoids and warts are the sites of secretion of a sticky white poison, which in some species can paralyze or kill predators. Some predators, however, can eat toads with no apparent ill effects. Distinguishing features between Alberta species are differences in size, shape and distribution of the parotoids, conspicuousness and arrangement of the cranial crests, the extent of wartiness, form of the foot tubercles, and colour. Colour, however, may change from light to dark in response to temperature. Breeding in bufonids occurs in spring and summer, usually after rains. Adult males of most species have a dark throat. All develop brown nuptial pads on the thumb and inner fingers, which help them to cling to the slippery body of the female. Amplexus is pectoral.

The family Pelobatidae is represented by a single species in Alberta. The spadefoots are distinguished from the true toads by their cat-like eyes, single black, sharp-edged spade on the hind foot, teeth in the upper jaw, rather smooth skin, and the absence of parotoid glands. Males may have a dusky throat and dark nuptial pads on the innermost front toes; amplexus is pelvic. Spadefoots breed in pools that form after heavy rains, or in slow streams, reservoirs or irrigation ditches. The developmental stages are very rapid, as the eggs are often deposited in bodies of water that are only transient. Dry periods are spent in burrows either constructed by other animals or by themselves. When burrowing, spadefoots back into the ground.

The family Hylidae is also represented by only a single species in Alberta. The hylids are a large family of slim-waisted, long-legged frogs mostly of small size. Many are arboreal and have well-developed toe pads set off from the rest of the toe by a small, extra segment. These frogs are found on all continents but are most abundant and varied in the New World tropics.

The remaining group of amphibians that occurs in Alberta is the family Ranidae. This is composed of typically slim-waisted and long-legged frogs with a smooth skin. On land they jump, and the feet are webbed. There are dorsolateral folds which are very prominent, and these act as distinguishing features for ranids in western North America. Again there are representatives on all continents. Distinction between species is often extremely difficult as colour patterns may be quite variable.

With respect to Alberta's reptiles, there is but one species of turtle, six species of snake and one species of lizard. The turtle is *Chrysemys picta*, the western painted turtle. It has been found in the Milk River of southeastern Alberta and is an aquatic form which frequents ponds, marshes, small lakes, ditches and streams where the water is quiet or sluggish and the bottom muddy and overgrown with aquatic plants.

The lizard is *Phrynosoma hernandesi,* one of the horned lizards. These lizards are armed with head spines and sharp, projecting scales on the dorsal surface of the body. They are usually solitary in habits and when approached often crouch low, their markings and spiny skin blending with the ground. They feed chiefly on ants. This food resource and fine soil for burrowing appear to be essential environmental features for these lizards. When picked up, they may inflate themselves by gulping air, may jab with the horns, or, rarely, spurt blood from the eyes. The Alberta species is not known to employ the latter tactic. This blood comes from a sinus at the base of the nictitating membrane and is thought to repel predators.

There are three species of garter snake in Alberta, and these are all moderately slender snakes with a head slightly wider than the neck. The dorsal scales are keeled, and the anal scale is usually single. Dorsal scale counts are important in identification. Most species have a conspicuous pale yellow or orange vertebral (mid-dorsal) stripe and a pale stripe low on each side. Garter snakes occupy a great variety of habitats from sea level to high in the mountains. Many are aquatic or semi-aquatic, but some are completely terrestrial. When caught, they often void feces and expel musk from their anal scent glands. They are viviparous.

One species of *Pituophis* occurs in Alberta. This is the gopher snake or bullsnake (*P. catenifer*), a large yellow or cream-coloured snake with black, brown, or reddish brown dorsal blotches. This species lives in a variety of habitats throughout North America, from the lowlands high into the mountains and from coast to coast. It frequents desert, prairie, brushland, woodland, coniferous forests, and farmland. It is a good climber and burrower and is active chiefly by day, except in hot weather. When aroused, it hisses loudly and sometimes flattens its head and vibrates its tail. This behaviour, along with the diamond-shaped markings, causes these snakes to be mistaken for rattlesnakes.

The western hog-nosed snake, *Heterodon nasicus,* is a heavy bodied, blotched snake with a broad neck and upturned snout, which it uses in digging. This species frequents sandy or gravelly prairies, farmlands, and flood plains of rivers. In the extreme western part of its range, it occurs in semi-desert habitats and occasionally in mountain canyon bottoms.

The prairie rattlesnake, *Crotalus viridis,* is the only venomous snake found in Alberta. It belongs to the family Viperidae and the subfamily Crotalinae. This family has the most highly developed

Table 3.1. Breakdown of the Numbers of Species of Amphibians and Reptiles Occurring in Canadian Provinces and Territories[1]

	Caudata	Anura	Testudinata	Sauria	Serpentes	Total	Source
Alberta[2]	2	8	1	1	6	18[3]	This Book
B.C.	9	12	1	3	9	34	Green and Campbell 1984; Gregory and Campbell 1984; Corkran and Thoms 1996; Weller and Green 1997
Manitoba	4	12	2	1	5	24	Preston 1982; Cook, F.R. 1984; Weller and Green 1997; Duncan 1997
N.B.	7	9	3	0	4	23	Gorham 1970; Cook, F.R. 1984; Weller and Green 1997
Nfld.	2	6	0	0	0	8	Bleakney 1958; Maunder 1983; Maunder 1997; Weller and Green 1997
N.W.T.	0	5	0	0	1	6	Hodge 1976; Cook, F.R. 1984; Fournier 1997; Weller and Green 1997
N.S.	5	8	4	0	5	22	Bleakney 1952; Gilhen 1984; Cook, F.R. 1984; Weller and Green 1997
Ont.	14	14	11	1	18	58	Logier 1939, 1958; Cook, F.R. 1984; Johnson 1989; Weller and Green 1997; Oldham 1997
P.E.I.	4	5	0	0	3	12	Cook, F.R. 1967, 1984; Weller and Green 1997
P.Q.	10	11	8	0	7	36	Mélançon 1961; Cook, F.R. 1984; Bider and Matte 1990; Chabot and St. Hilaire 1991; Weller and Green 1997
Sask.	1	6	2	1	9	19	Cook, F.R. 1967, 1984; Didiuk 1997; Weller and Green 1997
Yukon	0	3	0	0	0	3	Hodge 1976; Cook, F.R. 1984; Mennell 1997; Weller and Green 1997
Canada Total	21	24	8	5	25	83	Cook, F.R. 1984; Weller and Green 1997
Montana[1]	4	12	3	4	10	33	Stebbins 1985; Reichel and Flath, 1995

[1] Montana is also included for comparison as it lies adjacent to Alberta.
[2] There is the possibility of four other species occurring in Alberta (see Chapter 5).
[3] Previous counts were 16 (Mills 1948); 17 (Logier and Toner 1955, 1961); 18 (Cook, F.R. 1984; Alberta Fish and Wildlife 1985).

venom injection mechanism among snakes. Large, hollow, moveable fangs are located at the front of the upper jaw. In biting, they are swung forward from their folded resting position, and the victim is stabbed and poisoned in a rapid thrust. The crotalids are known as pit vipers because they bear pits in the facial region that act as temperature sensitive structures, by means of which they can sense the location of their prey by detecting infra-red radiation.

Significant references: Alberta Recreation and Parks 1986; Anon 1964a, b, 1971, 1972; Beck and Beck 1988; Black 1967, 1969, 1970a, b, 1971; Black and Brunson 1971; Blair 1963, 1972; Boulenger 1920; Bow Valley Naturalists 1978; Breitenback et al. 1984; Burns (no date); Butler 1980; Campbell, et al. 1982; Carl 1959, 1960; Cook, F.R. 1965, 1966, 1983a, b, c, d; Corkran and Thoms 1996; Corn et al. 1984; Fowler 1934; Green and Campbell 1984; Greene 1997; Gregory and Campbell 1984; Griffiths 1979; Hardy, W.G. 1967; Harper 1931a; Hodge 1971, 1972, 1976; Holman 1972; Lewin 1963; Logier and Toner 1955, 1961; Mills 1948; Mosimann and Rabb 1952; Nelson 1979; Nelson and Paetz 1972; Nussbaum et al. 1983; Preble 1908; Roberts 1982a, b; Russell and Bauer 1991; Salt 1977, 1979; Smith, H.C. 1972; Smith, H.C. et al. 1970; Smith, W.W. 1972, 1975; Soper 1949; Spalding 1971, 1973, 1980; Tebby and Smith 1977; Watt, 1971; Weller and Green 1997; Williams 1946.

4 How to Observe Amphibians and Reptiles

As pointed out in the Introduction, reptiles and amphibians tend to be rather elusive and thus chance encounters are rare. They are generally small, cryptic and often tend to range over long distances during the active season, all of which make them rather difficult to locate. There are, however, certain ways in which the chances of encountering these animals can be increased. Obviously, reference to the distribution maps provided for each species will give some indication of areas where they are likely to occur, but these are not specific enough to locate particular sites. Thus, what can be determined from these is that the vicinity is appropriate, but from there on the search is up to you. It is also imperative that permission be obtained from the landowner if the particular site is on private land, before you enter and make a search. It is also significant that we advocate here only observation, not collection of specimens. For identification purposes, individuals may be handled, if you know how to do so competently without injuring yourself or the animal, but they should always be gently released again at the same site. Most amphibians and reptiles are afforded some level of protection under appropriate legislative acts of the Fisheries and Wildlife departments of each province. In Alberta, the local Fisheries and Wildlife office should be consulted about current regulations and legislation. No animals should be handled or removed before the regulations in force at the time have been consulted. Remember also not to disturb any habitat or handle any animals in provincial and national parks.

The first thing to remember is that many of our native amphibians and reptiles have activity patterns that are different from our own. Frogs, salamanders and snakes are often active at night. While this does not preclude their activity during the daytime, for some species, the chances of encounter are greatly increased if you can look for them after sunset. For frogs and toads, your task will often be assisted by the characteristic calls that these animals emit. After sunset, anurans can often be approached much more readily than they can in the daytime and will reveal themselves by their calls. Patience is still required, but once the calls are heard, usually at a water body, the source of the sound can be approached. This may cause the sound to cease, but if you stand still it should begin again fairly soon, and the singer can then be located with a flashlight. Once located like this, frogs and toads will often continue to sing while the beam of the flashlight is trained on them. This will give you an opportunity to observe the vocal sacs. Frogs and toads can also often be located simply by walking slowly around the perimeter of a likely body of water, again usually after dark, with a flashlight trained on the ground. Often frogs and toads will emerge into the vegetation to forage and will leap back into the water at your approach. The sound of the animal entering the water will enable you to locate the ripples with a flashlight, and again a short time spent waiting at the same spot may well see the animal come to the surface and attempt to exit the water once more. Toads often venture much further from water than frogs and so may also be encountered moving through the undergrowth along woodland paths.

Salamanders are a little more difficult to locate as they do not emit sounds. Often the best way of finding them is to walk the perimeter of likely ponds or sloughs, turning debris, such as logs and stones, as you go. Often they can be found hiding under such pieces of cover. Remember to always replace the turned item to its original position after investigating whether there is anything beneath it, and remember also not to injure the animal if there is one there when you replace the item. Frogs and toads may also be located in the same way, often in daylight hours when they are at rest. Another sign of amphibian activity, especially in the spring and early summer, is the presence of eggs in bodies of water. To locate these, one must again walk the periphery of the pond and carefully examine the vegetation near the shore. Often, eggs can be found attached to such vegetation (see colour plates), or tadpoles can be seen swimming in and out of the vegetation near shore. In some instances, tadpoles can be located in relatively small isolated puddles where females lay the eggs to avoid the potential pressures of predation that may exist in the main body of the pond.

Amphibian activity may be particularly great after a heavy spring or early summer rainfall. In conditions of relatively high humidity, amphibians tend to emerge in great numbers, and such falls of rain may actually initiate the breeding activities for the year. Such effects may be particularly noticeable in the southeastern corner of the province, where water is rather scarce. Mating in species such as the spadefoot toad occurs after heavy spring rains, and activity may be very intense after dark. The temporary pools left by such rainfalls often serve as the sites for egg deposition, and the tadpoles may be present in them in very high numbers.

Reptiles may be somewhat more difficult to locate as they generally have no preferred sites of aggregation where they remain obvious for extended periods of time. Some species of snake occupy communal den sites during the winter. If these can be located, then either spring emergence or fall aggregation can provide very spectacular views of large numbers of animals. Very soon after emergence in spring, they disperse, however, and very soon after arriving at the den site in fall, they enter the hibernaculum and thus disappear from sight.

Garter snakes can often be located close to water bodies as they tend to eat frogs and toads. Walking the periphery of a pond can often turn up a garter snake. Many snakes will bask during the day on warm surfaces and are thus often seen along roads where they pick up heat from the road surface or from rocks at the side of the road. Rocks in other areas are also likely sunning sites. For the same reason, driving slowly along minor roads (not major highways!) after dark may result in the location of snakes. They often emerge onto road surfaces to pick up heat being radiated from the road after a hot day. Such animals are most easily seen simply by an observer (a passenger) paying attention to the beam cast by the headlights and scanning this for the presence of basking animals. Snakes may also be found basking beneath sheets of metal and other man-made objects that have been left lying in fields. Always remember to be careful when turning such objects as, if you are in the right area, you may meet up with a rattlesnake!

Less direct ways of attempting to locate animals are by signs that they leave behind. Shed skins of reptiles (see colour plates) give a clue that you are in a likely spot, as do scats (droppings). Once you know what to look for, particular sorts of burrows may also give an indication of the likelihood of locating snakes. The only lizard and only turtle in the province are both very localized in their distribution and are extremely difficult to locate. For the lizards, walking along the tops of south-facing coulee slopes and staring at the ground is about the only method available, and you will usually see nothing. The only real way of locating turtles is to travel by canoe along the Milk River on its course in Alberta and to closely observe the banks and logs emerging from the water, on which the turtles may be basking.

It may often be difficult to approach amphibians and reptiles closely without disturbing them, so patience in your searches is very important. It is also good practice to record what you see in a field notebook. Minimally, such details as location, species, time of day and weather conditions should be recorded. Also helpful will be such aspects as behaviour and any pertinent ecological notes, such as habitat details. As your dossier of records builds, you will learn more about the circumstances in which a particular species might be encountered.

The following references provide information about a variety of techniques used in the study of amphibians and reptiles. Some are of general applicability, while others will be of use primarily for more advanced students of herpetology. In addition to the works listed here, the journal *Herpetological Review* regularly publishes descriptions of new or improved field and laboratory techniques in herpetology.

Significant references: Alberta Forestry, Lands and Wildlife, 1990; Anon 1988; Bull et al. 1983; Bishop and Pettit, 1992; Bury and Corn 1991; Cagle 1953, 1956; Camp and Lovell 1989; Clark, D.B. and Gillingham 1984; Corn and Bury 1990; Etheridge (no date); Ferner 1979; Fisher and Muth 1989; Green 1997; Gregory 1983; Guerra 1976; Haneline and Rhodin 1976; Hero 1989; Heyer et al. 1994; Hudnall 1982; Ireland 1986; Karns 1986; King and Duvall 1984; Lillywhite 1982; Lohoefener and Wolfe 1984; MacCulloch and Gordon 1978; Mazzotti and Brandt 1988; Mengak and Gwynn 1987; Olson et al. 1997; Parker 1971; Pisani 1973; Robertson 1984; Schueler 1981; Simmons 1987; Stanner and Farhi 1989; Stark 1985, 1986b; Vogt 1987; Zucker 1988; Zwickel and Allison 1983.

5 A Guide to the Amphibians and Reptiles of Alberta

IN THIS CHAPTER WE begin by providing a list of the scientific and common names of species of amphibian and reptile either known to occur or suspected of occurring in Alberta. In this list, we employ the names used by Collins (1997) as this is the standard guide to the current common and scientific names of amphibians and reptiles of North America (except in the cases of *Phrynosoma hernandesi* and *Charina bottae*, where we disagree with Collins' allocation), and constancy of application of names makes cross-reference easier. This checklist is followed by illustrated keys to adult amphibians and reptiles, and to the larvae and eggs of the frogs and salamanders. The bulk of the chapter consists of accounts that provide a general description of each Alberta species, an outline of age- and sex-related variation, a summary of natural history and reproductive characteristics of the species and a statement of the distribution of each animal, both in Alberta and throughout its range. Additional remarks about its biology as well as a list of significant references appear at the end of each account. Every species is illustrated and a point locality map of its Alberta distribution is provided. In each of these maps, Calgary is designated as a large open circle (○) and Edmonton as a large open star (☆); solid black circles represent point locations based on museum and literature records. For additional species, abbreviated accounts are provided at the end of this chapter. Wright and Wright (1932) include notes on a variety of snake species that may occur in Alberta, but for which there are no definite records.

A Checklist of the Amphibians and Reptiles of Alberta

Chordata
 Vertebrata
  Amphibia
   Caudata
    Family Ambystomatidae
     Ambystoma macrodactylum Baird 1849 — long-toed salamander
     Ambystoma tigrinum (Green 1825) — tiger salamander
   Anura
    Family Ascaphidae
     *Ascaphus truei** Stejneger 1899 — tailed frog
    Family Pelobatidae
     Spea bombifrons (Cope 1863) — plains spadefoot toad
    Family Bufonidae
     Bufo boreas Baird and Girard 1852 — western toad
     Bufo cognatus Say 1823 — Great Plains toad
     Bufo hemiophrys Cope 1886 — Canadian toad
    Family Hylidae
     Pseudacris maculata (Agassiz 1850) — boreal chorus frog
    Family Ranidae
     Rana luteiventris (Thompson 1913) — Columbia spotted frog
     Rana pipiens Schreber 1782 — northern leopard frog
     Rana sylvatica LeConte 1825 — wood frog

Reptilia	
Testudinata	
Family Chelydridae	
*Chelydra serpentina** (Linnaeus 1758)	snapping turtle
Family Emydidae	
Chrysemys picta (Schneider 1783)	painted turtle
Squamata	
Sauria	
Family Phrynosomatidae	
Phrynosoma hernandesi (Girard 1858)	mountain short-horned lizard
Serpentes	
Family Boidae	
*Charina bottae** (Blainville 1835)	rubber boa
Family Colubridae	
*Coluber constrictor** Linnaeus 1758	racer
Heterodon nasicus (Baird and Girard 1852)	western hog-nosed snake
Pituophis catenifer (Blainville 1835)	bullsnake
Thamnophis elegans (Kennicott 1859)	wandering garter snake
Thamnophis radix (Baird and Girard 1853)	plains garter snake
Thamnophis sirtalis (Linnaeus 1758)	red-sided garter snake
Family Viperidae	
Crotalus viridis Rafinesque 1818	prairie rattlesnake

Key to the Adult Amphibians and Reptiles of Alberta

			Go to
1A.	Skin covered with keratinous scales	Reptilia	12
B.	Skin naked	Amphibia	2
2A.	Body elongate, fore and hindlimbs subequal	Caudata, Family Ambystomatidae	3
B.	Body short, hindlimbs much longer than forelimbs	*Anura*	4
3A.	Digits short and stubby, pattern does not consist of middorsal stripes	*Ambystoma tigrinum*	
B.	Digits slender and elongate, pattern of middorsal stripe or blotches	*Ambystoma macrodactylum*	
4A.	Fifth (outermost) toe of hind foot broader than other toes	*Ascaphus truei*	
B.	Fifth (outermost) toe of hind foot not broader than other toes		5
5A.	Parotoid glands present (Fig. 5.1)	Family Bufonidae	6
B.	Parotoid glands absent		8
6A.	Prominent boss between eyes (Fig. 5.1)	*Bufo hemiophrys*	
B.	No boss between eyes		7
7A.	Cranial crests prominent (Fig. 5.1)	*Bufo cognatus*	
B.	Cranial crests weakly developed	*Bufo boreas*	

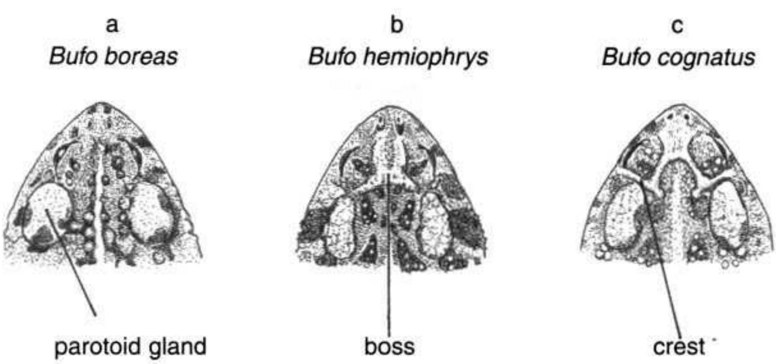


Figure.5.1

8A. Pupil vertical, black "spade" on heel (Fig. 5.2) .... *Spea bombifrons*
B. Pupil not vertical, no "spade" on heel 9

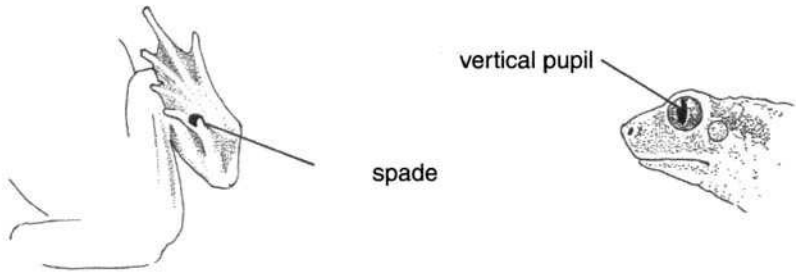
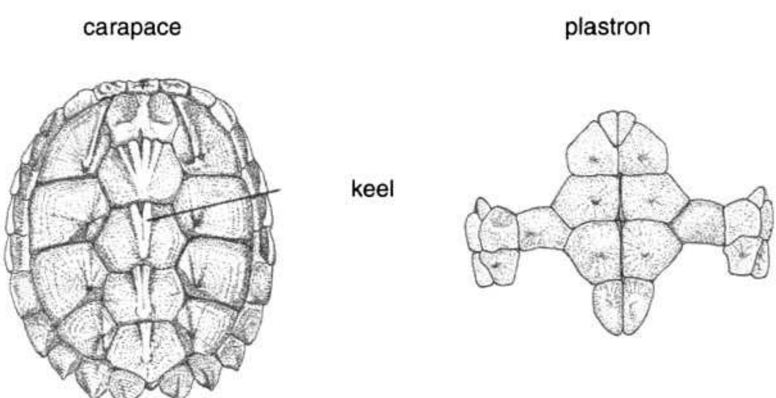


Figure 5.2

9A. Venter (belly) granular, small disks on tips of digits .... *Pseudacris maculata*
B. Venter (belly) smooth, no disks on tips of digits .... Family Ranidae
10A. Conspicuous dark eye mask .... *Rana sylvatica*
B. No dark eye mask 11
11A. Venter (belly) white .... *Rana pipiens*
B. Venter (belly) red, yellow or orange .... *Rana luteiventris*
12A. Carapace present (Fig. 5.3a, b) .... Testudinata 13
B. No carapace 14
13A. Carapace keeled, plastron small (Fig. 5.3a), head very large .... *Chelydra serpentina*



Chelydra serpentina
Figure 5.3a

B. Carapace smooth (Fig. 5.3b), plastron large (Fig. 5.3b), head small, retractable .... *Chrysemys picta*

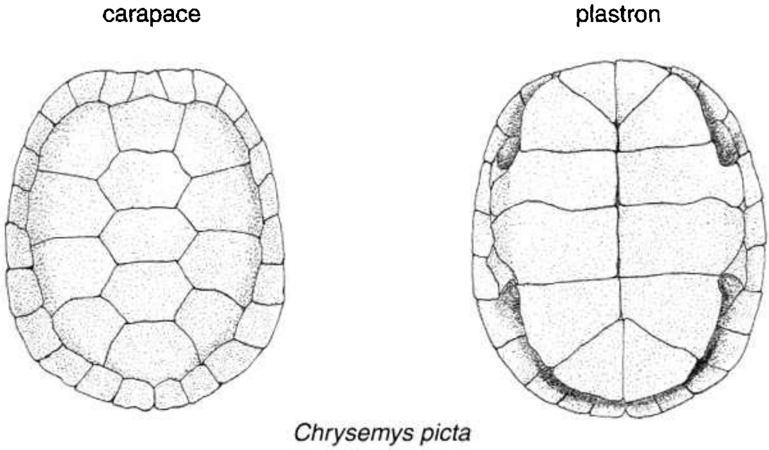


Figure 5.3b

14A. Legs present .... Sauria, *Phrynosoma hernandesi*
B. Legs absent .... Serpentes 15
15A. Tail with rattle, body stout, head distinctly triangular, facial pits .... *Crotalus viridis*
B. Tail without rattles, head not expanded laterally, no facial pits 16
16A. Chin shields (scales between the front part of the lower jaws) all small .... *Charina bottae*
B. Some chin shields (scales between the front part of the lower jaws) enlarged .... Family Colubridae 17
17A. Rostral enlarged, upturned (Fig. 5.4) .... *Heterodon nasicus*
B. Rostral not enlarged or upturned 18

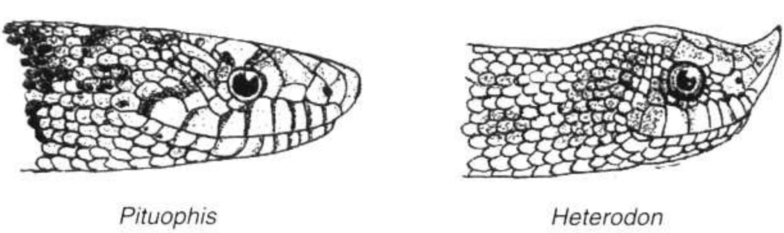


Figure 5.4

18A. Dorsal scales keeled (Fig. 5.5) 19
B. Dorsal scales smooth .... *Coluber constrictor*
19A. Four prefrontal scales (Fig. 5.5) .... *Pituophis catenifer*
B. Two prefrontal scales (Fig. 5.5) .... genus *Thamnophis* 20

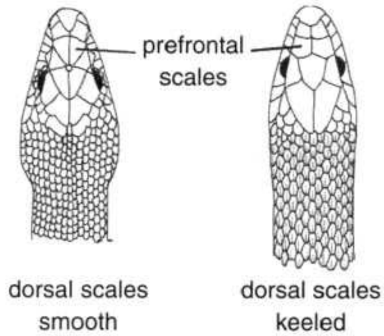


Figure 5.5

20A. Lateral stripes on 3rd and 4th rows of dorsal scales .... *Thamnophis radix*
B. Lateral stripes on 2nd and 3rd rows of dorsal scales 21
21A. Eight upper labial scales (Fig. 5.6), both pairs of chin shields approximately equal in size .... *Thamnophis elegans*
B. Seven upper labials (Fig. 5.6), posterior chin shields longer than anterior .... *Thamnophis sirtalis*

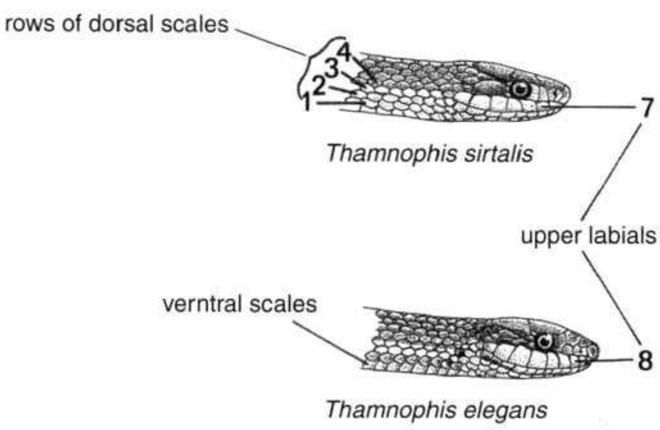


Figure 5.6

Key to the Larval Amphibians of Alberta (Late Stages)

		Go to
1A.	Body elongate, both front and hind limbs present, conspicuous external gills (Fig. 5.7)	2
B.	Body short and stocky, no distinction between head and trunk, limbs small if present (Fig. 5.7)	3

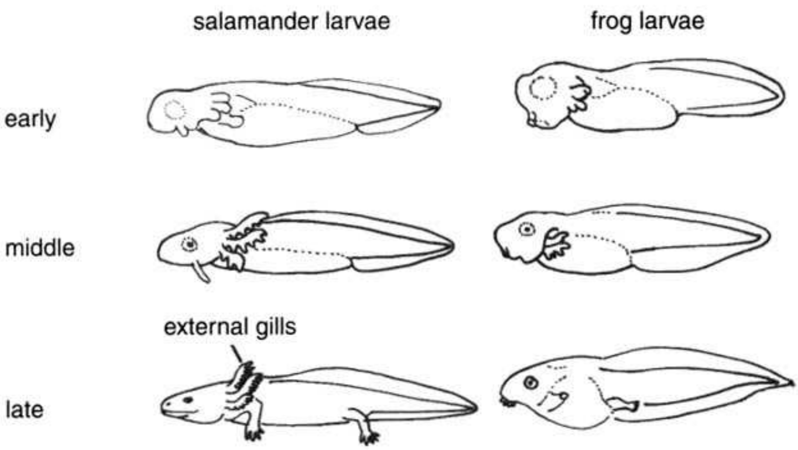


Figure 5.7

2A. 9-13 gill rakers on anterior face of third gill arch (Fig. 5.8), larva small, <8 cm .... *Ambystoma macrodactylum*

B. 15-24 gill rakers on anterior face of third gill arch (Fig. 5.8), larva large, to 25 cm .... *Ambystoma tigrinum*

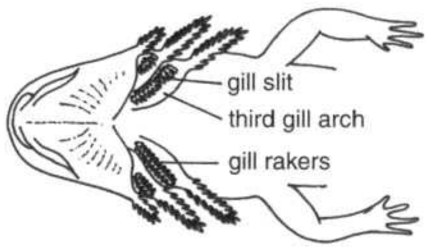


Figure 5.8

3A. Spiracle medial (Fig. 5.9), oral discoral disc large and ventral, some tooth rows biserial .... *Ascaphus truei*

B. Spiracle sinistral, all tooth rows uniserial 4

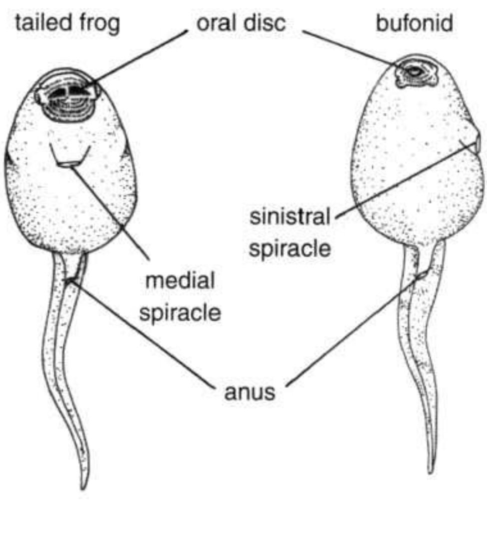


Figure 5.9

4A. Anus medial 5

B. Anus dextral 8

5A. Papillary border of mouth with a ventral gap
(Fig. 5.10) .... Family Bufonidae 6

B. Papillary border without a ventral gap
(Fig. 5.10) .... *Spea bombifrons*

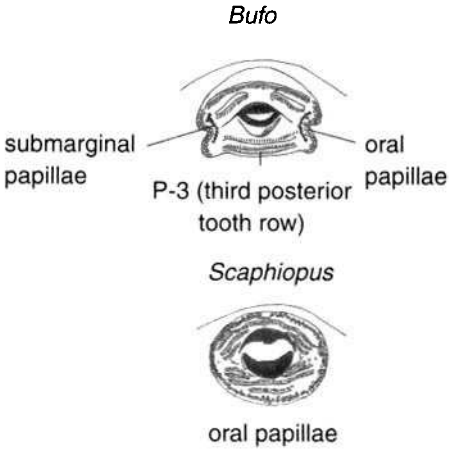


Figure 5.10

6A. Several to many submarginal papillae
at lateral tips of P-3 .... *Bufo cognatus*

B. Submarginal papillae at lateral tips
of P-3 reduced or absent...7

7A. Throat and fins pigmented .... *Bufo boreas*

B. Throat and fins at least partly
unpigmented .... *Bufo hemiophrys*

8A. Oral disc emarginate (Fig. 5.11) .... Family Ranidae 9

B. Oral disc not emarginate (Fig. 5.11) .... *Pseudacris maculata*

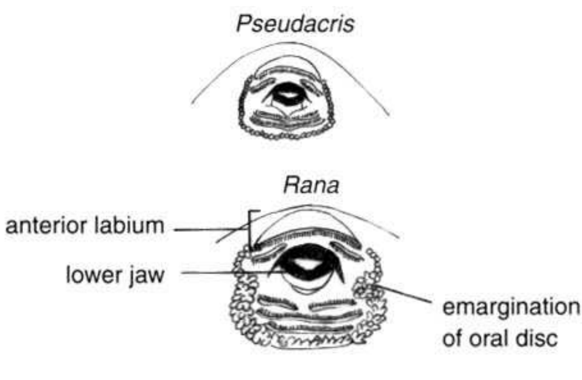


Figure 5.11

9A. Four or more rows of teeth
on posterior labium .... *Rana sylvatica*

B. One to three rows of teeth
on posterior labium.. 10

10A. Lower jaw much wider than upper jaw .... *Rana pipiens*

B. Lower jaw not wider than upper jaw .... *Rana luteiventris*

Key to Eggs of the Amphibians of Alberta

Go to

1A. Ovum unpigmented .... *Ascaphus truei*

B. Ovum pigmented.. 2

2A. Eggs in cylindrical strings (Fig. 5.12) ...... Family Bufonidae 3

B. Eggs in clusters or single (Fig. 5.12)... 5

3A. Eggs enclosed by two envelopes (Fig. 5.12) 4

B. Eggs enclosed by a single envelope
(Fig. 5.12) .... *Bufo hemiophrys*

4A. Egg strings decidedly scalloped
(Fig. 5.12) .... *Bufo cognatus*

B. Egg strings not scalloped,
often in double row (Fig. 5.12).............................. *Bufo boreas*

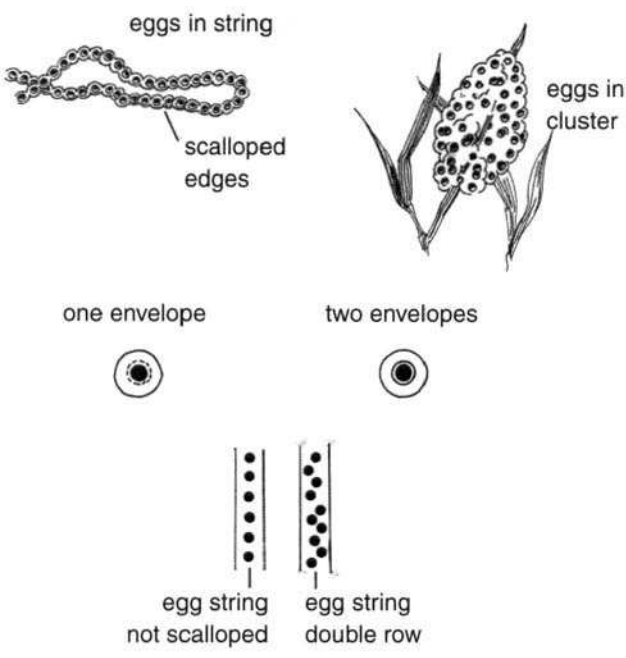


Figure 5.12

5A. Eggs single or in small clusters (<4 cm in diameter) 6
B. Eggs in larger clusters
(>5 cm in diameter) .... Family Ranidae 9
6A. Eggs single or in compact clusters
.... Family Ambystomatidae 7
B. Eggs in loose clusters <2.5 cm in diameter 8
7A. In mountainous regions of the province
.... *Ambystoma macrodactylum*
B. Normally below ca. 1,000 m elevation
.... *Ambystoma tigrinum*
8A. Egg mass cylindrical or elliptical, one envelope,
SE corner of province only .... *Spea bombifrons*
B. Egg mass irregular, one indistinct envelope,
widespread .... *Pseudacris maculata*
9A. Mass spherical, egg diameter to 5.5 mm .... *Rana sylvatica*
B. Mass globular 10
10A. Egg diameter 2.5-6 mm .... *Rana pipiens*
B. Egg diameter 10-15 mm .... *Rana luteiventris*

Significant references for keys: Altig 1970; Altig et al. 1998; Anon 1964a, b; Corkran and Thoms 1966; Livezey and Wright 1947; Orton 1952; Petranka 1998; Powell et al. 1998; Savage 1959; Wright 1929.

Species Accounts

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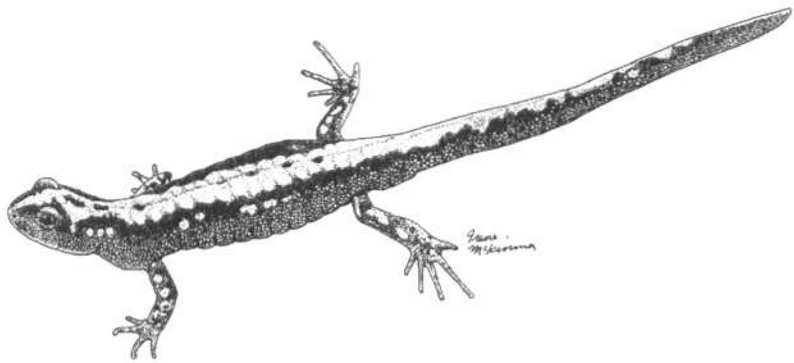
LONG-TOED SALAMANDER
Ambystoma macrodactylum

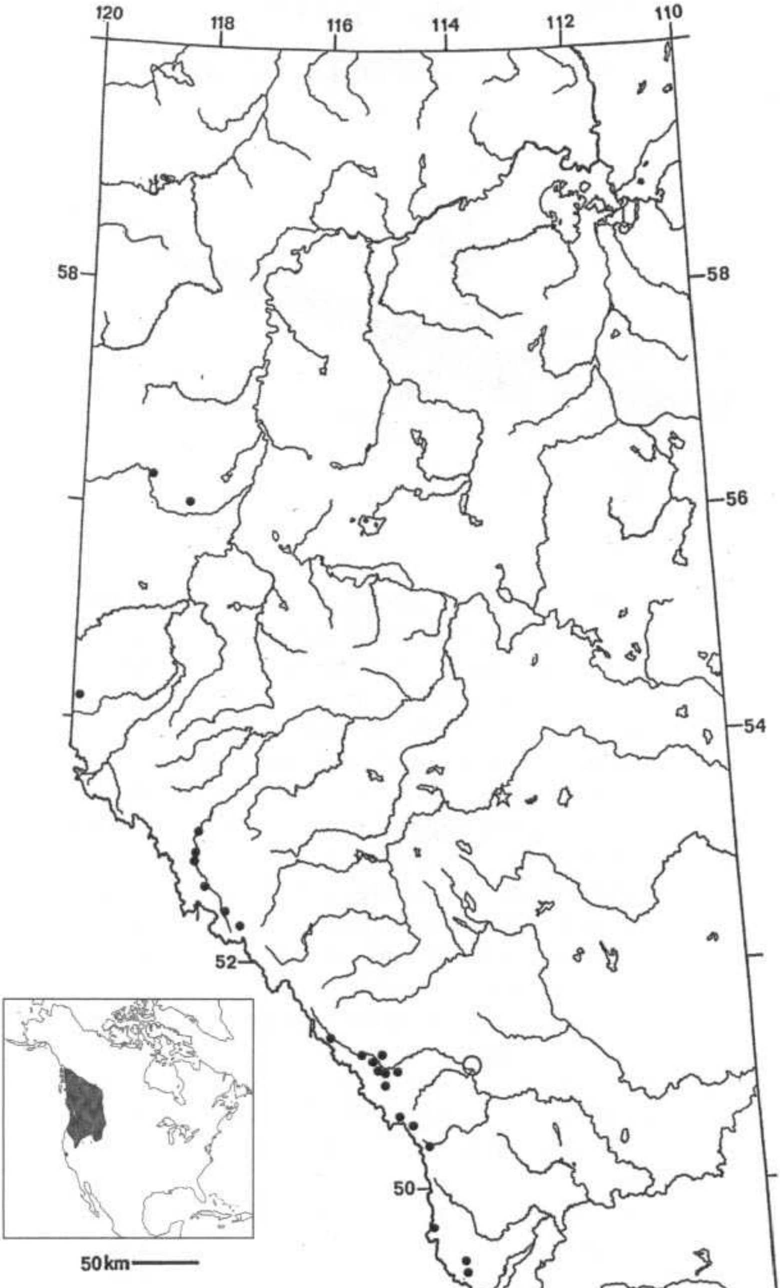


Description: Adult: Total length 80-120 mm (snout-vent length about 37-58 mm). A relatively slender salamander with an oval head, blunt snout and rather large eyes with the iris tinged with bronze. Normally twelve costal grooves on each side of the body. Limbs slender, toes narrow, elongate and unwebbed. Tail long, cylindrical in section at the base, but becoming compressed distally. Background colour dark greenish-grey to black, with a narrow yellow dorsal stripe running from snout to tail tip. Large yellow patches on eyelids and white flecks on the flanks. Belly greyish.

Larvae: Total length up to 70 mm. Grey or light brown with irregular darker flecks and a silvery belly. Fewer than fourteen gill rakers on the anterior surface of the third gill arch. Balancers (lateral outgrowths below each eye) present.

Variation: Postmetamorphic juveniles typically more brightly patterned than adults, often with fewer light flecks or speckles on the flanks and dorsum. Males with proportionately longer limbs and tails than females. In breeding season the cloacal region is swollen in males. Cloaca longer in males than females. Vent of males lined with papillae.

Natural history: In Alberta, active from early spring to early fall, although, in the United States, it may be active throughout the winter, especially during rainy periods. Most conspicuous in Alberta in April and May when the adults migrate to the breeding sites (typically in periods of high humidity), and in September when the juveniles leave for hibernation sites. Adults usually



Distribution of Long-toed Salamander in Alberta remain at the breeding pond for only about one month or less. Typically found under rocks, rotting logs and other debris near ponds, lakes or occasionally streams. Population sizes can be very large, numbering in the thousands. Feeds on small invertebrates, chiefly arthropods. Rarely seen in the open, except during the breeding season. Adults on average live six to seven years, with a maximum of ten having been recorded, and are almost exclusively nocturnal. Birds and shrews are the most frequent terrestrial predators. Larvae feed primarily on zooplankton and select prey items in proportion to their own body size. Natural predators include garter snakes.

Reproduction: Mating occurs in early spring, often before breeding ponds are clear of ice. Generally prefers shallow areas of permanent ponds. Males hold females in pectoral amplexus and rub their mental (chin) glands across the female's snout. After terminating amplexus the male swims ahead of the female and deposits a spermatophore (packet of sperm) on the substrate. The female picks this up with her cloaca, and lays eggs soon after. Eggs laid singly or in clumps, on vegetation or twigs. Eggs hatch after approximately three weeks, but the time for hatching varies considerably with water temperature. In Alberta, larvae sometimes overwinter before metamorphosing. Sexual maturity is attained in the second or third year.

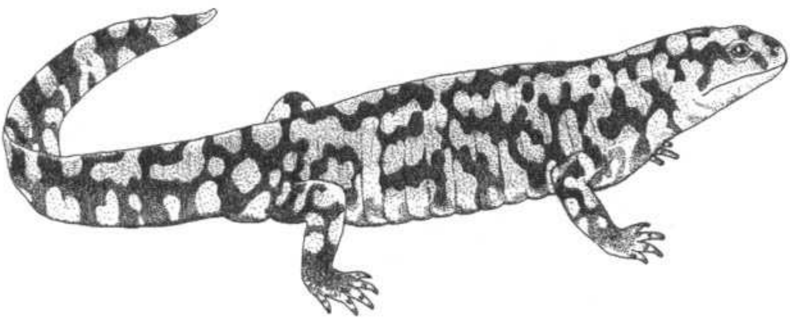
Distribution: In Alberta, occurs at elevations of 1,075-2,800 m in subalpine to alpine areas, from the Montana border north through Jasper National Park (except for the Icefields region). A recent range extension record reports this species from aspen parkland near Fairview. Most often encountered in valley bottoms with fluvial or glaciofluvial unconsolidated substrates, and high groundwater probability. Range in Alberta probably continuous to about 54°30′ N. Northern populations occur as low as 549 m. Elsewhere, it occurs from southeastern Alaska to northeastern California, including Vancouver Island, east to the eastern foothills of the Rockies in Idaho, Montana and Alberta. Isolated populations exist in Santa Cruz and Monterrey counties, California.

Conservation status: Previously considered rare, this taxon has been the subject of extensive field monitoring programs. These have revealed that it is much more common than previously believed, but that its distribution is patchy. Currently not thought to be in decline.

Remarks: Five subspecies are recognized. *Ambystoma macrodactylum krausei* is the Alberta form, occurring from the eastern Kootenays in east central British Columbia, south through the Rockies and their foothills into western Montana and east central Idaho.

Significant references: Anderson 1961, 1967; 1968a, b; Beneski et al. 1986; Ferguson 1961, 1963; Fukumoto 1995; Graham 1997; Graham and Powell 1999; Hamilton et al. 1996; Howard and Wallace 1985; Kleinschroth, 1985; Knudsen 1960; Mittleman 1948, 1949; Nelson et al. 1995; Oseen et al. 1995a, b; Nussbaum 1985; Petranka 1998; Powell and Russell 1996a; Powell, Nelson and Russell 1993; Powell et al. 1997b, c; Russell et al. 1996; Rodgers and Jellison 1942; Salt 1979; Shepard, 1977; Slater 1936; Tyler 1996; Walsh 1998.

Tiger Salamander
Ambystoma tigrinum



Description: Adult: Total length 140-180 mm, rarely to 200 mm (snout-vent length 70-90 mm). A large, robust salamander with a short, round head and relatively small eyes. Normally thirteen costal grooves on each side of the body. Limbs robust, toes relatively short, stout and unwebbed. A pair of tubercles on the underside of the feet. General colour blotched, barred or reticulate pattern of yellow (or white) and black (or grey, dark brown or olive green). Boundaries of blotches not always sharp. Belly sooty grey.

Larvae: Hatch at about 15 mm total length and may reach 75-80 mm, but neotenic individuals exist that may be as large as fully grown, metamorphosed tiger salamanders. General colour dull yellow to olive green or dark brown, with pale undersides. There are prominent external gills, with fifteen or more gill rakers on the anterior surface of the third gill arch, and a conspicuous tail fin. The larvae lack balancers.

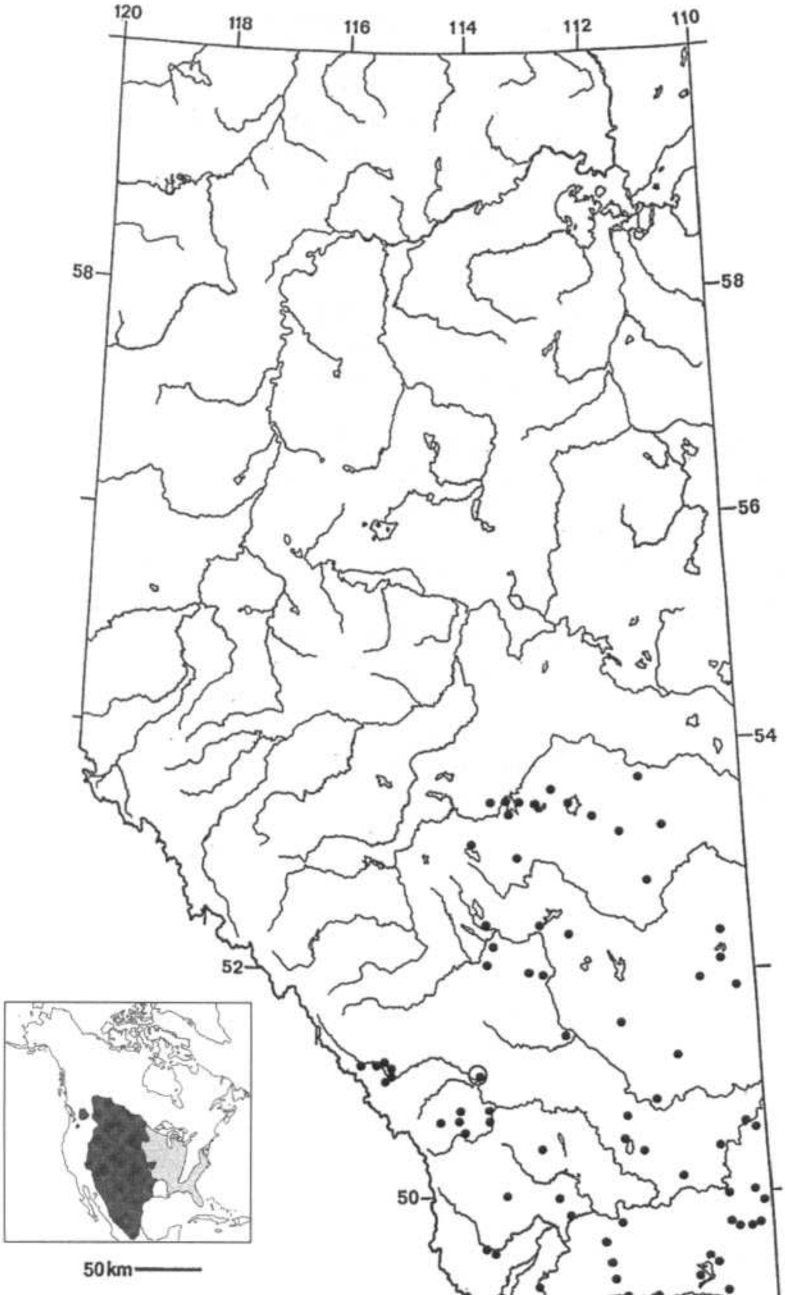
Variation: Juvenile metamorphosed individuals with smaller and brighter markings than adults. Old individuals may become uniform olive, brown or black in colour. Males with proportionately longer tails and hind legs than those of females. In the breeding season, the cloacal region is swollen in males.

Natural history: In Alberta, active from early spring to early fall; particularly active in spring rains. Although tolerant of very dry conditions, usually found near small lakes, ponds or dugouts, often in subterranean burrows which may be excavated by the salamanders themselves. Feeds on insects, mites, earthworms, molluscs and small vertebrates. Hatchlings feed mainly on zooplankton and crustaceans; older larvae and neotenic adults may eat fish, insect egg masses and larvae, worms, frogs and other salamanders. Larvae may be cannibalistic. Metamorphosed adults are rarely seen in the open except during the breeding season. Primarily nocturnal in activity patterns.

Reproduction: Mating occurs after early spring migration to breeding sites in permanent or semi-permanent standing water. No amplexus occurs, but males push and nuzzle females in courtship, then lead them to deposited spermatophores. Males may be aggressive towards each other during courtship bouts and may even cover previously deposited spermatophores with their own. Breeding may take place in water of less than 10°C. Eggs (2-5 mm in diameter) are laid singly or in small groups shortly after mating, and are attached to stones, plants or debris. Eggs hatch after approximately three weeks and metamorphosis occurs (if at all) after three to four months, usually in August. Larval development may often take two years.

Distribution: In Alberta, occurs at elevations of up to 2,800 m. Found in short-grass prairie, aspen parkland, boreal forest and subalpine habitats. Widely distributed south from Edmonton, with an isolated population near Grande Prairie. Probably introduced in many areas throughout the province. Extralimitally, broadly distributed east of the Rockies, south to the Mexican plateau (absent from parts of the Gulf Coast, Florida, the Appalachians, the northern United States and Eastern Canada). Scattered isolated populations throughout the west, south from the Okanagan Valley, B.C. The inset map showing the total range of *Ambystoma tigrinum* indicates some of the uncertainty surrounding the taxonomic status of this taxon and its component parts. The light grey area to the east represents the distribution of *Ambystoma tigrinum tigrinum*. The remainder of the distribution, indicated in black, represents the other subspecies. Those portions occupying Canada and the U.S.A. have recently been advocated to belong to a separate species, *Ambystoma mavortium*, but this opinion has not yet won widespread acceptance. The taxonomic status of the Mexican populations is uncertain—hence the question mark.

Conservation status: The former range of this species has probably become fragmented as a result of human activities, but the species remains common in suitable habitats and shows no signs of broad scale population decline.

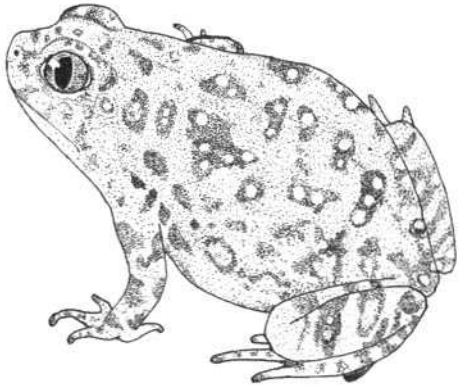


Distribution of Tiger Salamander in Alberta

Remarks: Five to seven subspecies are recognized, although the validity of some of these, including *Ambystoma tigrinum melanostictum* (the Alberta form) is questionable. *A. tigrinum melanostictum* occurs south to Idaho and Wyoming and east to eastern South Dakota. Disjunct populations occur in eastern Washington and adjacent parts of British Columbia, the Idaho panhandle and the Columbia River Valley. Neoteny is particularly common in *A. t. melanostictum.* This species has been widely used as live bait and this has influenced its distribution. Individuals may live for up to 16 years. Stebbins (1985) shows in his distribution map *Ambystoma tigrinum diaboli* present marginally in east central Alberta. As yet we have no confirmation of this.

Significant references: Anderson 1968b, 1970; Anderson et al. 1971; Arnold 1976; Bizer 1978; Brophy 1980; Burger 1950; Clark and Chandler, 1991; Delson and Whitford 1973; Dodson and Dodson 1971; Dunn 1940; Else and Bennett 1987; Fowler 1935; Franz 1971; Gehlbach 1967; Gruberg and Sterling 1972; Hassinger et al. 1970; Heath 1975, 1976; Hetherington and Lombard 1983; Holomuzki 1986, 1989; Holomuzki and Collins 1987; Kristensen 1981; Kumpf 1934; Lannoo and Bachman 1984; Lannoo et al. 1989; Larsen, J.H. and Guthrie 1975; Lauder and Shaffer 1985, 1986; Lewin 1963a; Malvin and Heisler 1988; Moore and Strickland 1955; Nussbaum 1985; Patch and Stewart 1924; Pedersen 1991; Petranka 1998; Pierce et al. 1983; Rohrbach and Stiffler 1987; Salt 1979; Semlitsch 1983a, b; Shaffer and Lauder 1985; Shaffer and McKnight 1996; Sprules 1974; Stark 1986a; Stebbins 1985; Whitford and Massey 1970.

Plains Spadefoot Toad
Spea bombifrons

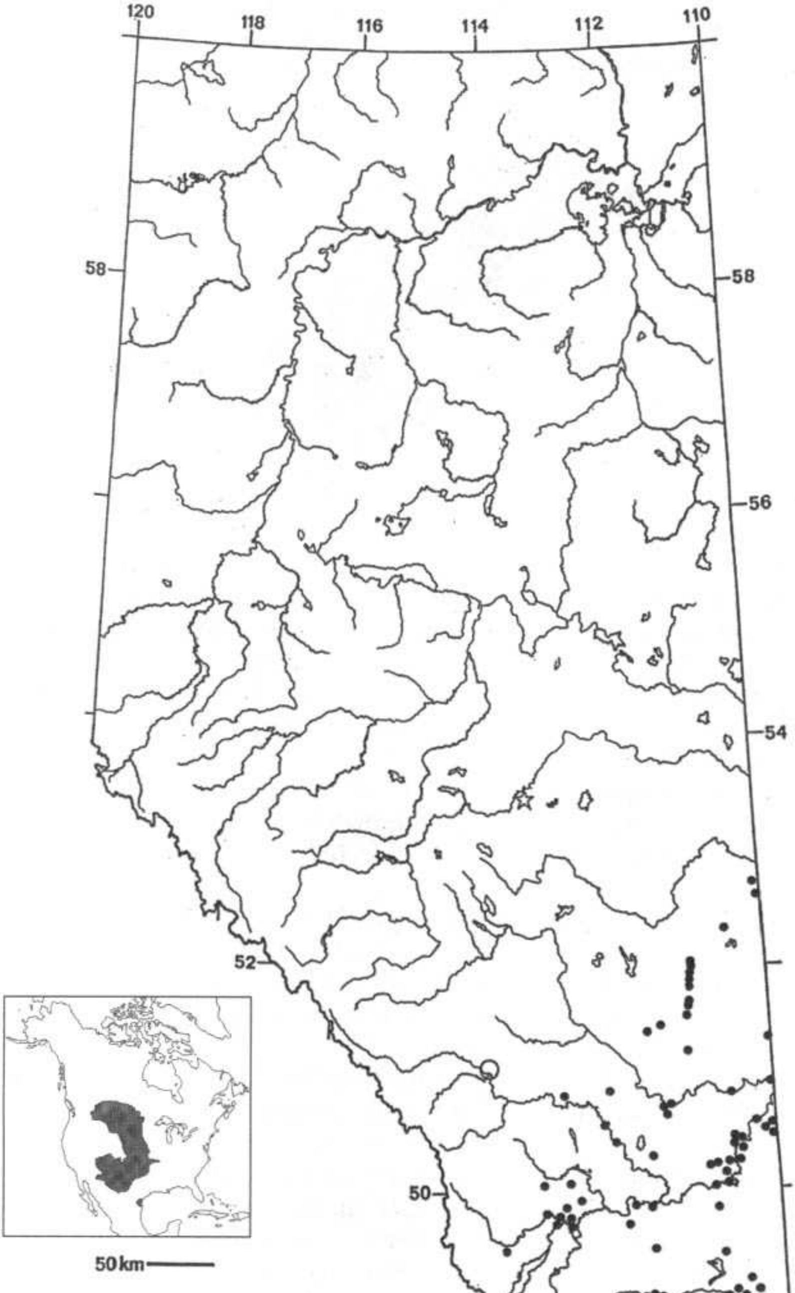


Description: Adult: Head and body length 35-60 mm. A robust, thick-bodied frog with relatively short limbs and a short, blunt snout. Eyes large and protruding, with vertical pupils. Tympanum small. A prominent boss present between the eyes. No enlarged parotoid glands. Dorsum of body covered with small to moderate-sized scattered tubercles. Digits short, hind feet partially webbed. A black, wedge-shaped spade present at the "heel." General colour ranges from various shades of brown to dull green, usually with four lighter stripes along the back. Tubercles tipped with yellow or orange. Belly white.

Larvae: Tadpoles reach a total length of 68 mm. Body widest behind the eyes, snout narrowed. Anus median, spiracle sinistral. Labial tooth rows usually 4/4. Light grey or brown above, lighter below. Caudal fins lightly pigmented. Tadpoles gulp air in areas where they are highly concentrated.

Variation: In some individuals the tip of the snout may be covered with black, keratinized skin. Females are slightly larger than males. Males have a blackish throat and keratinization on the fingers.

Natural history: In Alberta, active from late May until fall, but rarely seen outside of breeding periods. (In the United States, it is generally most active in the summer, in association with the rainy season). Typically found near permanent or temporary bodies of water, usually in areas of sandy or friable soil appropriate for burrowing. Uses the spades on the hind feet to dig backwards into soil to depths of almost one metre. It is able to supercool, which



Distribution of Plains Spadefoot Toad in Alberta may decrease the depth to which it has to burrow in winter to protect itself from freezing. Feeds on small invertebrates, particularly nocturnal forms such as moths, ants and beetles. A sticky defensive secretion is exuded when molested. The larvae feed on plankton and detritus. Tadpoles may be cannibalistic, and may be able to withstand brief periods of almost total evaporation of their pools. Adults are seldom seen, but their presence in owl pellets suggests that they may be more widespread than generally recognized.

Reproduction: Breeds during spring or summer periods of rain, usually in vernal ponds or other temporary water bodies. Males call while floating in the water. Males hold females in pelvic amplexus. Eggs are laid in clusters of 10-250 and hatch in about 48 hours. Metamorphosis is completed about 21-40 days after hatching. Upon metamorphosis the spades are already well-formed and the young individuals are able to burrow.

Voice: A short, duck-like scream of 0.2-0.7 seconds duration.

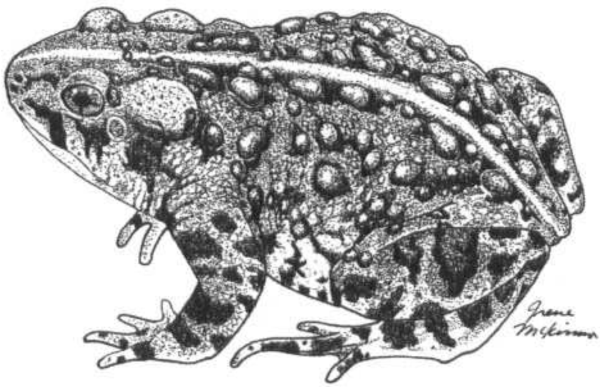
Distribution: In Alberta, occurs at elevations up to 1,200 m, primarily in short-grass prairie, from the Montana and Saskatchewan borders north and west to the Red Deer River and Pincher Creek. Extralimitally, it occurs east to western Manitoba and south through the plains states to Chihuahua and eastern Arizona. Populations are probably continuous along the Missouri River to the Mississippi. An isolated population is known from extreme southern Texas and adjacent Mexico.

Conservation status: There is no evidence that this species has declined in recent years, but our knowledge of its populations within its limited range in Alberta is fragmentary. More evidence is needed to accurately assess its conservation status.

Remarks: Tadpoles may be preyed upon by aquatic arthropods. In order to survive the winter, spadefoots must locate sources of moisture in their arid surroundings. They burrow downward until they locate a damp resting spot, and have been found at depths of almost one metre. Collins (1990) places this species in the genus *Spea,* although Conant and Collins (1991) retain it in *Scaphiopus.* We have placed this species in the genus Spea following current usage (Wiens and Titus 1991, Collins 1997).

Significant references: Black 1970a; Bragg 1941, 1944, 1965; Bragg and Bragg 1959; Farrar and Hey 1998; Hoyt 1960; Klassen 1990, 1998; Lauzon and Balagus 1998; Lewin 1963a; Moore 1952; Morlan and Matthews 1992; Nero 1959; Pfennig et al. 1993; Seymour 1973; Swanson and Graves 1995; Tanner 1939; Trowbridge 1941, 1942.

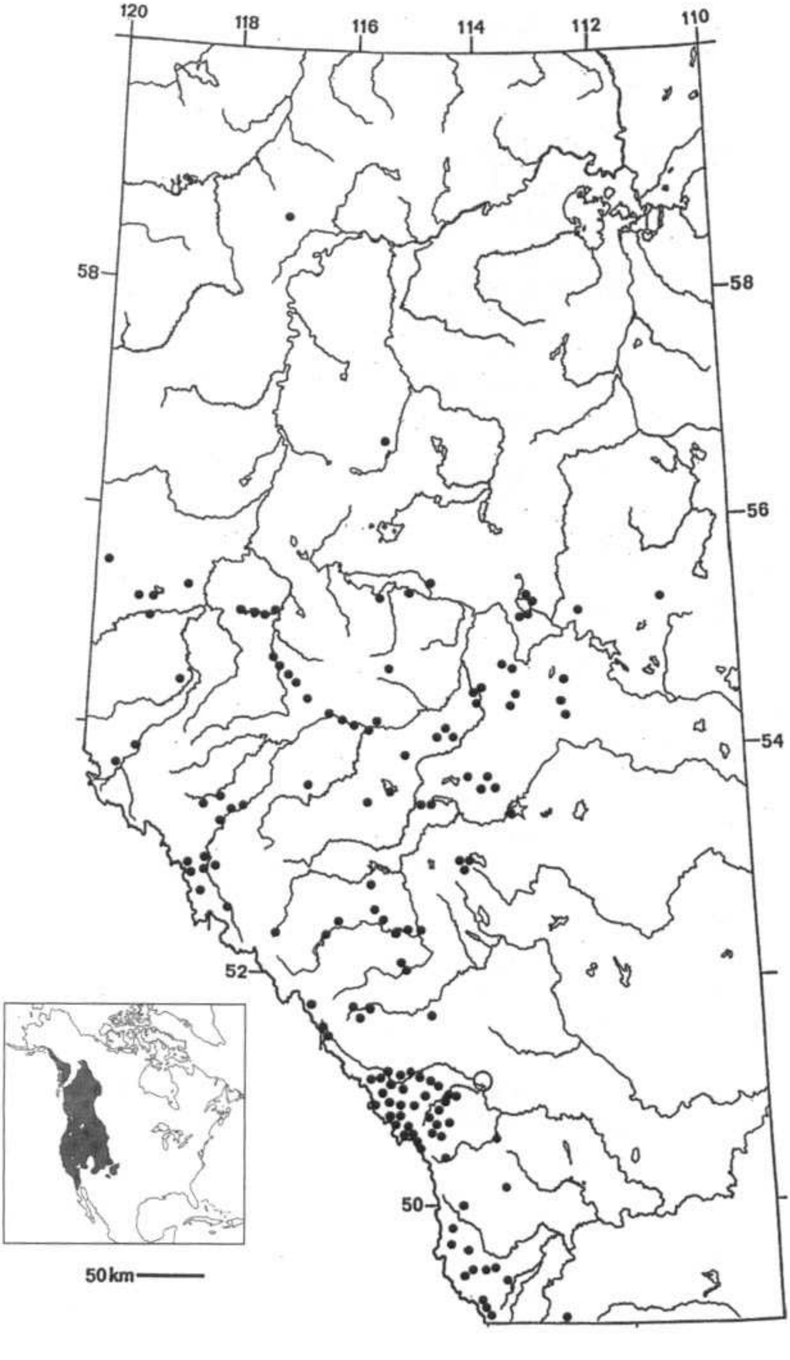
Western Toad
Bufo boreas



Description: Adult: A relatively large toad, with a head and body length of 55-125 mm. The dorsal and lateral skin, and that of the upper portions of the limbs, is covered with small round or oval warts. Parotid glands are prominent, oblong and larger than the eye. The tympanum is smaller than the eye. The pupils are horizontal. Cranial crests are weakly developed. The limbs are relatively short and the hind toes partially webbed. Keratinized tubercles for digging are found on the ventral surfaces of the feet. Background colour usually green or brown, with a light vertebral stripe from the snout to the vent. Warts may be reddish-brown and/or may be encircled by a ring of dark pigment. The venter is pale, with dark mottlings on the abdomen and black marks on the throat. Numerous scattered tubercles with black tips occur on the belly.

Larvae: Tadpoles hatch at about 10 mm, and grow to reach 25-30 mm total length. The eyes are placed high on the head. Metamorphosed toadlets are about 12 mm snout-vent length. The tail fin of the tadpole is low and rounded. Labial teeth in two rows anterior and three rows posterior to the mouth—the second anterior row has a gap in the midline. Tadpoles are blackish dorsally and somewhat lighter ventrally. The fins are pigmented, but diffusely so. Anus medial, spiracle sinistral.

Variation: Toadlets are typically dark, with little patterning. Males have nuptial pads. The dark marks on the throat are more prominent in males. This species exhibits physiological colour change, with individuals becoming lighter at higher temperatures. The



Distribution of Western Toad in Alberta

dorsal colour is highly variable, but the dorsal stripe is rarely lacking. Males have relatively narrower heads and longer arms, and females are generally considerably larger than males. Males lack a vocal sac.

Natural history: In Alberta, active from April until September. Typically found around ponds, streams, rivers and lakes. Active primarily at night at lower elevations, but diurnal at higher elevations and at higher latitudes. It is a largely terrestrial species that may burrow into loose soil or seek shelter in pre-existing burrows of small rodents. It digs hibernacula up to 1.3 m deep. Western toads tend to walk rather than hop. Secretions from the parotid glands and warts are used in defence. They generally prefer damp conditions and have a ventral pelvic patch of skin that allows them to absorb moisture from the ground. They feed on worms, slugs, insects and other arthropods. In Alberta, beetles and ants appear to predominate in the diet, although other insects and spiders are also taken. They are eaten by snakes, owls, magpies, shrikes, gulls, crows and especially ravens as well as mustelids, bears, foxes and coyotes. They have a distinctive behaviour of inflating themselves with air and standing high on all four limbs when threatened. If all else fails they may urinate on the attacker if molested. The tadpoles exhibit synchronized behaviour and will school. This may be mediated, in part, by alarm substances released by damaged individuals. Tadpoles eat algae, seek out the warmer microhabitats in the bodies of water in which they live, and may fall prey to tiger salamander larvae. Juveniles may be found in basking aggregations at the edges of ponds. Tadpoles and metamorphosing toadlets are consumed by a wide variety of predators, including dragonfly larvae, mallards, sandpipers, American robins, and red foxes. In captivity individuals have survived for up to thirty-six years.

Reproduction: Breeds in Alberta in April to June. In spring they congregate in bodies of water, usually pools or small ponds, to breed. May breed in water below 10°C. They prefer shallow water with a sandy bottom and will breed in either permanent or temporary bodies of water. Males have a mating call. Males clasp females in pectoral amplexus. If males grasp other males, a release call is emitted. Nearly all breeding activity ceases at night. Eggs of 1.5-1.7 mm diameter are laid in long strings, typically entwined about submerged vegetation. Up to 16,500 eggs may be produced by a female in a single clutch. Hatching is rapid and takes three to twelve days. Tadpole densities may be extremely high. A further six to eight weeks are required for metamorphosis. By mid-September in the Rockies, all larvae have metamorphosed and have left the breeding ponds. The animals reach sexual maturity in two to three years. Egg laying at a particular site tends to be synchronized, and all females laying at that site will do so in less than a week.

Certain individuals of each batch of tadpoles grow rapidly at first, and release a growth-inhibiting substance that acts upon the smaller tadpoles. This results in metamorphosis occurring in waves rather than all at once. The outcome of this is that mass mortality due to predation or unfavourable climatic conditions may be lessened.

Voice: A repeated, quiet peeping. A slightly more emphatic version of the same sound is used as a release call when molested.

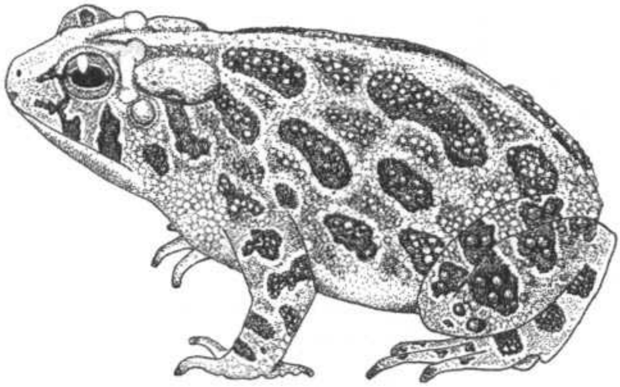
Distribution: In Alberta, it occurs to at least 2,300 m north from the Montana border to at least as far as Lesser Slave Lake. Isolated records are also known from the Loon Lake and High Level areas. Distribution in the northern part of the province may be more extensive, but lack of access to most areas has made observation and verification difficult. Absent from the drier eastern regions of the province, where it is replaced by *Bufo cognatus* in the extreme southeast and *Bufo hemiophrys* in the east. There is some range overlap with the latter. It occurs at all elevations within its range, but is found primarily in boreal forest, sub-alpine and alpine habitats. It occurs marginally in aspen parkland and short-grass prairie. Extralimitally, it is found from coastal Alaska and the southern Yukon south to northern Baja California, east as far as western Wyoming. Isolated populations occur in central Wyoming and Colorado, and northern New Mexico.

Conservation status: This species appears secure in its range in Alberta. There is no evidence of recent declines.

Remarks: Two subspecies are recognized, that occurring in Alberta is *Bufo boreas boreas*. This has the same range as the species as a whole, except for California and Baja California. Amplexus has been observed in Alberta between this species and *Bufo hemiophrys*.

Significant references: Black 1970a, 1971a, b; Black and Black 1969; Black and Brunson 1971; Burger and Bragg 1947; Clarke 1974; Cook 1977a; Eaton et al. in press; Feder 1979; Ferguson 1954; Hews 1988; Hews and Blaustein 1985; Huey 1980; Jones et al. 1999; Karlstrom 1962; Lillywhite et al. 1973; Lillywhite and Wassersug 1974; Logier 1932; Moore and Strickland 1954, 1955; Mullally 1956; O'Hara and Blaustein 1982; Rodgers and Jellison 1942; Salt 1979; Sander, 1987; Schueler 1982a.

Great Plains Toad
Bufo cognatus

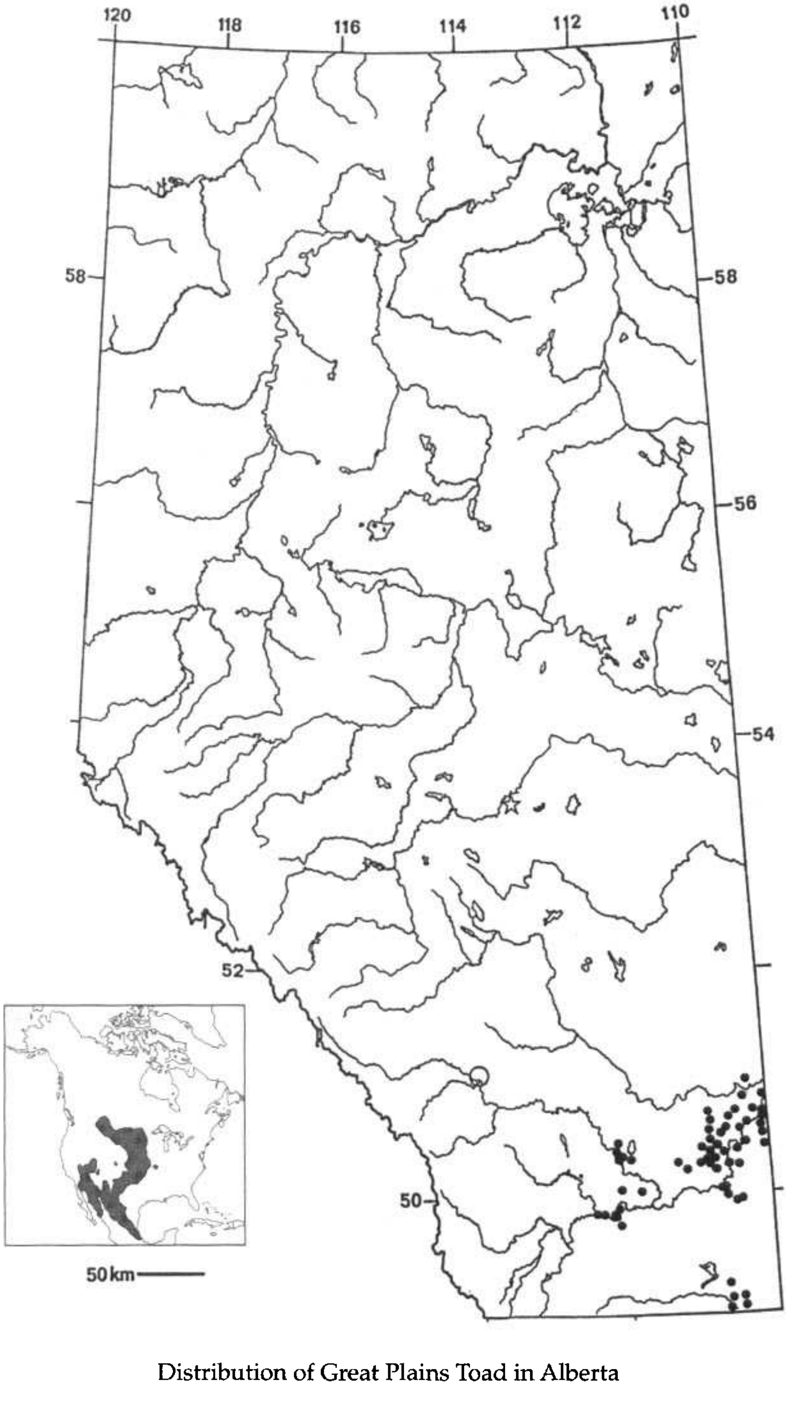


Description: Adult: A moderately large toad, with a head and body length of 45-110 mm. Parotids large, oval. Cranial crests form an "*L*" around each eye and fuse anteriorly to form a boss. Tympanum smaller than eye. Skin covered with small warts. Toes of hind feet weakly webbed. Hind feet with sharp-edged tubercles on the ventral surface. Background colour pale brown-grey or olive, with an irregular pattern of darker blotches, some of which may have even darker borders. A vertebral stripe may be present. Venter immaculate white.

Larvae: Tadpoles reach about 25 mm total length. Labial teeth 2/3. Dorsal fin arched. Anus median, spiracle sinistral. Mottled brown and grey or blackish dorsally, light green below. The venter may be iridescent.

Variation: Toadlets with many small reddish tubercles and cranial crests forming a '*V.*' Males have a single, elongate vocal sac, equivalent to about one third of the body volume when inflated.

Natural history: Active in Alberta from April until September. Generally nocturnal in its activity patterns. A good burrower that spends much of its time underground. When exposed to high temperatures it burrows. It frequents irrigation canals, river flood plains, temporary rain pools and dugouts. If threatened the great plains toad inflates itself with air, depresses its head and stands high on all four legs. It is known to eat moths, flies and beetles.



Distribution of Great Plains Toad in Alberta

Reproduction: Breeding takes place after rains in spring or summer, and occurs in temporary ponds, dugouts, ditches, flooded fields, marshes or streams. Breeding takes place in clear, shallow water and this species will not breed in muddy water. Amplexus is pectoral. Female may produce a clutch of 20,000 eggs. The eggs are produced in long strings, hatch in about two days, and the tadpoles metamorphose in about six weeks. Tadpoles naturally aggregate, possibly as a defensive strategy. It may be diurnal during the breeding period. Sexual maturity is attained in three to five years.

Voice: A repeated, harsh clatter of great intensity and long duration (up to 50 seconds). Males also produce a release call if molested. Females are basically voiceless. The type of water habitat, permanent or temporary, may play a role in determining the intensity of the chorus.

Distribution: In Alberta, limited to the extreme southeastern corner of the province, south of the Red Deer River and east of a line connecting Brooks, Vauxhall and Taber. Most localities are in the vicinity of the South Saskatchewan River and its tributaries. Restricted to short-grass prairie habitats. Occurs at elevations up to 900 m. Extralimitally, it occurs from southwestern Saskatchewan through central Montana, south through the plains states to San Luis Potosi, Mexico. Also from central Utah and the Colorado River south into western Mexico. Several additional isolated populations exist.

Conservation status: This species has experienced population declines since the 1980s. This appears to be due to habitat loss (largely through agriculture) and drought.

Remarks: This species is known to be active at a range of temperatures normally not tolerated by other members of the genus *Bufo*. This is particularly significant for activity at the relatively high ambient temperatures encountered by *Bufo cognatus* when compared to those encountered by its relatives in the province.

Significant references: Bieniak and Watka 1962; Black 1971a; Blair 1963; Bragg 1936, 1940; Brown and Pierce 1967; Clark and Chandler, 1991; Clarke 1974; Flowers and Graves 1995; Graves et al. 1993; James 1998a; Logier 1931; Moore 1953b; Roberts, 1992; Rogers 1973; Ruibal 1962b; Sanders, 1987; Smith 1946; Tester et al. 1965; Turner et al. 1965.

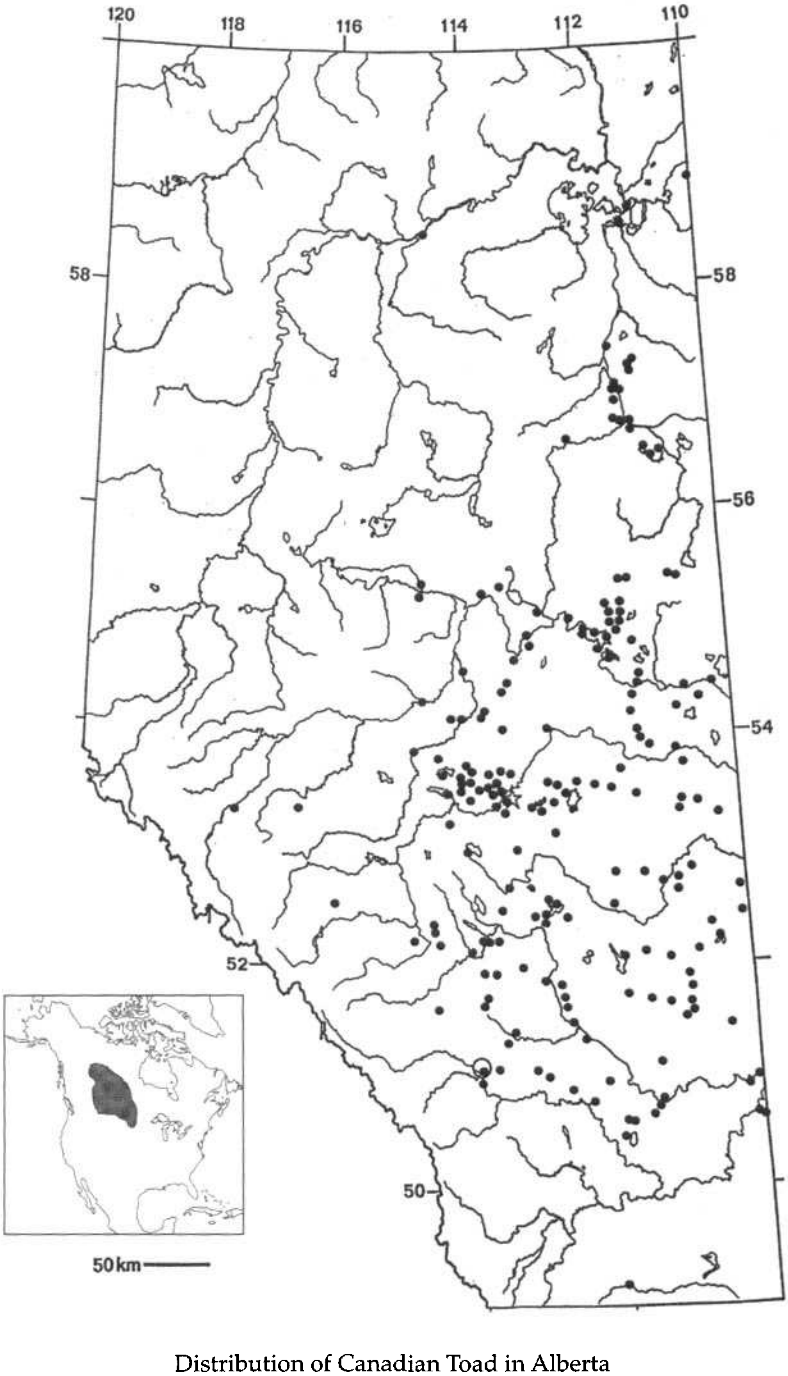
Canadian Toad
Bufo hemiophrys

Description: Adult: A small toad, reaching a head and body length of 37-75 mm. It has a short body and a skin covered with small, irregular warts. The parotids are large and oval or kidney-shaped. The interorbital region bears a large, solid boss that may be flat, convex or slightly furrowed. Tympanum smaller than eye. Toes of hind feet feebly webbed. Two prominent, dark-coloured tubercles on the hind feet, the inner one large and the outer one small. Background colour generally grey-green or brown, with reddish tubercles encompassed by dark spots. Typically with a whitish vertebral stripe (not as contrasting with the background colour as that of *Bufo boreas*). Belly white, spotted with grey, becoming pale yellowish laterally.

Larvae: The tadpoles are blackish above and lighter below, with a transparent region in the anterior part of the venter. The tail musculature is dark and the caudal fin is slightly pigmented. The labial teeth are 2/3. The spiracle is sinistral, the anus medial.

Variation: Toadlets have weakly developed cranial crests that become accentuated and fuse with age to form the adult boss. Males with a dark throat. In females, the throat is the same colour as the belly. Males have a single, rounded vocal sac.

Natural history: In Alberta, active from April until September. It is usually diurnal and burrows at night, although it may also be nocturnally active if the temperature is high enough. In high temperatures it seeks shade. When threatened Canadian toads may swim far from shore to seek protection. Four species of helminth parasite have been recorded, with an incidence of eighteen to seventy-three percent.



Distribution of Canadian Toad in Alberta

Reproduction: Breeding occurs from May to July. Males may be active and call at temperatures as low as 5°C. Breeding usually takes place in the shallows of lakes, ponds, ditches, marshes and other temporary bodies of water. Amplexus is pectoral. A long, single string of eggs of 1.0 mm diameter is laid.

Voice: A short (1-5 seconds), soft trill repeated after intervals of about thirty seconds.

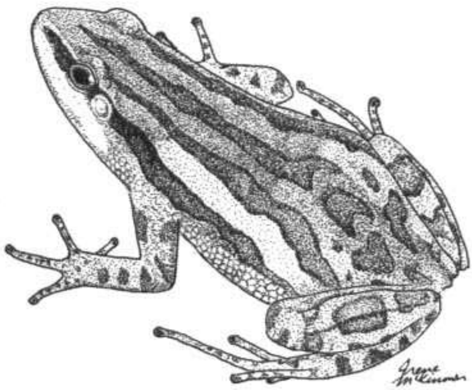
Distribution: In Alberta, this species occurs from north and east of the Bow River to the Northwest Territories border. It is confined essentially to the eastern half of the province. There is extensive overlap with *Bufo boreas* to the west and north of Edmonton. Scattered records exist that indicate that this species extends into the foothills of the Rockies, but these may be doubtful. It occurs at elevations of up to 1,200 m, primarily in boreal forest and aspen parkland, with some records from the short-grass prairie. Extralimitally, it occurs from the southern Northwest Territories through all of Saskatchewan, except the extreme north east corner, to south central Manitoba, western Minnesota, north east South Dakota and northern North Dakota and Montana. Isolated populations previously reported to exist in southeastern Wyoming have now been recognized as a full species, *B. baxteri.* In southeastern Manitoba *B. hemiophrys* hybridizes with *B. americanus,* producing fertile offspring in the ecotone between prairie and forest. Some authors accept this as evidence that *B. hemiophrys* should be considered as a subspecies of *B. americanus.*

Conservation status: This species has declined in recent years, especially in the more heavily populated areas of the province, apparently as a result of the destruction of appropriate wetland habitat. A volunteer monitoring program that operated largely in the southern part of the province yielded no positive reports of this species, indicating that the decline may be both continuing and truly alarming.

Remarks: In Elk Island National Park, the numbers of this species declined significantly from 1971 to the mid-1980s. This trend is consistent with that for this species in central Alberta as a whole. Adults emerge in the spring earlier than immatures, but both sexes in each age class emerge at about the same time. In conditions of high ambient temperatures, individuals move into the shade. In Minnesota, this species has been observed to burrow at the onset of winter in such a way as to keep ahead of the frost line, and follow it back up for spring emergence. Large numbers of toads may overwinter in communal sites. Two subspecies are recognized. That occurring in Alberta is *Bufo hemiophrys hemiophrys.* Amplexus has been observed in Alberta between this species and *Bufo boreas.*

Significant references: Black 1970a, 1971; Blair 1957; Breckenridge and Tester 1961, 1964; Burns (no date); Bursey and Goldberg, 1998; Clarke 1974; Cook 1964b, 1983e; Eaton et al. 1999; Green 1983; Hamilton et al. 1996; Hamilton et al. 1998; Henrich 1968; Kelleher and Tester 1969; Kuyt 1991; Powell et al. 1996; Roberts, 1992; Roberts and Lewin 1979; Sanders, 1987; Smith et al. 1998; Tester and Breckenridge 1964; Tester et al. 1965; Turner et al. 1965; Underhill 1961.

Boreal Chorus Frog
Pseudacris maculata

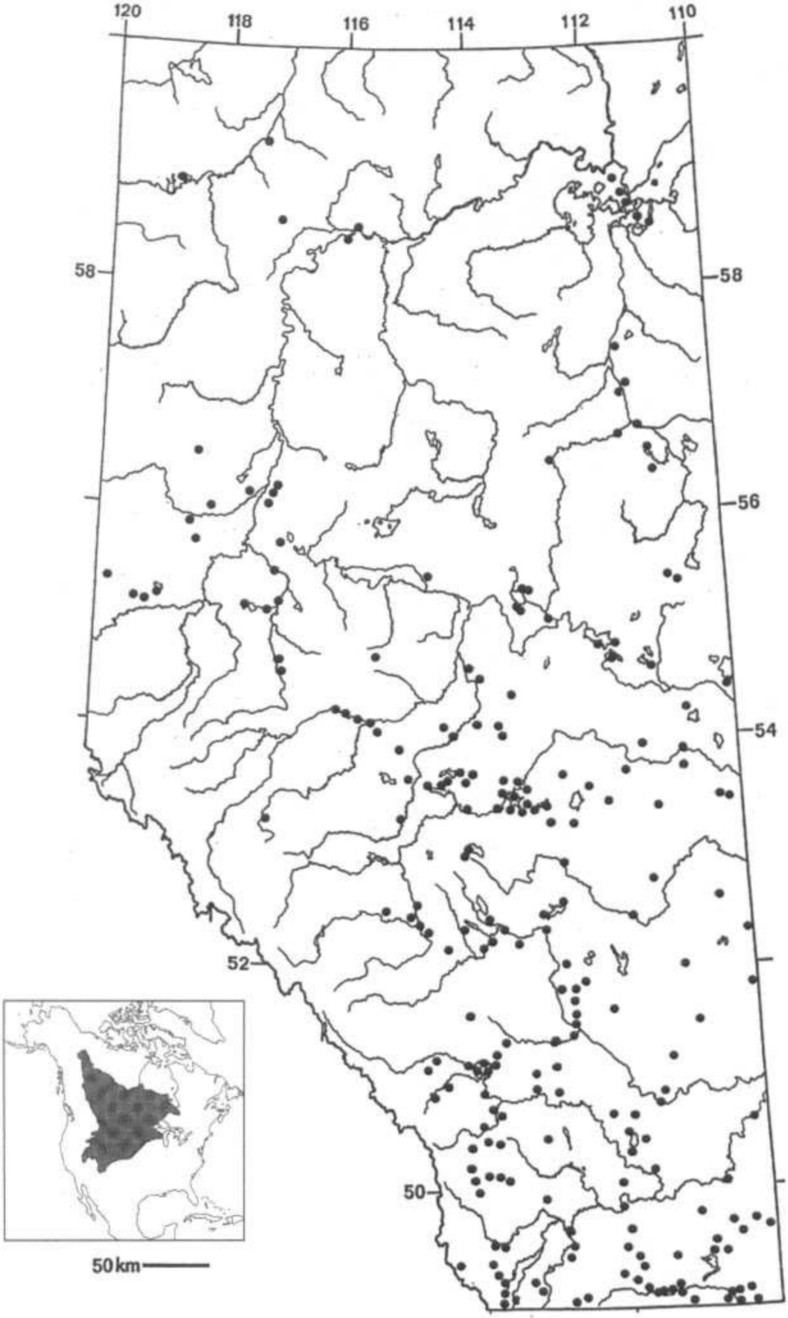


Description: Adult: A small frog with a head and body length of 20-40 mm. Overall build is gracile, with a relatively long body. The snout is pointed, the eyes are prominent and the tympanum is smaller than the eye. The toes are relatively long and do not bear terminal pads. The toes of the hindfoot are feebly webbed. The skin is granularly textured. Colour is highly variable with the background colour ranging from grey to brown to green. A dark stripe extends from the snout, through the eye to the groin. The upper jaw has a white stripe. There are usually three, often broken, irregular dark longitudinal stripes on the back. There is often a pale, triangular patch between the eyes. The venter may be white, yellow or a diffuse olive colour, with few or no dark markings.

Larvae: Tadpoles hatch at about 4-7 mm total length and reach about 30 mm. Froglets are 7-12 mm long just after metamorphosis. The tadpole's labial teeth are 2/3. Tadpoles are dark olive to black above and silver with a coppery sheen below. The eyes are more or less lateral. The dorsal fin is greatly arched and lightly to moderately pigmented. The anus is dextral and the spiracle sinistral.

Variation: Males have a greenish throat and a single, rounded vocal sac, and are slightly smaller than females. Males develop a nuptial pad on the first finger in the breeding season.

Natural history: This species frequents grassy pools, lakes, marshes and almost any other body of water. It occurs on farms and in cities, where suitable habitat is present, except in areas where pesticides are heavily used. It eats ground-dwelling insects, snails, millipedes



Distribution of Boreal Chorus Frog in Alberta and other small invertebrates. Larvae are taken by diving beetles and other aquatic predators. Its habits are little known outside of the breeding season. It may spend the non-breeding season in damp marshy or woody areas and overwinter in relatively dry sites. Individuals may climb into low vegetation. When moving on the ground, they hop.

Reproduction: Breeding usually occurs in April to June. It will breed in almost any body of water, both shallow and deep. Males begin to call before the snow melts. During the height of the breeding season calling may occur both night and day. Males usually call from concealed sites. Amplexus is pectoral. Eggs are laid in small clumps attached to vegetation. From 150 to 1500 eggs are laid over a number of days. Each egg is about 1.0 mm in diameter. They hatch in ten to fourteen days. Development and metamorphosis occur in about two months. Individuals reach maturity and breed in the following year, and they do not live to breed for a second season.

Voice: A terminally inflected trill of short duration (1-1.5 seconds). Such trills may be strung together in continuous phrases. The sound produced is much like that generated when one's finger is run along the teeth of a stiff plastic pocket comb.

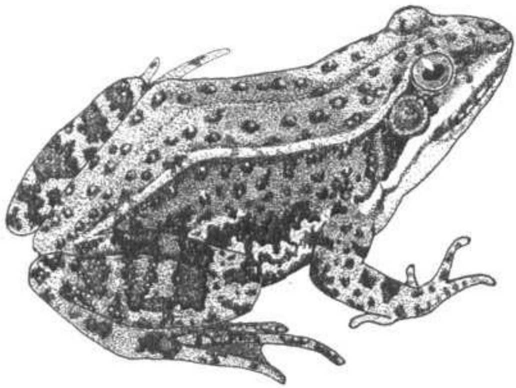
Distribution: The boreal chorus frog occurs throughout the province, except in true alpine habitats. Extralimitally, it is found from west central Northwest Territories east to southern James Bay and south to the upper mid-west and Great Plains states as far as northern New Mexico and Arizona.

Conservation status: The boreal chorus frog shows no signs of decline across its broad range in Alberta.

Remarks: Although some authors refer to this taxon as *Pseudacris triseriata maculata*, Collins (1997) affords it full species status.

Significant references: Bleakney 1959; Brown, L.E. and Pierce 1967; Dunlap 1980; Gaudin 1974; Kramer 1973, 1974; MacArthur and Dandy 1982; Matthews 1971; Mosimann and Rabb 1952; Roberts and Lewin 1979; Smith, D.C. 1983; Smith 1956; Travis 1981; Wassersug and Sperry 1977.

Columbia Spotted Frog
Rana luteiventris

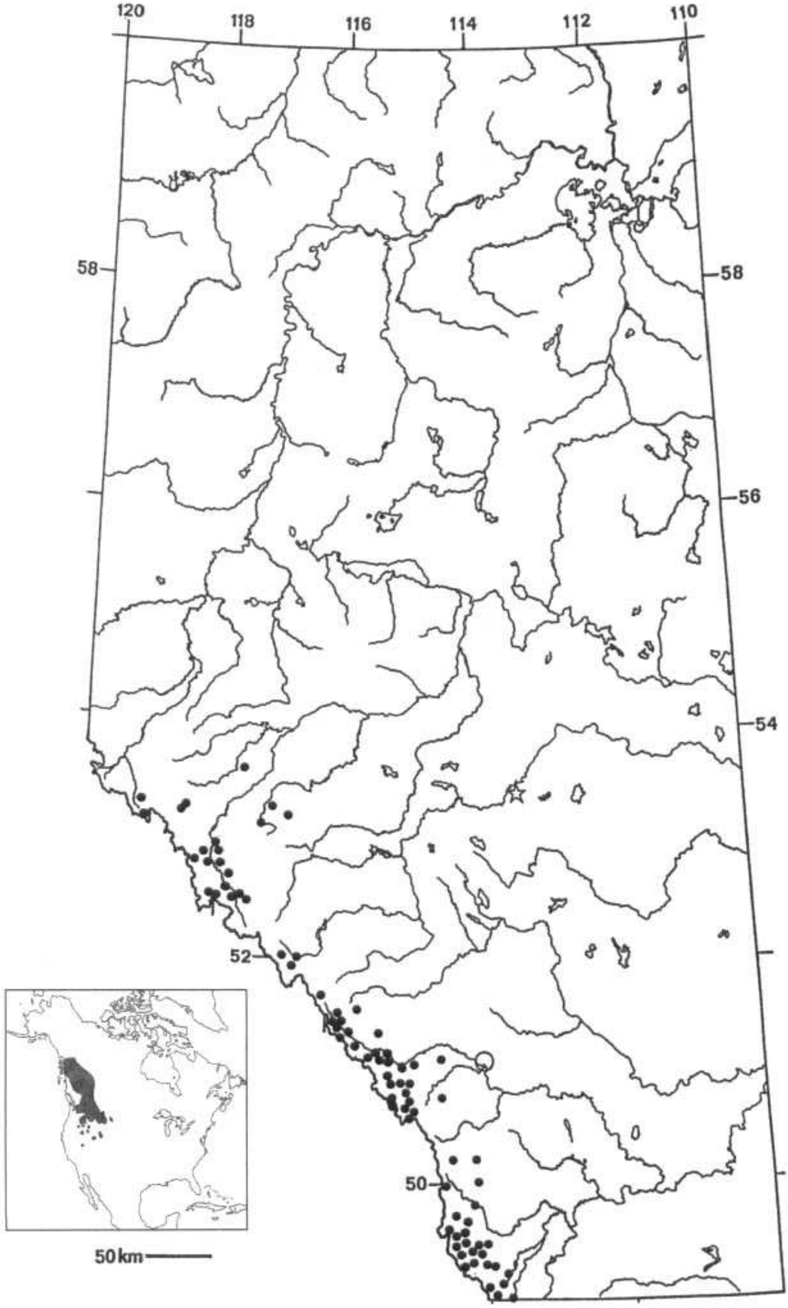


Description: Adult: A medium-sized frog with a head and body length of 45-100 mm. Its body form is similar to that of *Rana pipiens,* but it is slightly more robust. The eyes are large and are oriented somewhat dorsally. The tympanum is prominent and smaller than the eye. Dorsolateral folds are present but they are rather indistinct. The toes of the hind feet are fully webbed. The hindlimbs are relatively shorter than those of *R. pipiens.* The skin is textured with scattered small bumps. Generally dark brown above with many small, irregular spots of even darker colour. A dark mask running from the nostril to the tympanum may be discernible. A light jaw stripe is present from the snout to the insertion of the forelimb. In Alberta, the venter is salmon to red in colour, especially in the region of the hind limbs. This colour is very vivid and appears to be very superficial. The throat and other parts of the venter may be spotted or mottled with grey.

Larvae: Tadpoles are dark dorsally, flecked with gold. The venter is iridescent bronze. The anus is dextral and the spiracle sinistral. Newly transformed froglets have a total length of about 25 mm.

Variation: In very young specimens, the bright ventral colour may be faint or absent. Males have nuptial pads in the breeding season. Females are considerably larger than the males.

Natural history: The spotted frog is highly aquatic and is usually found associated with permanent water, particularly in regions of mixed coniferous forest and subalpine forest from 995 to above 2,150 m. It is rather slow in its movements and appears to be



Distribution of Columbia Spotted Frog in Alberta generally unwary. Its fright response is to swim to the bottom and then remain motionless, often hidden under submerged vegetation. It sometimes forages away from the water and is chiefly nocturnal in its activity patterns. The adults eat worms, insects, arachnids, molluscs and crustaceans and they feed both above and below the water. Tadpoles may be eaten by passerine birds or aquatic insect larvae. Adults may be taken by hawks, ravens, gulls, owls, garter snakes, mustelids, and coyotes. Extralimitally cannibalistic predation of adults on larvae has been observed, and it has been suggested that such behavior may be particularly important in resource-limited high elevation (and high latitude) regions.

Reproduction: Pre-reproductive life span may be as long as four to six years. The spotted frog breeds as early as winter thaws will permit. Males call from the water near shore. There is no distinctive mating call, but the males make short grunting noises. The males are not territorial during the breeding period. Amplexus is pectoral. The breeding period lasts only a few weeks. Large eggs (5-12 mm in diameter) are laid in communal masses. 700-1,500 eggs are laid in a clutch. Time from laying to hatching appears to be very variable—four days to three weeks. The larvae normally metamorphose during the summer of the year of their hatching, but in more northerly locations they may overwinter as tadpoles and metamorphose the following year.

Voice: A series of rapid, low-pitched clicks, building in intensity. The duration of individual calls is highly variable, but they usually last less than ten seconds.

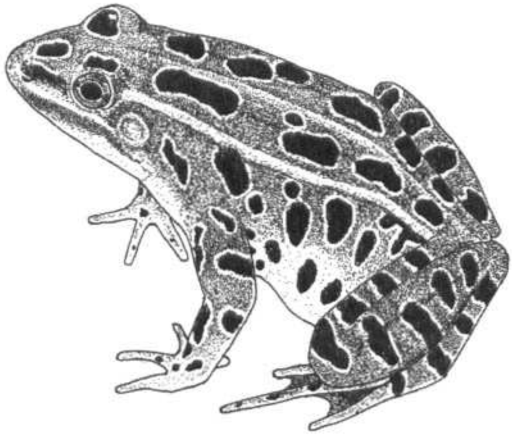
Distribution: In Alberta, the Columbia spotted frog is limited to subalpine and alpine regions and occurs at elevations of about 2,000 m. It occurs from Waterton Lakes National Park north through Jasper to perhaps as far as 55° N. Extralimitally, it occurs from the extreme southern Yukon through most of B.C., Washington, Oregon, Idaho, Montana and Wyoming, with isolated populations in Nevada and Utah. Its range in the United States is highly fragmented. It is absent from Vancouver Island.

Conservation status: Some populations, especially in areas of human disturbance, have disappeared. The status of remaining populations is uncertain, although some declines have been proposed.

Remarks: *Rana luteiventris* has recently been separated from *Rana pretiosa,* within which it was formerly included, on the basis of genetic differences. No morphological characters to distinguish these two species have yet been identified, but all spotted frogs in Canada, except extreme southwestern B.C., are referrable to *R. luteiventris.*

Significant references: Black 1969; Green 1985; Green et al. 1996, 1997; Hovingh 1993; James 1998b; Logier 1932; Moore and Strickland 1955; Pilliod 1999; Roberts 1992; Rodgers and Jellison 1942; Ross et al. 1999; Salt 1979; Svilha 1935; Turner 1958, 1959, 1960; Turner and Dumas 1972.

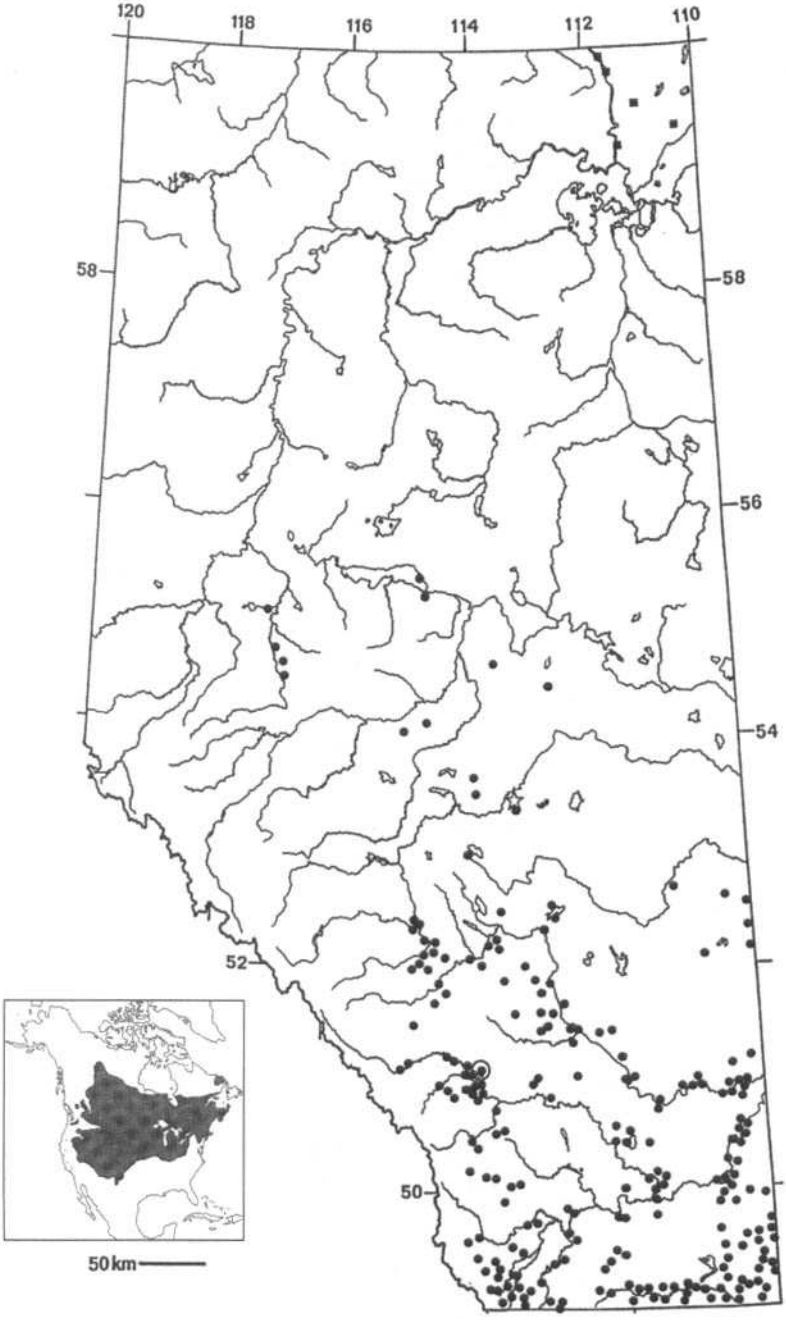
NORTHERN LEOPARD FROG
Rana pipiens



Description: Adult: A medium-sized frog with a head and body length of 50-100 mm. It is gracile, with a pointed snout, large and prominent eyes and a prominent tympanum that is about three-quarters the size of the eye. There are continuous, parallel dorsolateral folds that extend from behind the eye to the insertion of the hind limb. This fold is usually lighter than the background colour. The hind legs are elongate and the hind feet are strongly webbed. The background colour is greenish or brownish, punctuated with well-defined darker ovals or spots bordered with pale rings. These spots cover all but the venter, although the legs may be barred rather than spotted. There is a white stripe on the upper lip from the snout to the insertion of the forelimb. The belly is white or cream, with this colour extending part way up the flanks.

Larvae: Tadpoles hatch at about 8-10 mm total length and grow to a length of about 75 mm. The eyes of the tadpoles are dorsally placed, the dorsal fin moderately arched and slightly pigmented. Labial tooth rows 2/3. The froglets measure about 20 mm just after metamorphosis. The tadpoles are dark grey, olive or brown above, with fine gold flecks, and cream to white below. The ventral part of the abdomen is weakly pigmented. The anus is dextral and the spiracle sinistral.

Variation: The spotting typical of adults may be reduced or absent in froglets, and in rare instances, may result in a yellow morph. Males have enlarged, darkened nuptial pads during the breeding



Distribution of Northern Leopard Frog in Alberta season. Males have paired vocal sacs over the forelimb insertions. Females are slightly larger than the males.

Natural history: This is the most cold-adapted of all leopard frogs. It inhabits springs, streams, marshes and other permanent water bodies, usually those with abundant aquatic vegetation. Streams are used for dispersal. Individuals may travel up to two kilometres in a single active season. It may forage far from water, but generally uses water as a safe refuge if threatened. It eats insects, spiders and other small invertebrates, but will also eat birds, garter snakes, tadpoles, small frogs and fish if given the opportunity and prey items of an appropriate size. Cannibalism has been reported. Tadpoles are preyed upon by larval tiger salamanders, the garter snakes *Thamnophis elegans* and *T. sirtalis,* and adults by snakes, small carnivores and birds. In winter it hibernates in the mud at the bottom of bodies of standing water or under rocks in streams and springs. The species is generally found in areas where the vegetation provides a good deal of ground cover. This species has survived up to nine years in captivity.

Reproduction: The leopard frog breeds from April to June and may enter into breeding behaviour while ice is still on the pond. For a given population the actual period of spawning activity may be somewhat reduced. Migration from sites of hibernation to preferred breeding sites may take place. Males call while floating in the water, the call being a long, low guttural rumble. In the breeding season, males are territorial. Amplexus is pectoral. Egg masses may be laid on vegetation or the pond bottom, and up to 6,000 may be deposited by a single female. The eggs are about 1.7 mm in diameter and generally require from ten days to three weeks to hatch, depending upon water temperature. After metamorphosis individuals take from two to three years to become sexually mature.

Voice: A mixed repertoire of low frequency sounds that may be described as "grunts," "chuckles" and "snores." A higher pitched release scream may be emitted when handled. Both sexes can croak, but females rarely do and the voice is weak.

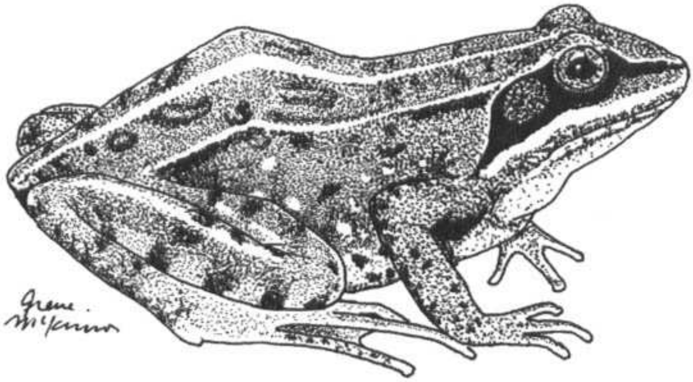
Distribution: In Alberta, the leopard frog occurs from the Montana border north and west to the Little Smoky River area. Locality records exist as far north as the Slave River, but the true distribution north of about 55° N is poorly known. The western extent of the range is in the foothills and lower elevations of the Rockies. It is distributed extensively in regions of short-grass prairie, as well as aspen parkland and boreal forest. It also occurs in the Cypress Hills. On the accompanying range map, solid circles represent populations occurring within the current range of this species. Solid squares represent pre-1981 reports that lie outside of the present range and probably depict extirpated populations. Extralimitally, it is broadly distributed from south central Northwest Territories to California in the west, extreme southern New Mexico in the south, through the northern plains states, east through the Ohio Valley to New England, Quebec and the Maritime provinces.

Conservation status: The range of the northern leopard frog has contracted greatly over the last several decades. A variety of causes, perhaps including disease, have wiped out populations everywhere except the southeastern (and probably the extreme northeastern) corner of the province, where relatively few breeding populations remain. These populations, however, appear to be recovering and although still in jeopardy the status of this species in Alberta appears to be improving. Extensive monitoring by Alberta Fish and Wildlife has probably contributed significantly to the arrest of its decline.

Remarks: *Rana pipiens* is part of a large complex of very similar leopard frogs that range across all of North America. The abundance of *Rana pipiens* in Alberta appears to have declined markedly since 1978. It is not known why this decline has taken place, but there is some speculation that it may be due to the effects of herbicides and pesticides. Several consecutive drought years may also have had an effect, destroying some breeding sites and resulting in overwinter freezing deaths of adults. It has been widely used in laboratory studies.

Significant references: Black 1969; Briggs 1949; Browder and Davison 1964; Cunjak 1986; de Benedictis 1974; Di Berrardino 1962; Emery et al. 1972; Gilbert et al. 1994; Greenwald 1971; Hunter et al. 1989; Klassen 1991; Layne, 1992; Licht 1991; McClelland and Wilczynski 1989; Moore 1949; Mosimann and Rabb 1952; Post and Pettus 1966; Roberts 1981, 1992; Ruibal 1959, 1962a; Sage and Selander 1979; Schueler 1982b; Scott and Jennings 1985; Seburn et al. 1997; Shivers and James 1970; Shumway 1940; Smith et al. 1988; Smithberg 1954; Taylor and Kollross 1946; Verma 1965; Wagner 1997; Yaremko 1994.

Wood Frog
Rana sylvatica

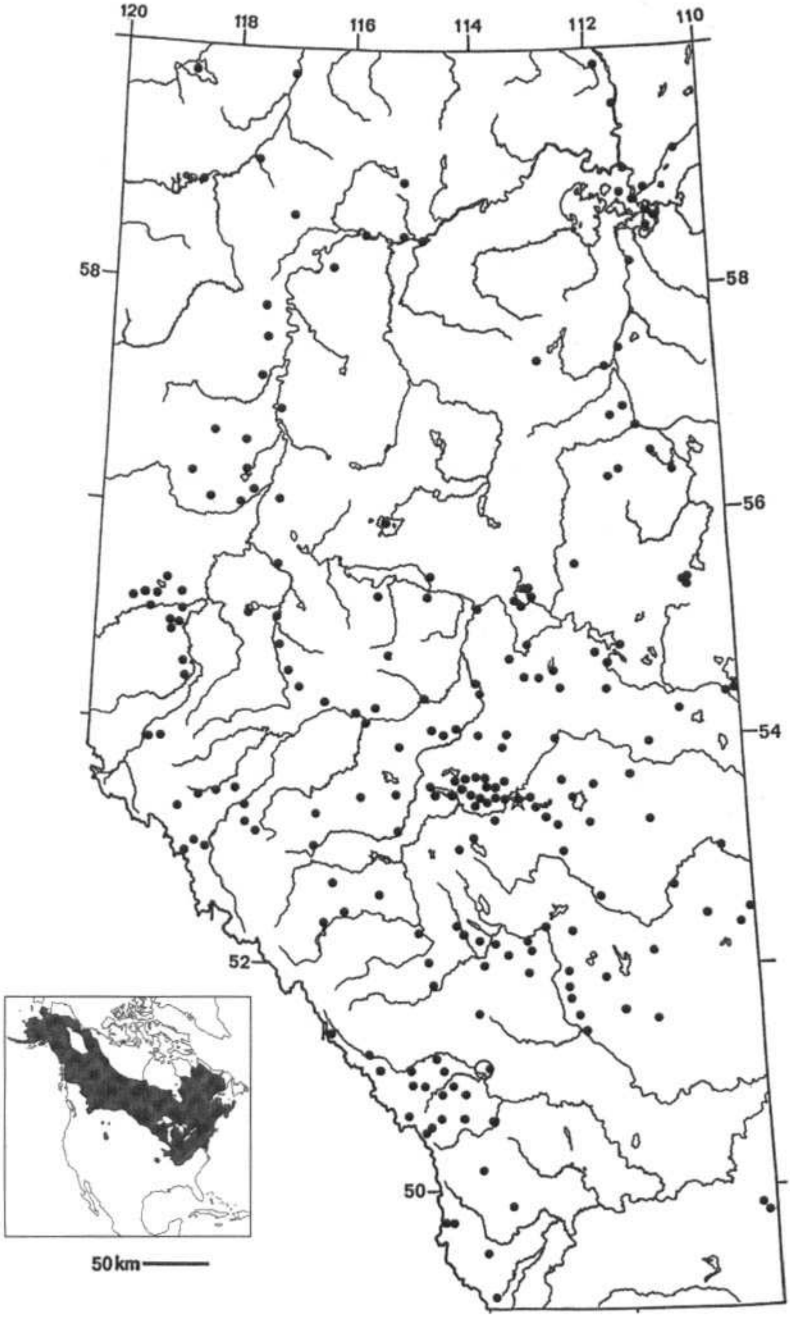


Description: Adult: A smallish to medium-sized frog, with a head and body length of 30-60 mm. The eyes are moderately large and protruding and the tympanum is smaller than the eye. The dorsolateral folds are prominent and the limbs are relatively short. The skin is relatively smooth, although there may be some tubercles laterally. It is brownish above, often with two light-coloured dorsal stripes. There may also be a whitish vertebral stripe. The lateral surfaces bear dark spots. The venter is white with dark markings laterally, on the throat and occasionally on the chest. There is a dark spot at the base of each foreleg and the hindlimbs are usually barred. There is a prominent dark brown or black mask extending from the snout, through the eye and tympanum, to the insertion of the forelimb. This is bordered below by a white stripe.

Larvae: Tadpoles hatch at about 7-10 mm total length and attain a maximum length of about 50 mm. The eyes are dorsally placed and the labial tooth rows are 2/4 or 3/4. The caudal fin is arched and the tail tip is pointed. The anus is dextral and the spiracle sinistral. Tadpoles are brownish or greenish above and creamy below, with a pinkish tint. A light line occurs along the edge of the mouth.

Variation: The males bear nuptial pads during the breeding season, and have paired vocal sacs, one being positioned over each forelimb insertion. Females are slightly larger than males, and subtle differences in colouration occur between the sexes.

Natural history: The wood frog is chiefly diurnal and is found in wooded areas or associated with open ponds. It occurs up to



Distribution of Wood Frog in Alberta

2,500 m elevation and is very cold-tolerant and hibernates on land beneath litter and humus. This species employs physicochemical mechanisms to protect against extreme cold and dryness. It forages widely, often far from water, and eats molluscs, worms, insects and other arthropods. It is largely terrestrial in the non-breeding season. Population densities may be very high. It produces repulsive skin secretions. Predation by fishes has been observed on adults in Wisconsin.

Reproduction: Breeding begins as soon as the ice begins to melt and occurs for a one to two week period from late April until June (depending upon latitude and/or altitude). After breeding, the adults disperse. They normally breed in shallow, clear ponds or in ephemeral water bodies. Males are non-territorial during the breeding period. They call while floating on the surface, and may call day and night. Amplexus is pectoral. Males clasp any female that is encountered and try to displace other males from amplexus with females. Such struggles are often intense and may result in death. Eggs are laid in globular masses, usually attached to plants, but they may be laid free in the water. Several females may lay their eggs in close proximity to each other. The eggs are somewhat resistant to desiccation. The number of eggs in a clutch varies greatly, but may average about 2,000-3,000. The number laid by females in Alberta is not known. Each egg is about 1.6 mm in diameter. Hatching occurs after three weeks or more. The tadpoles then grow quickly and metamorphosis occurs six to twelve weeks after hatching.

Voice: The voice of the wood frog is similar to that of *Rana pipiens,* but the calls are higher pitched, less intense and shorter in duration. Adults emit an escape scream if attacked by a predator.

Distribution: It occurs throughout the province except for short-grass prairie habitats. An isolated record for the Cypress Hills exists, and probably represents an outlying population in a persisting area of suitable habitat. Extralimitally, it occurs from northern Alaska and south central B.C. in the west to the Appalachians, Atlantic coastal states and Maritime provinces in the east. Isolated (primarily montane) populations are scattered west of the Mississippi River.

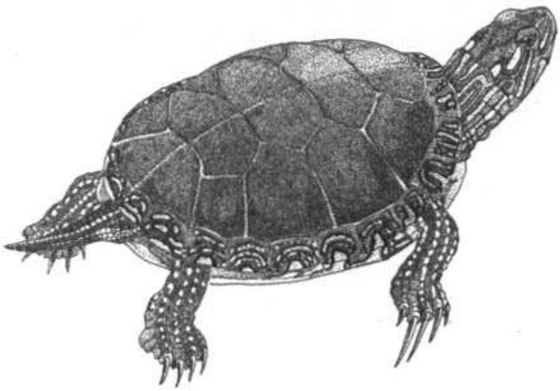
Conservation status: Alberta populations are robust and there is no evidence of decline.

Remarks: The wood frog is the only North American amphibian to cross the Arctic Circle.

Significant references: Banta 1914; Bastien and Leclair, 1992; Bellis 1961, 1962; Berven 1981, 1982a, b, 1987, 1988; Berven and Chadra 1988; Berven and Grudzien 1990; Clark 1998; Cochran 1999; de Benedictis 1974; Ferguson

1956; Forester and Lykens 1988; Gamboa et al. 1991; Heatwole 1961; Herreid and Kinney 1966, 1967; Howard 1980; Howe 1899; King and King 1991; Layne, 1992; Layne and Lee 1986; Licht 1991; Lotshaw 1977; Martof 1970; Martof and Humphries 1959; Moore 1951; Moore and Strickland 1955; Patch 1939; Pierce et al. 1987; Pollister and Moore 1937; Roberts and Lewin 1979; Salt 1979; Storey, J.M. and Storey 1985a; Storey, K.B. 1984, 1987; Wilbur 1972, 1976, 1977.

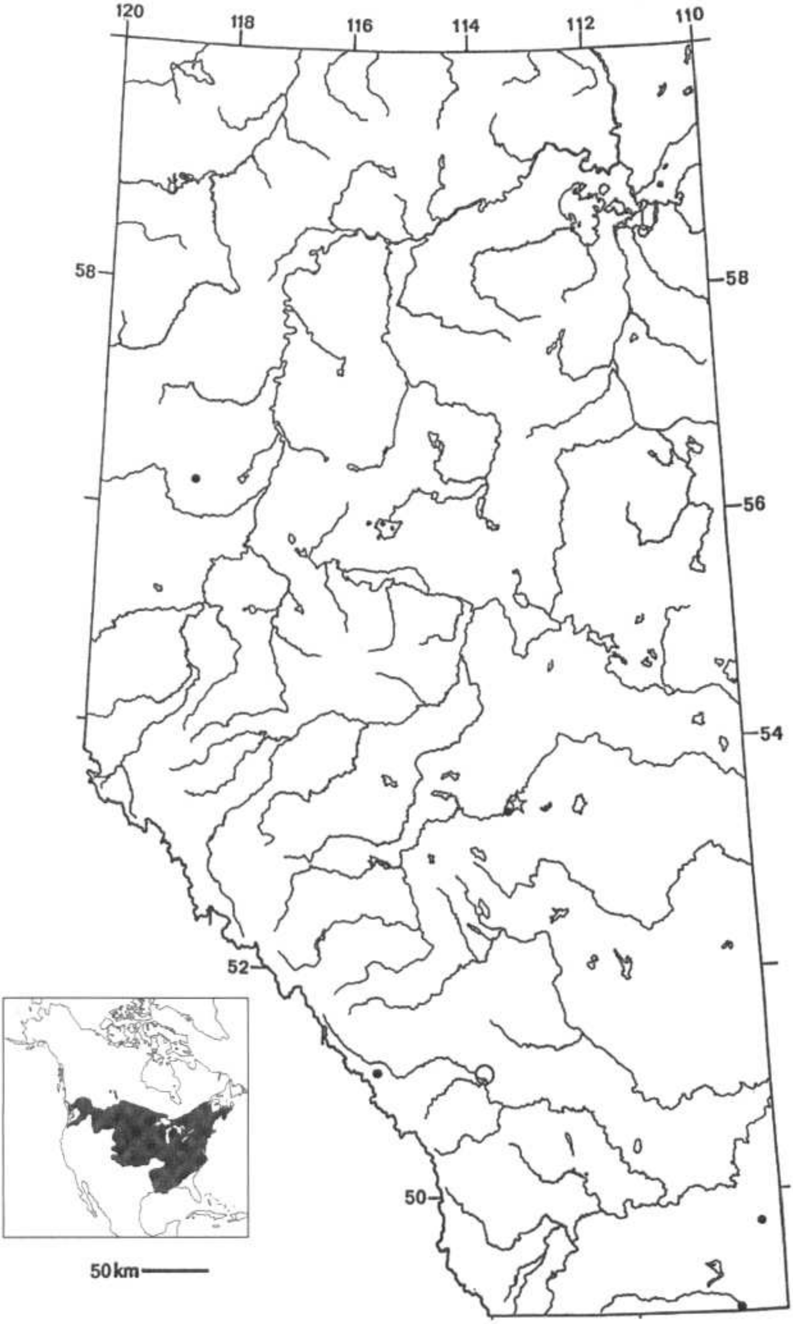
Painted Turtle
Chrysemys picta



Description: Carapace length 60-250 mm. Carapace low, smooth and unkeeled; oval in outline. Rear of carapace with a smooth border. Hind feet strongly webbed. Carapace generally olive, brown or black, with contrasting olive, yellow or red borders along the front edge of the shields. Yellow lines on the head and limbs. A red bar or blotch behind the eye. Plastron usually marked with red, and having a dark central patch that sends extensions outward between the scutes.

Variation: Plastron red or orange, with well-pronounced dark markings. Males much smaller than females, with very elongate claws on the front feet and a slightly concave plastron. The vent is more distally positioned on the tail in males and lies outside the carapace margin. Hatchlings have a more rounded carapace with a middorsal keel. Hatchling carapace length is about 25 mm. Males mature at about four years of age, females at five.

Natural history: Aquatic and generally diurnal. Usually found in association with ponds, lakes, streams, ditches or marshes with quiet waters, muddy or sandy bottoms and abundant aquatic plants. Younger individuals occupy shallower water. Frequently bask on logs, rocks or banks near water. Under conditions of high density or high temperature *Chrysemys* may show aggressive behaviour towards conspecifics at basking sites. It hibernates in winter by burrowing into the mud beneath the water. These turtles may supercool, allowing them to survive temperatures well below freezing, but hatchlings can only survive brief periods of freezing



Distribution of Painted Turtle in Alberta of their bodily fluids. In appropriate conditions, with water-binding agents in the soil, painted turtles in nests can supercool to −17°C or more before spontaneously freezing. In Alberta, it probably does not emerge from hibernation until April. It eats insects, molluscs, earthworms, fish, frogs, tadpoles, aquatic plants and carrion. It may move extensively on land between bodies of water, or it may be restricted to a single body. The painted turtle is preyed upon by small carnivores at all stages of its life. It may also be parasitized by leeches. Individuals may reach an age of forty years.

Reproduction: Lays one or two clutches of eggs from late May through late summer. Mating occurs in the water. Males may be aggressive at that time. The male strokes the female with its elongate claws. Pre-mating courtship usually lasts five to fifteen minutes. Nesting occurs on land, and this usually begins in June. The female digs a nest in sandy or friable soil, near water. Females may carefully select their site of oviposition in order to manipulate the thermal regime of the nest. This is of special significance because painted turtles have temperature-dependent sex determination. Two to twenty eggs are laid. These may be up to 35 x 18 mm. The female covers the nest. The young may overwinter in the nest after hatching.

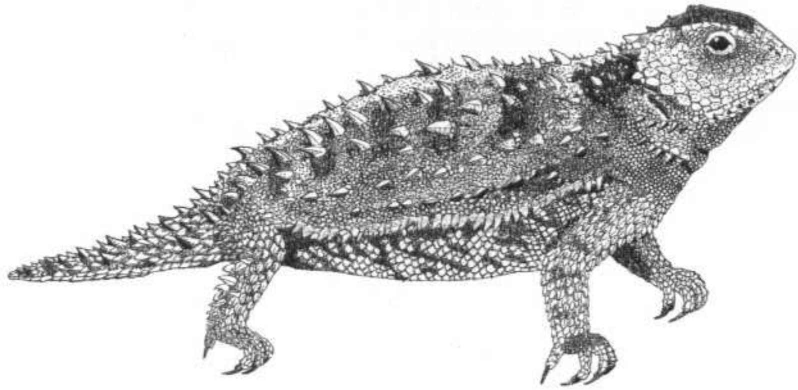
Distribution: In Alberta, this species occurs naturally only along the Milk River drainage. Localities in the Cypress Hills, Banff National Park, Edmonton and Hines Creek may be introductions. Extralimitally, it is widespread from Vancouver Island (probably introduced), southwestern coastal B.C. and the Columbia River Valley to the central Gulf coast and the Atlantic coast from North Carolina to Nova Scotia. It is absent from the extreme southeastern United States and much of the west.

Conservation status: Although details of the Milk River population are unknown, the very restricted range of this turtle in Alberta makes it of special conservation concern.

Remarks: Four subspecies are recognized. *Chrysemys picta belli* is the Alberta subspecies. It occurs as far east as central Ontario, northern Michigan, central Wisconsin, western Illinois and northern Missouri. This turtle has been extensively introduced as it is commonly kept as a pet and often released back into the wild. Probably at least some of the introduced populations are viable. Pattern of the carapace may be obscured in some animals by a growth of algae that peaks in density in the summer.

Significant references: Attaway et al. 1998; Beall and Privatera 1973; Bennett et al. 1970; Bishop and Schmidt 1931; Black 1970b; Breitenbach et al. 1984; Cagle 1954; Clark and Chandler, 1992; Congdon and Tinkle 1982; Congdon et al. 1992; Costanzo et al. 1998; Ernst 1971a, b; Ernst and Barbour 1972; Frazer et al. 1991; Froese and Burghardt 1975; Gibbons 1967a, b, 1968a, b, c, 1969; Hammer 1969; Hartweg 1946; Jackson and Ultsch 1982; Janzen 1994; Jones and Milsom 1979; Knight and Gibbons 1968; Lefevre and Brooks 1995; Legler 1954; Lewin 1963b; Lovich 1988; MacCulloch 1981; Milsom and Chan 1986; Milsom and Jones 1980; Mitchell 1983, 1985a, b; Moll 1973; Musacchia 1959; Paukstis and Shuman 1989; Rogers and Jellison 1942; Schueler 1983; Sexton 1958, 1959a, b; Sievert et al. 1988; Taylor and Nol 1989; Tinkle et al. 1981; Ultsch and Jackson 1982; Ward 1984; Wilbur 1975.

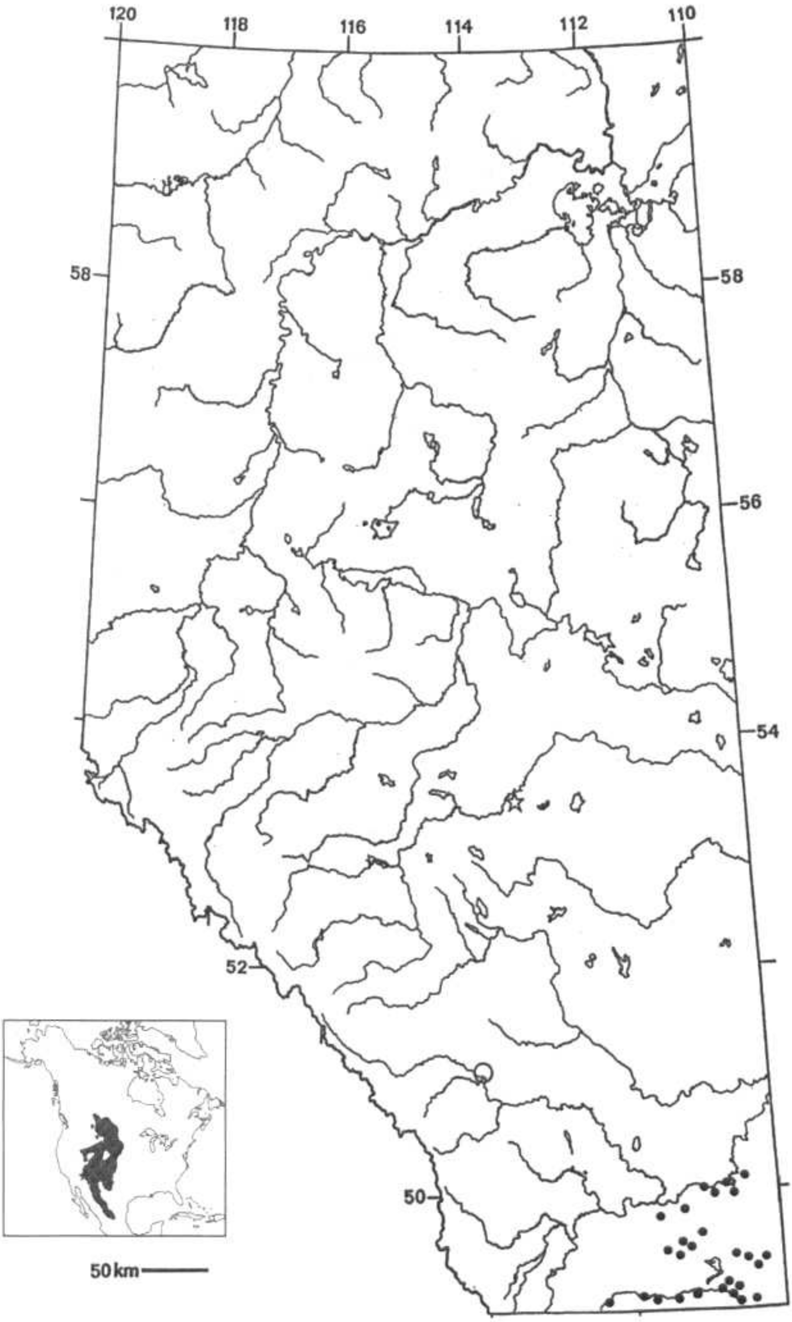
MOUNTAIN SHORT-HORNED LIZARD
Phrynosoma hernandesi



Description: A moderately small lizard with a snout-vent length of 40-70 mm. Body flattened and ovoid in outline, with short limbs and tail. Head short and snout blunt. Small horn-like scales at the back of the head. A single row of fringed scales along the sides of the body between the front and hind limbs. Throat scales small. Back covered with rows of enlarged tubercles amongst smaller granules. Beige or grey above, blotched with dark brown and speckled with white. Generally cryptic against its background. A pair of dark brown blotches above the shoulders. Area under the throat and on the chest may be tinged with yellow or beige; otherwise the venter is white.

Variation: Females are considerably larger than males. Males and females grow at the same rate, but males cease growing earlier than females and thus become sexually mature at a smaller size and younger age. Males may mate in their second summer; females not until their third. Juveniles have the appearance of miniature adults.

Natural history: Diurnal. In Alberta, lives at the interface of short-grass prairie and coulee rims, chiefly on south-facing slopes. Population densities in Alberta appear to be lower than those in adjacent regions to the south. Forages among sagebrush, to which the species is primarily restricted. Basically a sit-and-wait predator. Eats insects, chiefly beetles and ants, some grasshoppers and any other small invertebrates it can procure. It is quite cold-tolerant and is active from early April to mid-October. It is live-bearing.



Distribution of Short-horned Lizard in Albera

After mating, the females remain at the coulee rims while the males disperse into the short-grass prairie. Preyed upon primarily by birds. The horns may be a deterrent against potential snake and mammalian predators, but this is probably less effective than in other species with larger horns. Seeks shelter under sagebrush and other vegetation during the hottest part of the day. May also burrow to obtain shelter or use the burrows of small rodents. Complex shuttling behaviour is involved in temperature regulation throughout the day. Over the active season, individuals cover considerable distances, with the length of movements being greatest in the spring and fall. Shallow hibernacula are excavated in sheltered slopes. Insulation of snow cover may be significant in increasing survivorship through the winter, although winter mortality appears to be significant.

Reproduction: Mating takes place in spring, soon after emergence. The females give birth to live young, and up to ten individuals are born in late June or early July. Juveniles have a snout-vent length of about 20 mm at birth. While gravid, females exhibit restriction to a small home range.

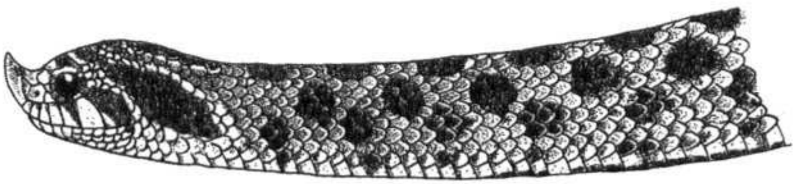
Distribution: Limited to the extreme southeastern corner of the province, and is found only in arid, short-grass prairie regions. It occurs south from the South Saskatchewan River valley to the Montana border, and west from the Saskatchewan border to the region of Del Bonito. Extralimitally, it occurs from the Continental Divide eastwards to the Great Plains. To the south, it extends through Utah and eastern Nevada to Arizona, New Mexico and west Texas. Populations as far south as Durango, Mexico may also be referrable to this species although the biogeography of horned lizards is in need of revision as a result of recent systematic analyses. It is chiefly found in mountainous areas in the southern parts of its range.

Conservation status: The mountain short-horned lizard has been the subject of considerable investigation over the past two decades. These studies have revealed that population densities are low but that, except where disturbed by oil and gas exploration, it seems to be maintaining itself at a sustainable level.

Remarks: Alberta short-horned lizards were formerly assigned to the species *Phrynosoma douglasi*. However, molecular data have revealed that lizards previously considered to belong to several different subspecies of *P. douglasi* are more appropriately allocated to *P. hernandesi*.

Significant references: Chandler 1965; Clark and Chandler, 1992; Clark, G.W. and Bradford 1969; Fitch 1985; Guyer 1978; Guyer and Linder 1985; Heath 1964, 1965; James et al. 1997; Laird and Leach 1980; Lynn 1965; Medica et al. 1973; Milner 1979b; Montanucci 1983, 1987, 1989; Montanucci and Bauer 1982; Mosimann and Rabb 1952; Nero 1957; Pianka and Parker 1975; Powell 1982; Powell and Russell 1984, 1985a, b, 1991a, b, 1992, 1993, 1994, 1996b, c; 1998; Prieto and Whitford 1971; Reeve 1952; Schowalter 1979; Scott 1976; Sherbrooke 1981, 1987; Sherbrooke and Montanucci 1988; Smith et al. 1999; Werschkul 1982; Williams 1946; Zamudio et al. 1997.

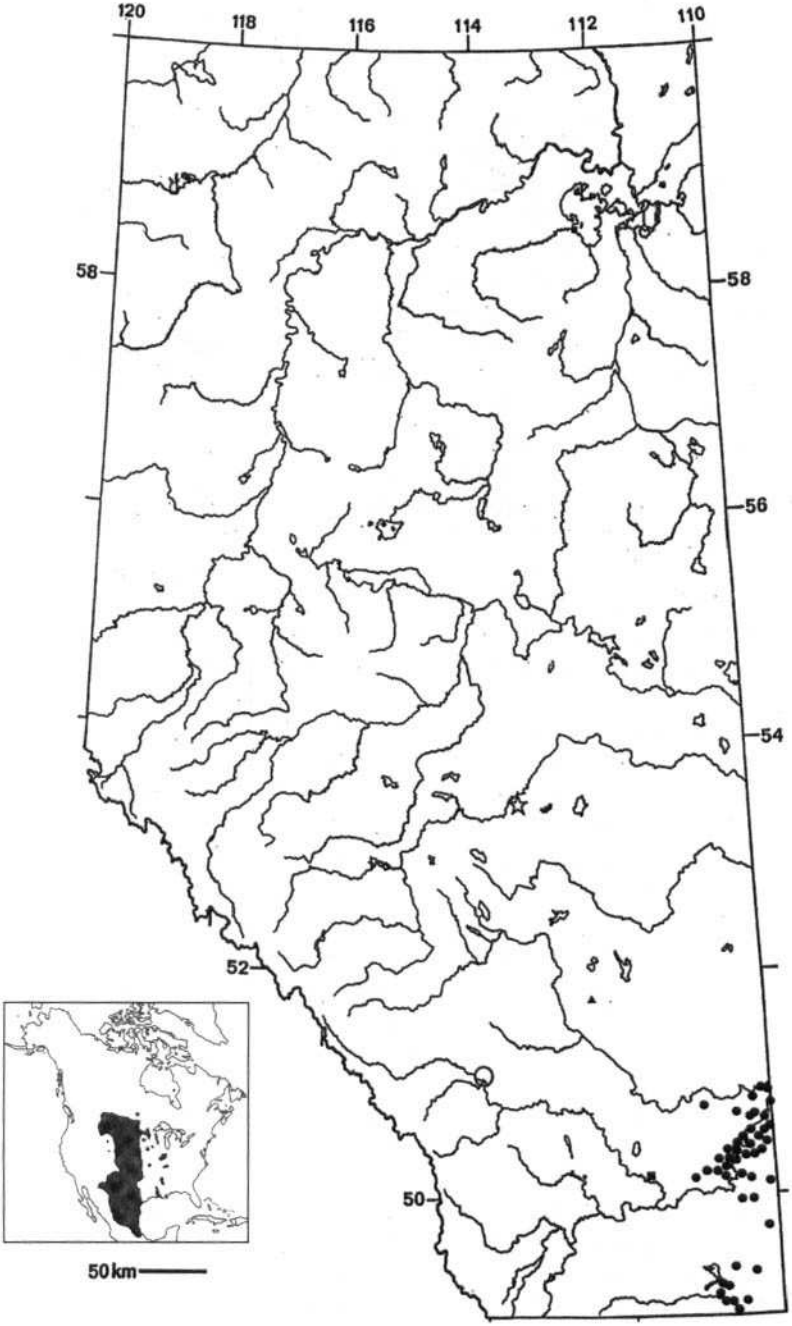
Western Hog-nosed Snake
Heterodon nasicus



Description: A small- to medium-sized snake, with a total length ranging from 400-900 mm. The snout-vent length of a large female is about 780 mm, while that of a large male is about 550 mm. This is a heavy-bodied snake. The rostral scale is keeled dorsally and turned sharply upward. There are no facial pits. The body scales are keeled. The anal scale is divided. There is no rattle at the end of the tail. Colour is light brown with three or four rows of dark brown blotches extending the length of the body on the dorsal surface. The pattern may be bold or faint. Smaller brown blotches occur along the sides. The throat is white and the venter is black or checkered black and white. In colour it superficially resembles *Crotalus* and *Pituophis.*

Variation: Females are larger than males. The tail of males is relatively longer than that of females, averaging twenty-two percent of the snout-vent length compared with fourteen percent for females. Males become sexually mature after one to two years, females after one-and-a-half to three years.

Natural history: Generally diurnal, but may also be active at night. Found in areas of friable soil and shows a preference for sandy locations and damp lowlands. It is found in sandy or gravelly areas with low-growing plants, sandhills, dry stream bottoms, often near areas of water in typical badlands country. Available habitat for this species has been much reduced by man's activities. The limiting factors affecting its distribution are soil and vegetation types, and proximity to water. The oddly shaped snout is used in digging.



Distribution of Western Hog-nosed Snake in Alberta

Heterodon eats toads, frogs, salamanders, other snakes, lizards, turtles, small rodents and various invertebrates. Its posterior teeth appear to function in puncturing toads that have inflated themselves. It is preyed upon by hawks, crows and coyotes. When molested it spreads a "hood" at the back of the head, hisses and strikes. It may, however, play dead in such circumstances, rolling on its back, writhing and then remaining motionless. It is very likely to bite if handled. It appears to be mildly venomous to its prey, but the venom has no demonstrable effects on man. It becomes active after soil temperatures reach about 15°C and in Alberta is most active in May, June and July. Males become active earlier than females, and both sexes are most active when air temperatures are very high. Individuals may live for eight years.

Reproduction: Mating and courtship behaviour are not known and have never been observed. Females lay between four and twenty-three eggs in the summer, with a mean of approximately nine. Each egg is about 31 x 22 mm. Females produce a clutch every other year. The eggs are laid in sandy soil at a depth of about 90 mm. The incubation period is about sixty days. In Alberta, egg laying occurs from the middle of June to the end of July. Hatchlings measure about 177 mm total length, with a snout-vent length of about 150 mm.

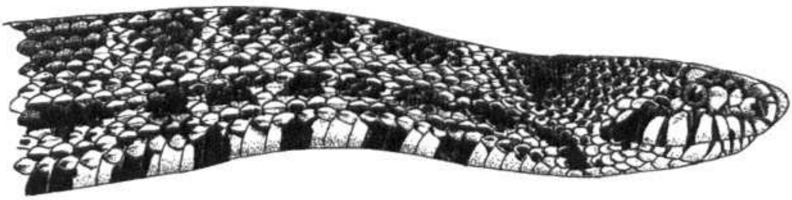
Distribution: In Alberta, the hog-nosed snake is limited to the short-grass prairie of the southeastern corner. It is found from the Montana border north to the Red Deer River, primarily east of Orion and Medicine Hat. It probably also occurs in suitable habitat as far north as the Drumheller area. Solid circles on the range map associated with this description indicate populations within the current range in Alberta. The solid triangle represents a report of this species by Moore (1953a) that lies far outside of any other reported occurrence in the province, and the solid square is a pre-1979 record that lies outside of the current range. Extralimitally, it occurs from southern Saskatchewan and southwestern Manitoba south through the plains states to San Luis Potosi, Mexico, and from central Montana and eastern Arizona in the west, east to central Illinois. The eastern limit comprises a suite of highly fragmented populations.

Conservation status: The hog-nosed snake has a very restricted range in southeastern Alberta and is now very infrequently encountered. It can be considered to be rare and intense study is needed to establish its actual status. Alberta Fish and Wildlife have been gathering data through a public awareness program.

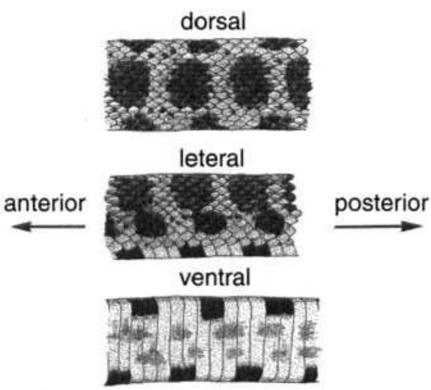
Remarks: Three subspecies are recognized. *Heterodon nasicus nasicus* occurs in Alberta. This subspecies ranges southward to Oklahoma, northern Texas and New Mexico. This snake has been severely affected in its distribution by human activities, and it is now much less common than it once was.

Significant references: Cook 1970, 1977b; Fitch, 1985; Lewin 1963a; Moore 1953a; Pendlebury 1976b; Platt 1969; Wright and Didiuk 1998.

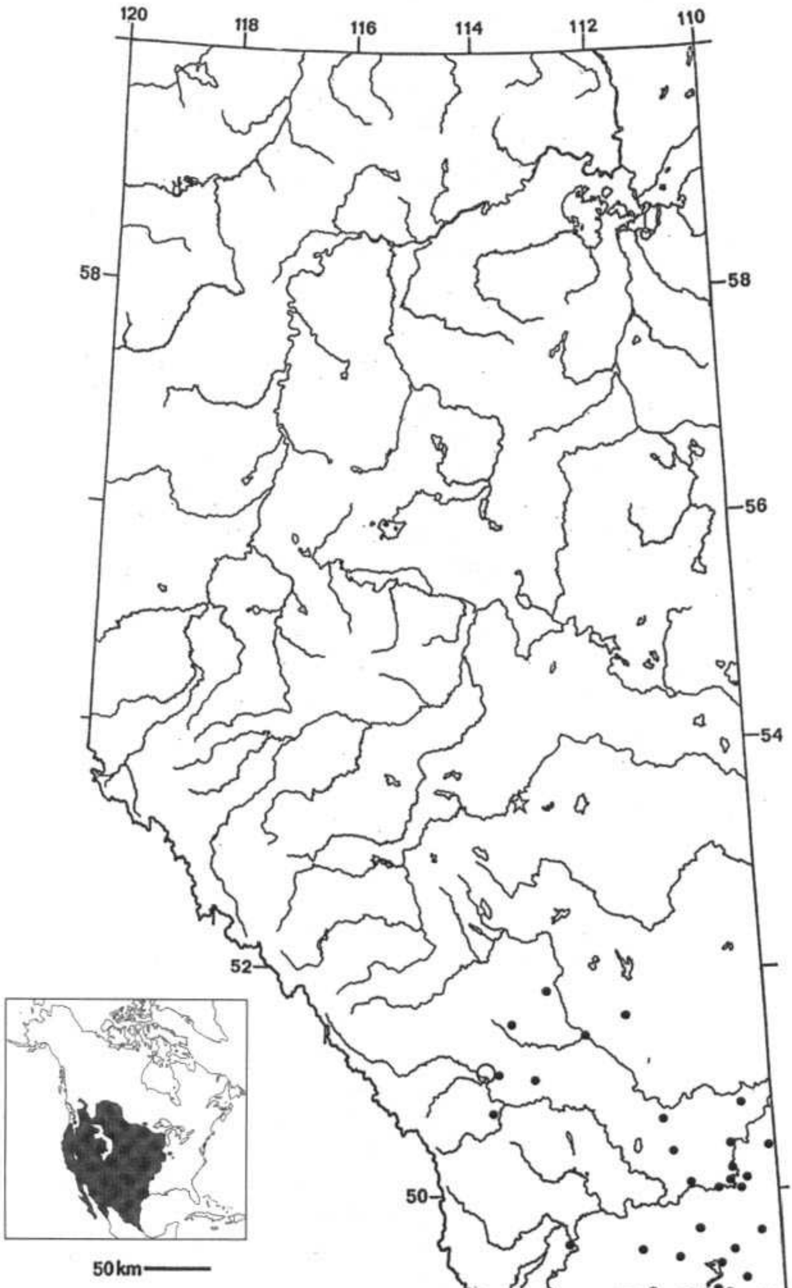
BULLSNAKE
Pituophis catenifer



Description: A large snake with a long, stout body and a moderately long tail. Total length ranges from 900-2,000 mm, with individuals generally being larger in the southern parts of the range. There are usually four prefrontal scales. There are no facial pits and the rostral scale is not upturned. The dorsal scales are keeled, in 27-37 rows at mid-body. The anal scale is single. There is no rattle on the tail. The general colour is yellowish, with black, brown or brick red dorsal blotches and rows of smaller lateral spots or dashes. The ventral scales are usually checkered brown and cream.



Variation: Males may be larger than females. Males mature at one to two years, females at three to five years.



Distribution of Bullsnake in Alberta

Natural history: It is mostly found in the drier areas of grassland or sagebrush, and may be found in farmlands and fields. It is typically found in areas of sandy soil, frequently in association with rock piles or boulders. It is diurnal or crepuscular (active at dawn and dusk). It is able to both burrow and climb. When molested it hisses loudly, strikes and may vibrate its tail. Individuals will almost certainly bite if handled. While not venomous, the bite may be quite painful. It is a generalist feeder and eats rodents, rabbits and other small mammals, birds, nesting birds and bird's eggs, lizards and arthropods. It kills by constriction and dens in the winter.

Reproduction: Males may engage in combat during the mating season. During copulation the male lies along and on top of the female and usually bites her on the back and neck. One or two clutches of between two and twenty-four eggs are laid each summer. Nest sites are often abandoned mammal burrows on south-facing slopes. The incubation period is fifty to sixty days. Hatchlings are between 200 and 400 mm total length and emerge from the eggs in late summer or early fall. The hatchlings may not feed until the next spring.

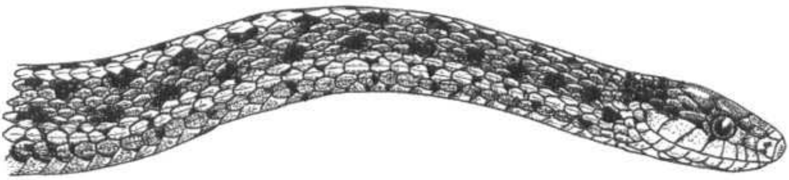
Distribution: In Alberta, the bullsnake is limited to short-grass prairie. It extends north from the Montana border to the Trochu region, and west from the Saskatchewan border to a line connecting Calgary with Waterton. It is found at elevations up to 2,000 m. Extralimitally, it occurs over much of the central and western United States and northern Mexico. Its range is fragmented in the Rockies of the United States and east of the Great Plains.

Conservation status: In the areas of Alberta in which it occurs the bullsnake is still frequently encountered and does not appear to be in decline, although its range is considerably more constrained than it appears to have been in the early years of the century.

Remarks: Six subspecies are recognized in Canada and the United States. *Pituophis catenifer sayi* occurs in Alberta. The range of this subspecies extends from Alberta and south western Saskatchewan south to north eastern Mexico, and west from the Idaho panhandle to western Indiana. It is probably the most economically beneficial snake in Alberta as it plays an important natural role in pest control. Although some authors (Sweet and Parker 1990; Conant and Collins 1991) place this species in *P. melanoleucus,* we here follow Collins (1997) in referring it to *P. catenifer.*

Significant references: Bullock 1981; Bullock and Tanner 1966; Burger 1991; Carpenter 1982; Clark and Chandler, 1992; Clark and Bradford 1969; Cook and van Zyll de Jong 1975; Corn and Bury 1986; Diller and Wallace 1996; Fitch 1985; Greenwald, O.E. 1971; Licht and Bennett 1972; Packard and Packard 1988; Parker and Brown 1980; Pendlebury 1972, 1973; Stinner 1987; Sweet and Parker 1990.

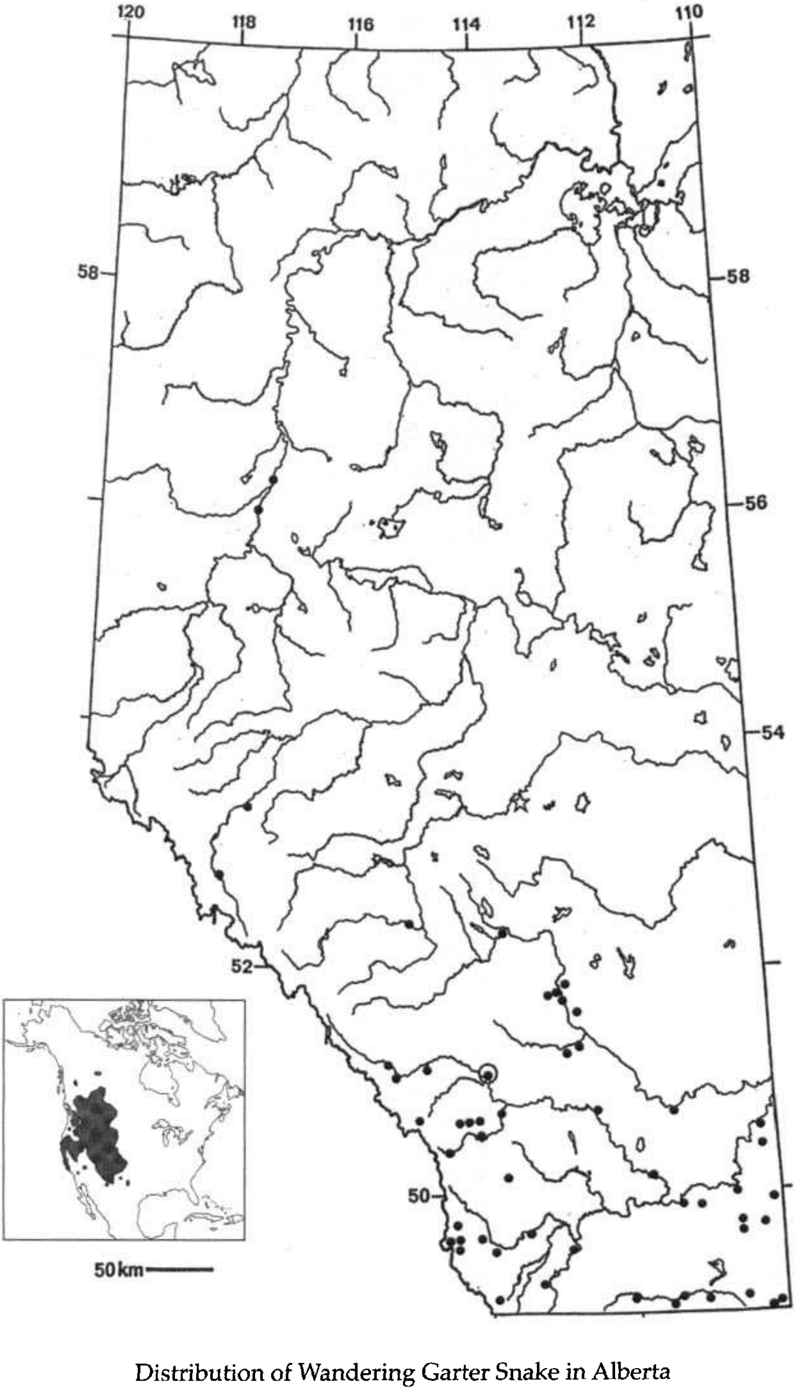
Wandering Garter Snake
Thamnophis elegans



Description: A slender, elongate snake that attains a total length of between 450 and 1,070 mm. There are usually eight upper labial scales, of which the sixth and seventh are often taller than wide. The internasal scales are usually broader than long. There are two pairs of chinshields of approximately equal length. The dorsal body scales are keeled and the anal scale is single. There are usually twenty-one scale rows at mid-body. The tail is moderately long. The background colour is primarily brown, grey or green, with a dull yellow or brown dorsal stripe, fading posteriorly. Side stripes, generally the same colour as the dorsal stripe, are present on the second and third rows of dorsal scales. Dark spots are generally present between the dorsal stripes and side stripes. The ventral surface is usually greyish, sometimes with darker markings. The underside of the head is white.

Variation: Females are larger than males.

Natural history: Often found near water, but it is not restricted to such locations. When associated with bodies of water, it may be found in close proximity to streams, lakes, ponds, marshes or ditches. In the spring, this species may occur in great numbers. When threatened it may seek refuge in water, beneath debris or in vegetation. It eats insects, molluscs, worms, fish, amphibians, reptiles, small birds and mammals, and carrion. It may bite when captured and / or emit a repulsive secretion from the cloacal glands, along with faeces. Wandering garter snakes are mildly venomous and may immobilize their prey with oral secretions, but the venom has no toxic



Distribution of Wandering Garter Snake in Alberta effects on man. This species occupies communal dens in winter. These may be in naturally occurring crevices or the abandoned burrows of small mammals. Home range size is extremely variable.

Reproduction: The wandering garter snake is a live-bearer. Mating occurs in the spring. Gravid females exhibit low rates of movement during gestation and prefer to occupy retreats that provide protection and more suitable thermoregulatory conditions. Four to nineteen young are born from July to September, measuring from 170 to 230 mm in total length.

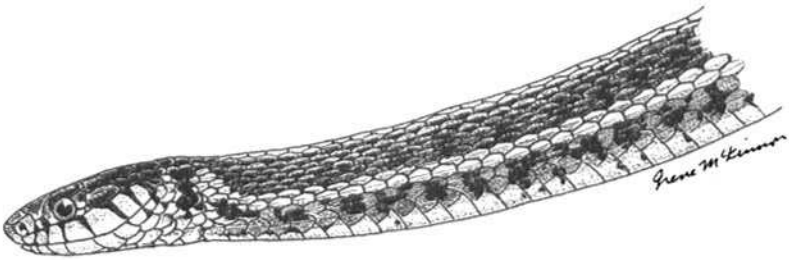
Distribution: In Alberta, this species is distributed widely south of 52°N, primarily south and west of the Red Deer River. There are scattered localities further north and west along the Athabasca and Peace Rivers. It is broadly distributed in all habitat types, although its status in the more northerly boreal forest sites remains unresolved. It occurs at altitudes of up to 2,000 m and its range overlaps that of both *Thamnophis radix* and *T. sirtalis* in south central Alberta. Extralimitally, it occurs from northern B.C. south to New Mexico, Arizona and Baja California. It is present on Vancouver Island. It occurs from the Pacific coast of California and Oregon east to extreme western South Dakota, Nebraska and Oklahoma. Populations at the periphery of the range are fragmented into isolates.

Conservation status: The wandering garter snake remains common throughout much of its range in Alberta, although localized extirpation has resulted in urban areas where wetlands have been destroyed. Such induced patchiness may ultimately prove to be problematic. The status of populations north of 54° requires further investigation.

Remarks: Five subspecies are recognized. *Thamnophis elegans vagrans* occurs in Alberta. This subspecies accounts for most of the range of the species, but is absent from California, Baja California, western Oregon and western Nevada.

Significant references: Arnold 1977b, 1980, 1981a, b; Ayres and Arnold 1983; Charland 1995; Charland and Gregory 1995; Clark and Chandler, 1992; Clark and Bradford 1969; Feder and Arnold 1982; Fitch 1940, 1983; Fox 1951; Garland and Arnold 1983; Gregory 1984a; Mutschmann 1995; Rosenberg et al. 1985a; Rossman et al. 1996; Ruthven 1908; Sweeney 1992; Tanner and Lowe 1989; Thompson 1917; Van Denburgh and Slevin 1918.

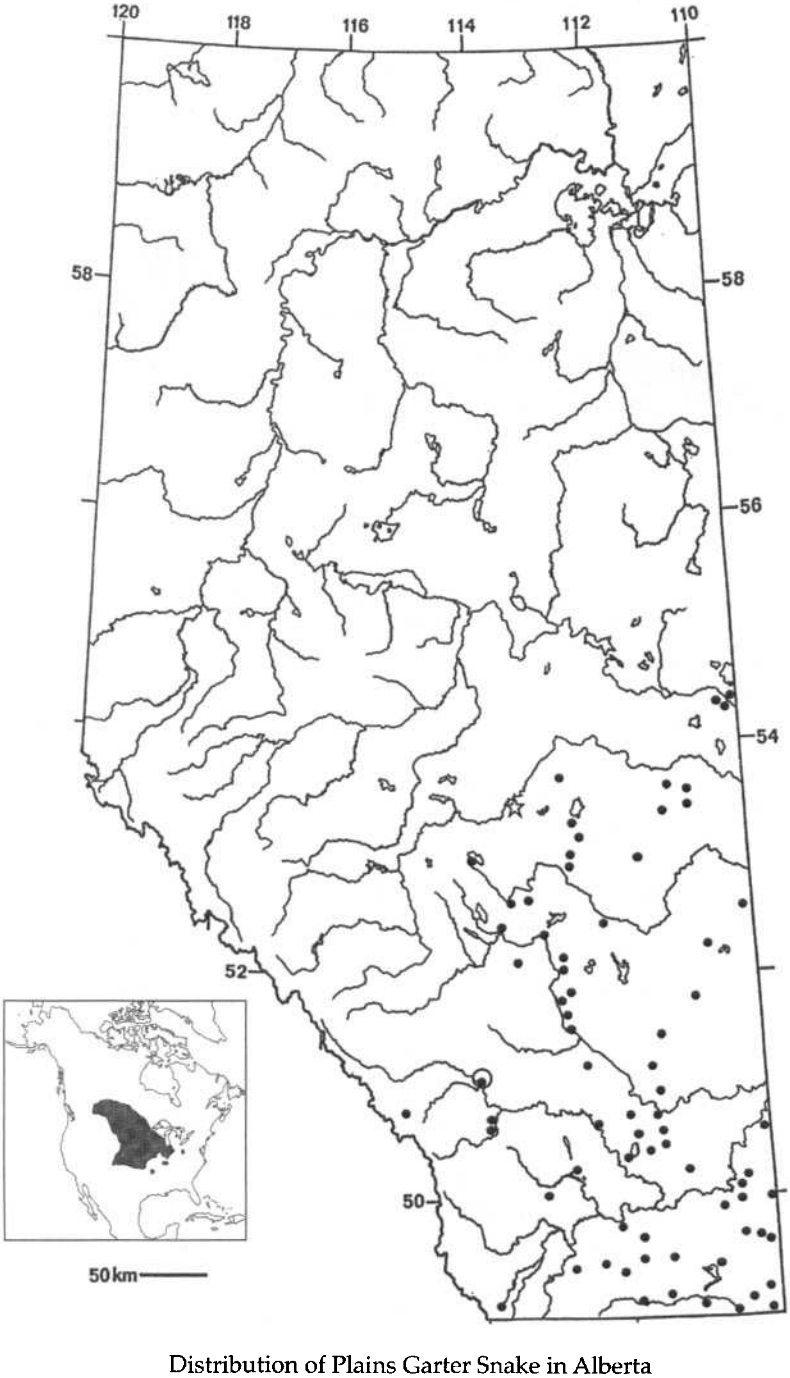
Plains Garter Snake
Thamnophis radix



Description: A medium-sized, slender, elongate snake attaining a total length of 500-1,000 mm. There are usually seven upper labial scales, and two pairs of chin shields, the posterior pair being longer and narrower from the anterior. The dorsal scales are keeled, there are normally twenty-one scale rows at mid-body and the anal scale is single. The tail is moderately long. Background colour is greenish grey, olive or brownish, with two rows of dark blotches forming a checkered pattern between the dorsal and lateral stripes. The dorsal stripe is usually orange to yellow, fading posteriorly. The lateral stripes are normally yellowish and are located on the third and fourth dorsal scale rows. Black bars are present on the yellowish upper labial scales. The ventral colour is variable and may be whitish, bluish green, or grey, with two rows of dark, diffuse spots.

Variation: Females are larger than males.

Natural history: This species has very wide habitat preferences and tolerances. It frequents ponds, lakes, streams, marshes and dugouts. It preys upon fish, amphibians, small mammals, worms, insects and carion. It possesses cloacal glands that secrete a foul-smelling liquid. If captured it may writhe and twist in an attempt to escape, but it rarely bites. It smears the secretions of the cloacal glands on the attacker, together with faeces. It may still be found in urban areas if suitable habitat persists. It may be active until mid-October on warm days. Like its congeners, this species uses hibernacula such as natural karst sink holes, mammal burrows



Distribution of Plains Garter Snake in Alberta and rock piles. It is mildly venomous and may immobilize its prey by injection of oral secretions. These secretions have no effect on man.

Reproduction: Mating may take place in spring or fall and is associated with denning congregations. It is a live-bearing species and may be very prolific, with from five to forty young being produced in a normal litter. On occasion, as many as ninety-two young have been produced in a single birth. The young are born from July onwards, and are about 180 mm in total length.

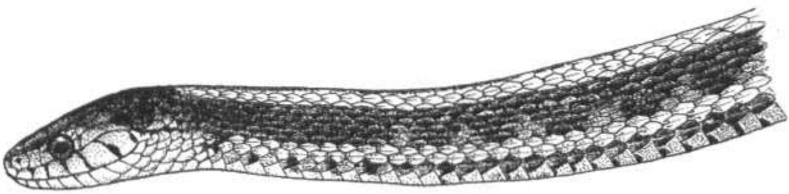
Distribution: In Alberta, the plains garter snake is widely distributed south of Cold Lake, primarily in the eastern half of the province. It inhabits short-grass prairie, aspen parkland and, marginally, boreal forest. It occurs as far west as Calgary, with a few records from subalpine areas near the B.C. border. Its range overlaps with those of *Thamnophis elegans* and *T. sirtalis* in south central Alberta. It is most common in the southeastern corner of the province. Extralimitally, it is found east through Saskatchewan and Manitoba, south through the great plains and upper midwestern United States from northeastern New Mexico to northwestern Indiana. Isolated populations occur in Ohio, the St. Louis area and northwestern Arkansas.

Conservation status: This species remains common in southeastern Alberta but populations around Calgary appear to have undergone decline.

Remarks: Two subspecies are recognized. *Thamnophis radix haydeni* occurs in Alberta. Its range extends to Minnesota, central Iowa, northwestern Missouri and Kansas. An outlier occurs in the Ozark Mountains.

Significant references: Arnold and Bennett 1984, 1988; Ballinger et al. 1979; Bauerle 1972; Bullock and Tanner 1966; Chiszar et al. 1976; Dalrymple and Reichenbach 1981; Gregory 1977a; Mutschmann 1995; Hart 1975, 1979; Ross and Crews 1977, 1978; Rossman et al. 1996; Ruthven 1908; Seibert, 1950; Smith 1949; Stewart 1965; Sweeney 1992; Van Denburgh and Slevin 1918.

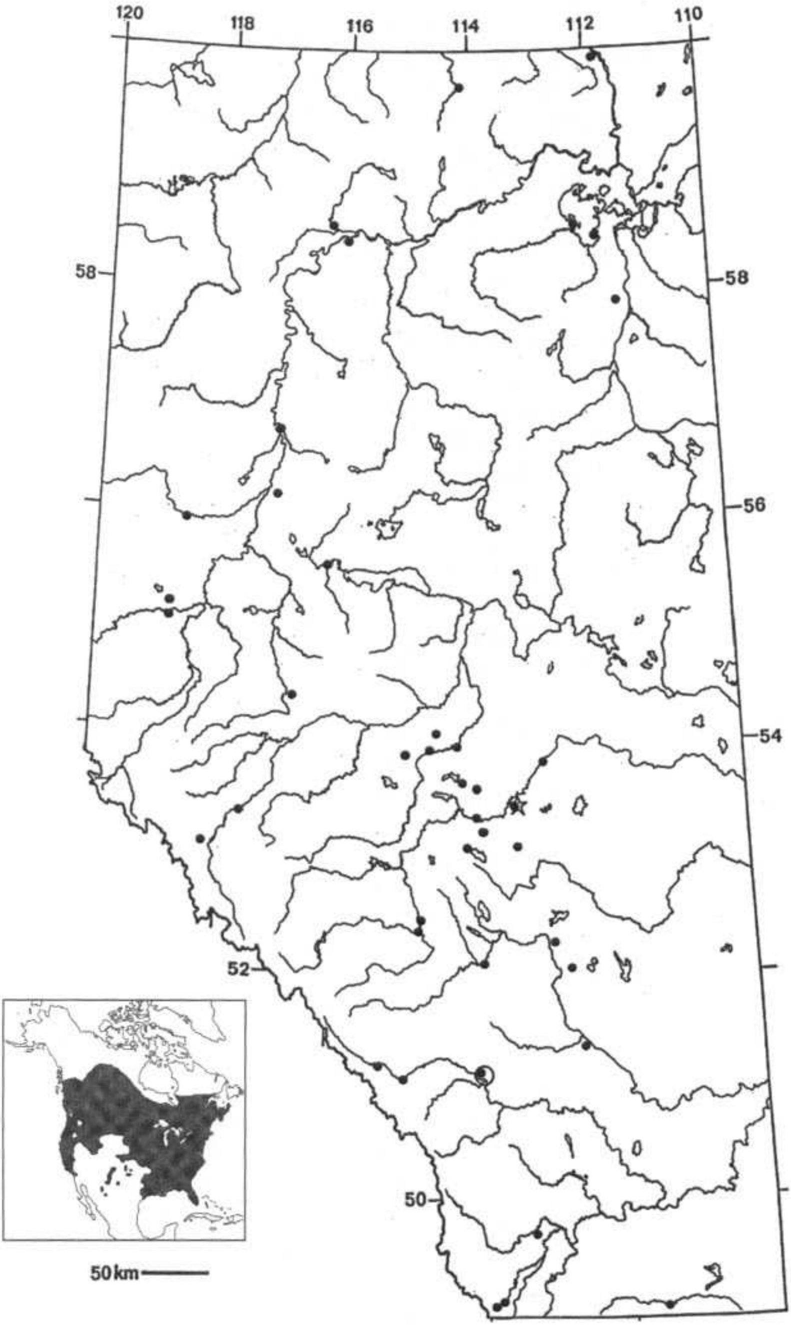
RED-SIDED GARTER SNAKE
Thamnophis sirtalis



Description: A medium-sized, slender, elongate snake, attaining a total length of between 460 and 1,300 mm. There are usually seven upper labial scales and ten lower labials, and two pairs of chin-shields, with the rear pair being longer than the anterior pair. The dorsal scales are keeled, there are usually nineteen scale rows at mid-body and the anal scale is single. The tail is moderately long. The background colour is dark olive to black. There are dark spots on the back and usually red or orange bars on the sides. The dorsum of the head is primarily olive in colour. The vertebral and lateral stripes are variable and may be yellow, greenish, orange or blue. The lateral stripe occurs on the second and third scale rows. The venter is bluish and is often darker posteriorly. The throat is whitish.

Variation: Males have knobbed keels on the scales above the vent. Females may be considerably larger than males. Males have relatively longer tails.

Natural history: This species has very broad habitat preferences and tolerances. It often lives in the vicinity of ponds, marshes, ditches, dugouts and streams. It may be found in forested habitat, farms or in urban situations. If molested, it may flee to water or, if captured, bite and / or smear the attacker with foul-smelling anal gland secretion and faeces. It eats fish, amphibians, reptiles, birds, small mammals, worms, molluscs and some arthropods. It is very cold-tolerant. Red-sided garter snakes are mildly venomous and may immobilize their prey with oral secretions. These secretions have no effect on man. In Alberta, this species emerges from hibernation



Distribution of Red-sided Garter Snake in Alberta as early as mid-April. The distance between hibernation sites and feeding grounds may be as much as nine kilometres.

Reproduction: This species is live-bearing and normally gives birth to twelve to eighteen young, although litters may range from as few as three to as many as eighty-five. The young may be born any time from May to October and average 200 mm in total length at birth. Litter sizes are smaller and individual neonates larger in western Canada than in the east. Mating usually occurs in spring, following emergence from hibernacula, but it may also occur in the fall. Males may mate with many different females and individual females may be inseminated by several males. Gravid females exhibit low rates of movement during gestation and prefer to occupy retreats that provide protection and more suitable thermoregulatory conditions. In the northern parts of its range, there is massive communal denning. Pheromonal cues may play a role in locating the dens.

Distribution: This species occurs at scattered localities throughout Alberta. Its status in the extreme northwest of the province and along most of the Saskatchewan border is uncertain. Although it may occur in all habitat types, it is chiefly a resident of the boreal forest and aspen parkland. It occurs at elevations up to 2,000 metres. Extralimitally, it occurs from south central Northwest Territories and James Bay, south to Florida and the Gulf coast in the east, and southern California in the west. It is absent from most of the arid south western United States, although it is present in parts of New Mexico and Chihuahua, Mexico.

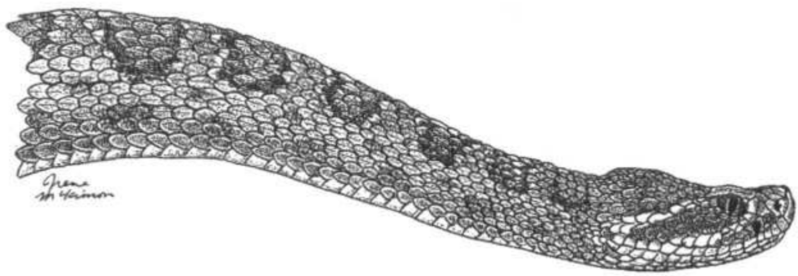
Conservation status: The most widespread reptile in the province, the red-sided garter snake appears at no imminent risk of decline.

Remarks: Twelve subspecies are recognized. *Thamnophis sirtalis parietalis* is the Alberta subspecies, and this subspecies occurs from the Northwest Territories and east central B.C. south to the Texas Gulf coast, and east from the Rockies to approximately the Mississippi.

Significant references: Aleksiuk 1970, 1971a, b, 1976a, b; Aleksiuk and Gregory 1974; Aleksiuk and Stewart 1971; Arnold 1978; Benton 1980; Blanchard 1943; Blanchard and Blanchard 1941, 1942; Bona-Gallo and Licht 1983; Burghardt 1975, 1983; Carpenter 1952a, b, 1953; Charland 1995; Charland and Gregory 1995; Clark and Chandler, 1992; Clark and Bradford 1969; Cooper et al. 1989; Costanzo 1985, 1986, 1988, 1989a, b, c; Costanzo and Claussen 1988; Crews 1976; Crews and Garstka 1982; Crews et al. 1984, 1986; Dalrymple and Reichenback 1981; Fitch 1940, 1965, 1980; Fitch and Maslin 1961; Garland 1988; Garstka et al. 1982, 1985; Gibson and Falls 1975, 1979; Gibson et al.

1989; Gregory 1974, 1977b; Gregory and Larsen 1993; Gregory and Nelson 1991; Gregory and Stewart 1975; Halpert et al. 1982; Hart 1975; Hawley and Aleksiuk 1975; Herzog and Bailey 1987; Herzog and Burghardt 1986; Hoskins and Aleksiuk 1973; Huey et al. 1989; Jansen and Foehring 1983; Joy and Crews 1985, 1986, 1988; Krohmer and Crews 1989; Larsen, K.W. 1987; Larsen and Gregory 1988, 1989; Larsen et al. 1993; Lawson 1989; Macartney et al. 1989; Mutschmann 1995; Peterson 1987; Pough 1977; Rodgers and Jellison 1942; Rosen 1991; Rossman et al. 1996; Ruthven 1908, Schwartz et al. 1989; Secoy and Ramaekers 1980; Seibert 1950; Shine and Crews 1988; Stewart 1965; Sweeney 1992; Tanner 1988; Van Denburgh and Slevin 1918; Whittier and Crews 1985, 1986; Whittier et al. 1985, 1987a, b; Wilde 1938; Young 1988, 1989.

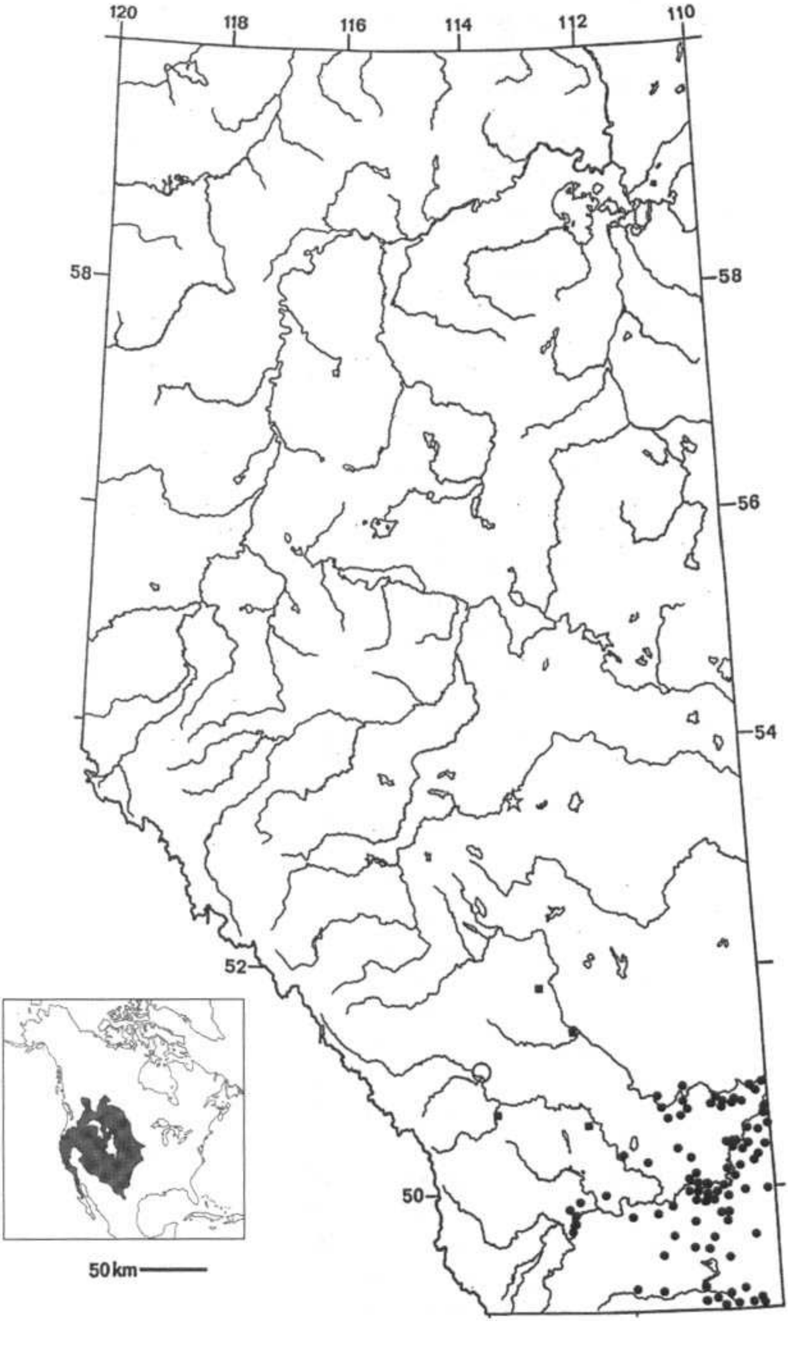
Prairie Rattlesnake
Crotalus viridis



Description: A medium-sized, thick and heavy-bodied snake that attains a total length of from 370 to 1,400 mm. The head is broad and triangular, and much wider than the neck. Facial pits are present behind and below the nostrils, one on each side of the head. The eyes have vertical pupils. Elongate, paired, retractile fangs are present in the upper jaw. The dorsal scales are keeled and the anal scale is single. The tail is short and bears a lobate rattle at the distal end. The general background colour is tan to brownish, with a repeating pattern of dark blotches or cross bands along the back. Smaller blotches are present along the sides. The tail usually has alternating light and dark rings. There is often a light stripe running from behind the eye to the corner of the mouth. The venter is a yellowy-cream.

Variation: Males are larger than females.

Natural history: This species is found mostly in the drier areas of grassland and sage brush. It may also be found in farmlands and fields. It is typically found in areas of sandy soil, frequently in association with rock piles or boulders. It dens in mammal burrows, rock crevices or caves, and may den communally. In these dens, body temperature is maintained only a few degrees above ambient, but they may move to warmer parts of the den during the period of "hibernation." Winter hibernacula may be a long distance from the summer foraging sites. Emergence from the dens will not occur until air temperature is about 10°C. It preys upon small mammals, birds, reptiles and amphibians. The heat-sensing



Distribution of Prairie Rattlesnake in Alberta facial pits are used to locate warm-blooded prey. Individuals may communicate with one another by way of an alarm pheromone secreted from the cloacal sacs. *Crotalus* usually enters hibernation in late September and emerges in late April or early May. It may remain active after the first frosts. It is generally crepuscular, but may be active at any time. When molested, it will coil, raise the head, shake the rattle, and strike. It may strike repeatedly. It is venomous and dangerous, but rarely fatal. It is capable of swimming. This species may live for up to fifteen years.

Reproduction: Sexual maturity is reached at five to seven years. Females may have their first litters in six to eight years. In the Okanagan Valley of British Columbia, mating occurs in late summer and parturition takes place in the following September or early October. Mating may take place in aggregations of several individuals. Multiple females may use a single rookery with preferred thermal conditions. The prairie rattlesnake is live-bearing and usually gives birth to four to twelve large young. They have a total length of about 280 mm at birth and weigh about 18 g. The female may give birth in or near the overwintering dens and may not feed during the period of gestation. Females probably breed only every second to fourth year. Males may engage in combat bouts near the dens during the breeding period.

Distribution: In Alberta, this species is found in the short-grass prairie regions of the south east. Older records suggest a range extending along the Red Deer River almost to the level of Red Deer, and along the Bow River valley almost to the level of Calgary. More recent collections and sightings, however, are confined to the areas east of 112°53′ W and south of 51°22′ N. On the range map accompanying this description, the current range of the prairie rattlesnake is indicated by solid circles. Solid squares represent pre-1978 reports that are now disjunct from the current distribution and probably represent extirpated populations. Extralimitally, this species occurs from south central B.C. and southern Saskatchewan south to Baja California and north central Mexico. Its range extends from the Pacific coast to eastern Nebraska. It is absent from Vancouver Island and much of its range is highly fragmented.

Conservation status: The range of the prairie rattlesnake has become reduced in recent decades and anecdotal reports have intimated that this animal is not as common as it once was in the southeastern corner of the province. Numbers still appear to be healthy, however, and a monitoring project is underway to attempt to determine if land use patterns have a direct effect on rattlesnake density. Special attention will be paid to such effects on den sites.

Remarks: Eight subspecies are recognized. *Crotalus viridis viridis* is the Alberta subspecies. The range of this subspecies essentially encompasses the range of the entire species east of the Rockies. It is of considerable economic value in controlling pests. In Alberta, the conversion of rangeland to cultivation may be responsible for a shrinking distribution.

Significant references: Cook1965; Cowles and Phelan 1958; Diller and Wallace 1996; Dobie 1965; Duvall 1986; Duvall et al. 1985;Ernst, 1992; Fitch 1985; Gannon 1978; Gloyd 1940; Graves and Duvall 1988, 1993; Hennessy and Owings 1988; Jacob and Painter 1980; Klauber 1936, 1937, 1972; Lewin 1963a; Logier 1932; Ludwig and Rahn 1943; Lynn, W.G. 1931; Macartney 1985; Macartney and Gregory 1988; Macartney and Weichel 1989; Marion and Sexton 1984; Melcer and Chiszar 1989; Melcer et al. 1988; Milner 1979a; Murphy and Crabtree 1988; Parker and Brown 1974; Pendlebury 1976a, 1977; Rahn 1942; Rodgers and Jellison 1942; Schaeffer et al. 1972, 1978; Sexton and Marion 1981; Stark 1984, 1985, 1986a, b; Watson and Russell 1997; White and Lasiewski 1971; Williams 1946; Zimmerman 1948.

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Species
Possibly Occurring in Alberta

TAILED FROG
Ascaphus truei

Description: Adult: A small frog, with a head and body length of 35-50 mm. The body is somewhat flattened and moderately slender. The eyes are large and prominent, with a vertical pupil. No tympanum is visible. The toes of the hind feet are webbed and the fifth (outermost) toe is considerably broader than the others. The skin is covered with small tubercles. Typically olive, grey or brown, with a dark eye stripe and a pale yellow or greenish triangle on the snout. Irregular dark stripes and spots are often present on the lateral surfaces of the limbs. Belly translucent pink.

Larvae: Tadpoles with a large, round sucking mouth. Tooth rows 2-3/7-10. Anus median, spiracle median. Attain a total length of 30 mm. Slate grey in general colour, with a usually white or pinkish tail bordered proximally by a dark band.

Variation: Males have a tail-like intromittent organ, as well as palmar and forearm tubercles in the breeding season. At this time, additional horny black pads develop on the male's chest. Females are larger than males.

Natural history: Nocturnal. Inhabits cold, clear, clean waters, typically in forested areas. Adults eat terrestrial and aquatic insects. They remain hidden beneath rocks during the day. Adults are highly site-faithful.

Reproduction: Breeding occurs in mid-summer to fall. Reproduction is not associated with aggressive or territorial behaviour. Amplexus is pelvic. The intromittent organ of the male is used for internal fertilization, with copulation lasting from twenty-four to thirty hours. Eggs are laid in small clumps under submerged stones. Multiple clutches may be found in a single nest. They are about 4.5 mm in diameter and are unpigmented. When the tadpoles hatch they have a total length of 10-15 mm. Tadpoles hang onto rocks with their mouth and feed on algae and diatoms. They may spend two to three years as tadpoles before transforming, and up to eight years before reaching sexual maturity. Individuals may survive up to fourteen years.

Voice: None.

Distribution: Known from southwestern B.C., the northern B.C. coast near Kittimat, the area of the Fraser Valley and extreme southeastern B.C. near the Flathead River. In the United States, it occurs south from the Canadian border to the Gualala River in northern California, and is found in extreme southeastern Washington and northeastern Oregon and throughout much of northern Idaho and western Montana, north to Glacier National Park (U.S.). The Flathead River and Glacier National Park localities are within 25 km of the Alberta border. This species may exist in suitable adjacent habitats in Waterton Lakes National Park and near the Castle River.

Remarks: This species does not seem to be able to tolerate water conditions in logged areas due to higher temperatures and increased amounts of particulate matter.

Significant references: Adams 1993; Altig 1969; Altig and Brodie 1972; Bury 1968; Daugherty and Sheldon 1982a, b; De Vlaming and Bury 1970; Gaige 1920; Gradwell 1971; Green et al. 1980; Metter 1964, 1967, 1968a, b; Mittleman and Myers 1949; Noble and Putnam 1931; Ritland 1955a, b; Rodgers and Jellison 1942; Slater 1931; Van Dijk 1955.

Snapping Turtle
Chelydra serpentina


© Wayne Lynch

Description: Carapace length up to 47 cm. Carapace with three prominent longitudinal keels, oval in outline with serrated posterior margin. Plastron cruciform (cross-shaped), greatly reduced. Head large, jaws hooked, neck extremely long and bearing numerous warty tubercles. Limbs are powerful and strongly clawed. Tail long, with dorsal crest of paired spines. Coloration generally olive, dark brown or black, with somewhat lighter, often greenish ventral surface.

Variation: As the animals become older the carapace becomes smoother. Skin colour varies from brown to grey. The females are smaller than the males and have a shorter preanal region of the tail. Hatchlings have an almost round carapace, which is 25-30 mm long. There may be a pattern on this, which disappears as maturity approaches.

Natural history: Highly aquatic. Generally prefers standing or slow-flowing waters with soft bottoms and aquatic vegetation. They spend much of their time on the bottom in shallow waters, or floating just beneath the surface. They are generally more active at night. Females generally travel further and occupy larger home ranges than do males. In Montana, snapping turtles hibernate in mud under the water from October to May. They accept a highly varied diet and typically take fish, frogs, crustaceans, reptiles, birds, plants and carrion. They will also eat various types of algae. This is a highly aggressive species which bites and produces a pungent musk as a defence. Snapping turtles do not appear to be strictly territorial, but aggressive interactions may affect individual spacing.

Reproduction: Females mature at eleven to sixteen years in the north-central U.S.A. Mating occurs in spring or early summer and eggs are laid between May and October. From eight to eighty eggs are placed in shallow pits. Incubation temperature of eggs determines sex. Temperatures of 22-28°C produce males, and higher or lower temperatures result in females. In the United States, hatching takes place after approximately four months. Survivorship of eggs and hatchlings is low, but near 100 percent for adults.

Distribution: Introduced in the Battle River area in Alberta. Naturally occurring throughout the eastern United States and parts of southern Canada. In the west, it extends into extreme southwestern Saskatchewan and adjacent north central Montana. It may occur naturally in the Milk River or in creeks to the south of the Cypress Hills.

Remarks: From two to four subspecies of snapping turtles are recognized. Only *Chelydra serpentina serpentina* occurs in northern North America. No specimens confirm the presence of *Chelydra* in Alberta, but Ernst and Barbour (1989) list the range as including the southeastern part of the province. This species may be dangerous to handle but may be safely picked up by the tail if held at arm's length from the body. It is of considerable economic importance, especially in eastern North America, where it forms the basis of most turtle soups.

Significant references: Christiansen and Burken 1979; Congdon et al. 1992, 1994; Dansereau et al. 1958; Ernst and Barbour 1972; Galbraith and Brooks 1986; Galbraith et al. 1987; Hammer 1971; Mosimann and Bider 1960; Obarrd and Brooks 1979, 1981; Pettit et al. 1995; Powell et al. 1997; Raney and Josephson 1954; Sexton 1958; White and Murphy 1973; Yntema 1979.

Rubber Boa
Charina bottae

Description: A small boa, less than 800 mm in total length. Head not set off from neck. Eye small, with vertical pupil. Head scales large and irregular. Chin shields small. Dorsal body scales small, smooth, in 32-53 rows; ventral scales 182-231. Anal plate entire. Subcaudal scales single, 24-43 in number. Tail short and blunt, capped by a rounded plate. Pelvic spurs present in both sexes, but more well-developed in males. Dorsal colour uniform olive green to tan or red brown to dark chocolate brown. Venter yellowish, with or without orange or brown mottling.

Variation: Juveniles pink to tan above, with light yellow to cream venter. There is some sexual dimorphism, with females achieving greater absolute size and maturing at a greater size.

Natural history: This species generally prefers moist coniferous forests and woodlands, but may be found in more open areas where sufficient cover exists. It is found from sea level up to 3,050 m. It is able to climb trees, swim and burrow. The diet consists chiefly of small mammals, which they constrict, but they are also known to take insects, lizards and salamanders. Musk is produced from anal glands.

Reproduction: This species is viviparous. The young are born from September to November. The litter size is two to eight, and young average about 7.5 gm and 220 mm in total length.

Distribution: Known to occur from Quesnel in the interior of B.C. south to the San Bernadino mountains of southern California, and east from the northern California and Oregon coasts to north central Wyoming and south central Montana. The northeastern species range limit appears to be the Continental Divide. Records from the Kootenay River area and Glacier National Park (U.S.) are within fifty kilometres of the Alberta border. If present in Alberta, it is probably restricted to the region between Crowsnest Pass and Waterton.

Remarks: Three subspecies are sometimes recognized. *Charina bottae utahensis* closely approaches the Alberta border.

Significant references: Cunningham 1966; Hoyer 1974; Nussbaum and Hoyer 1974; Rodgers and Jellison 1942; Stejneger 1890; Stewart 1977.

Racer
Coluber constrictor

Description: A moderately long and slender snake, adults 680-1,800 mm in length. Seven to eight supralabial scales, two of which enter the orbit. Anal plate divided. Fifteen to seventeen dorsal scale rows at midbody. Ventrals 158-191, caudals approximately 75. Dorsal coloration pattern uniform or spotted. In the west it is plain brown, olive or bluish above and whitish or pale yellow below, with a white throat.

Variation: Juveniles are generally lighter than adults and exhibit dorsal spots or blotches of chocolate brown on a pale olive background. Females are generally larger than males.

Natural history: Found in wooded or grassland regions. Individuals overwinter in protected areas or dens. The diet consists of small mammals, amphibians, birds, other snakes and insects. Primarily diurnal, but may be active at night.

Reproduction: In the United States, mating occurs in May or June. Fourteen to seventeen eggs are laid in rodent burrows or in purposely dug holes and then buried. The hatchlings emerge in late summer or early fall and are usually about 300 mm in length.

Distribution: Occurs naturally in south central B.C. and ranges to southern California in the west, and to the eastern United States and adjacent southern Canada in the east. It is absent from much of the south west, the northern mid-west and isolated montane regions of the west and north west. Populations in north central Montana approach the Alberta border closely. It may occur in

Alberta south of the Milk River and east of Coutts, although it is not common in adjacent regions of Montana.

Remarks: In the west this species has a similar distribution to *Crotalus viridis* and *Pituophis catenifer.* Two subspecies are recognized in western North America. *Coluber constrictor flaviventris* is the form occurring in central Montana and southern Saskatchewan.

Significant references: Auffenberg 1955; Brown 1973; Brown et al. 1974; Brown and Parker 1974, 1976; Cook and van Zyll de Jong 1975; Corn and Bury 1986; Fitch 1963, 1970; Rodgers and Jellison 1942; Sexton and Hunt 1980; Wilson 1978.

The long-toed salamander (*Ambystoma macrodactylum*), a secretive species found in subalpine and alpine areas of the province from Waterton to the Jasper region.

The blotched tiger salamander (*Ambystoma tigrinum*), a widespread and often locally abundant species of the short grass prairie, aspen parkland, boreal forest and subalpine regions of Alberta south of Edmonton.

The plains spadefoot toad (*Spea bombifrons*), a rarely seen inhabitant of the short grass prairie regions that is seldom active for long outside of its brief breeding period in the spring and early summer.

The western toad (*Bufo boreas*). This species occurs in the mountainous and cooler northern regions of the province and is typically found around ponds, streams, rivers and lakes.

The Great Plains toad (*Bufo cognatus*). This species is limited to the extreme southeastern corner of the province and is restricted to short grass prairie habitats.

The Canadian toad (*Bufo hemiophrys*), a species that is confined essentially to the eastern half of the province, although it avoids the very arid southeastern section.

The boreal chorus frog (*Pseudacris maculata*), a very small, noisy and widespread species that is found abundantly in all regions of the province except for the mountains.

The northern leopard frog (*Rana pipiens*), a once common species in the prairie and aspen parkland regions of the province. Its numbers have declined drastically over recent years and it is the focus of intensive study to try to figure out the reasons for its decline.

The Columbia spotted frog (*Rana luteiventris*). One of the least well-known species of amphibian that inhabits Alberta, it is highly aquatic and is limited to alpine and subalpine regions.

The wood frog (*Rana sylvatica*), a widespread and abundant species throughout the province except for short grass prairie habitats. It is chiefly diurnal and is found in wooded areas or those associated with open ponds. It is largely terrestrial in the non-breeding season.

Eggs of the wood frog (*Rana sylvatica*) on submerged vegetation. Sign such as this, in the spring and early summer, can reveal the presence of amphibians in the area even if the adults are not immediately visible or audible.

The painted turtle (*Chrysemys picta*). This species is severely limited in its natural distribution in the province, occurring only along the Milk River drainage. Other localities may be due to local introductions as the result of pet individuals being released into the wild.

The mountain short-horned lizard (*Phrynosoma hernandesi*), the only lizard found in Alberta. It is limited to the extreme southeastern corner of the province and is found on the faces and the upper margins of south-facing coulee slopes.

The rare western hog-nosed snake (*Heterodon nasicus*). An inhabitant of the arid southeast, its numbers have declined drastically in recent years. The oddly shaped, upturned snout is used in digging.

The largest of the snakes native to Alberta, the bullsnake (*Pituophis catenifer*). It is limited in its distribution to short grass prairie and is found in drier areas of grassland or sagebrush. It is an accomplished climber.

The wandering garter snake (*Thamnophis elegans*), a species widely distributed in Alberta south of 52°N, primarily south and west of the Red Deer River.

The plains garter snake (*Thamnophis radix*). This species is widely distributed south of Cold Lake and is found chiefly in short grass prairie and aspen parkland habitats in the eastern half of the province. It ranges further north than the wandering garter snake.

The red-sided garter snake (*Thamnophis sirtalis*). Although it may occur in all habitat types in Alberta, it is chiefly a resident of the boreal forest and aspen parkland. In the northern half of the province, it ranges the furthest west of the three species of garter snake.

The prairie rattlesnake (*Crotalus viridis*), the only snake found in Alberta that is venomous with respect to humans. It occurs in the drier areas of grassland and sage brush in the short grass prairie regions of the southeast.

A rattlesnake crossing a road in southeastern Alberta. Roads are often favourite places for snakes because they are able to pick up radiated heat from the road surface. Because of this, however, they may also be sites of high mortality as the snakes enter into conflict with traffic.

The shed skin of a bullsnake (*Pituophis catenifer*) that was found among vegetation. Such traces of the presence of reptiles can reveal likely areas for searching for these often rather elusive animals.

A typical short grass prairie scene in southeastern Alberta. Such areas are very warm and dry in the summer and support the greatest diversity of amphibian and reptile life in the province.

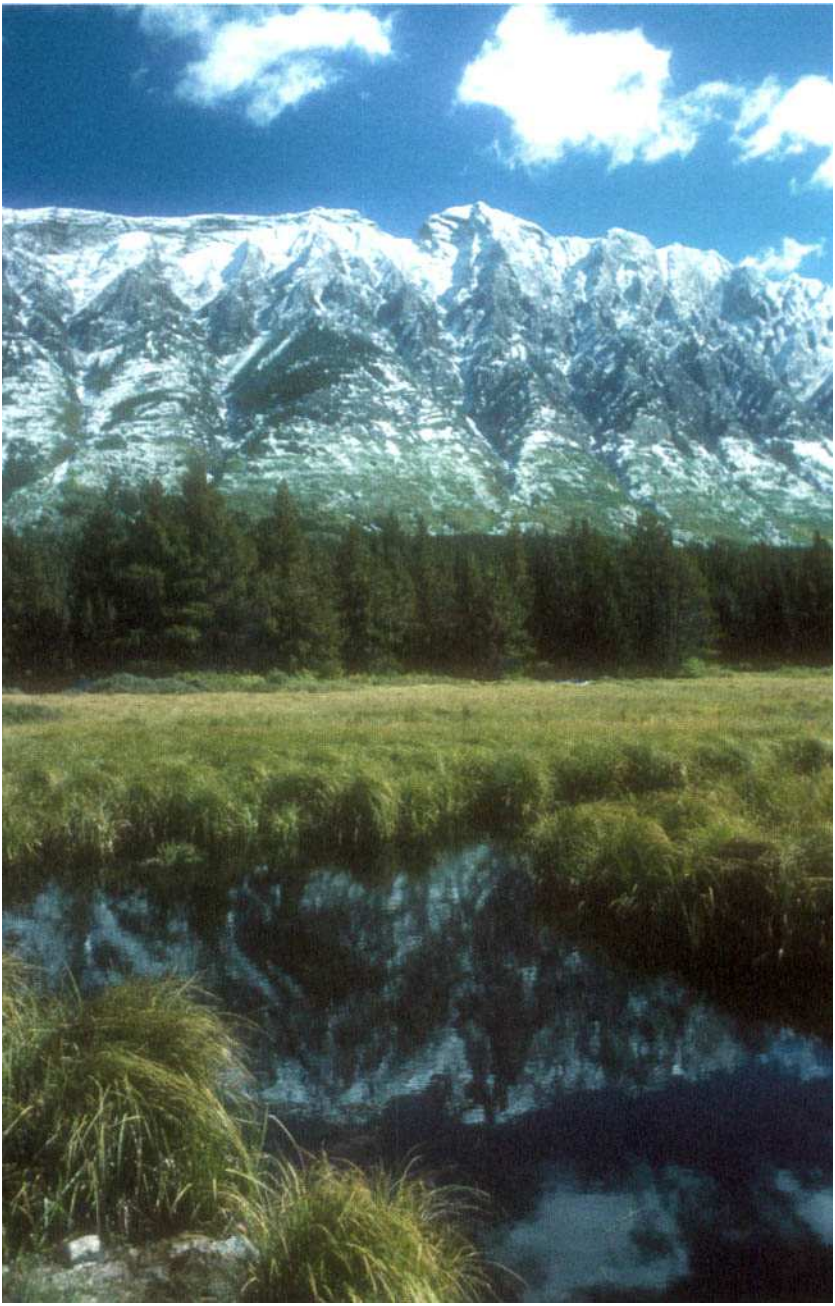
A prairie slough. Such water bodies provide breeding sites for a variety of amphibian species and also are often focal points for garter snakes that forage in and around the water.

Badlands scenery is found in a variety of locations in southeastern Alberta. This picture is of Dinosaur Provincial Park, near Brooks. Badlands provide a variety of habitat from the prairie at the top, through the coulee slopes to the river valleys at the bottom, and are often rich in amphibian and reptilian species.

A typical aspen parkland scene, offering more moderated climates than the prairie regions in the summers and providing homes for a less diverse but often quite abundant herpetofauna.

A view of the Cypress Hills. Straddling the border between southwestern Saskatchewan and southeastern Alberta, this isolated plateau is the only part of the prairies to have escaped the physical ravages of glaciation and harbours relictual populations of a variety of animal and plant species.

A boreal lake in northern Alberta. Such water bodies provide breeding habitat for frogs, toads and possibly tiger salamanders and suitable foraging habitats for garter snakes.



A view of mountainous terrain in southern Alberta. Species such as the long-toed salamander, western toad and Columbia spotted frog breed in water bodies at low to moderate elevations, and red-sided and wandering garter snakes may also be found in such locations.

6 Zoogeography of the Alberta Herpetofauna

THE 661,000 KM^2 OF ALBERTA may be divided into four major biomes (Fig. 6.1). Representative terrain from these biomes is presented in the colour plates. The bulk of the southern quarter of the province (121,000 km^2) falls within the prairie biome. This is a region characterized by relatively low rainfall (approximately 300 mm/year, chiefly in summer) and high summer temperatures. The dominant plants are grasses, with trees restricted primarily to water courses. The far southeast is exemplified by short-grass plains with arid-adapted plants such as sagebrush. Further north and west, mixed prairie with a more diverse and less arid-adapted flora grade into the other biomes of the province.

The base elevation of the prairie ranges from 760 metres in the east to 1,250 metres in the foothills of the Rockies (Fig. 6.2). The topographic relief of the region is relatively low, with sand hills and ridges scattered throughout. The Alberta prairie is drained by a series of rivers flowing in a generally eastward direction (Fig. 6.3). The southernmost river is the Milk, which flows south into the United States. Somewhat further north, the Oldman and Bow Rivers join to form the South Saskatchewan River. At the northern limits of the prairie, the Red Deer River, which has its origin in other biomes, flows to the south and east, exiting the province just north of the South Saskatchewan near Empress. Small streams and drainage channels from the prairie as well as tributaries to the major rivers form deep, often narrow and intricately sculpted gorges and coulees, characteristic of badland topography. These protected passages support a rich flora and fauna and serve as conduits, allowing for the penetration of prairie elements into the parkland to the north. Other coulees may be remnants of pre-glacial river valleys that now incise through the prairie, but no longer serve as major drainage channels.

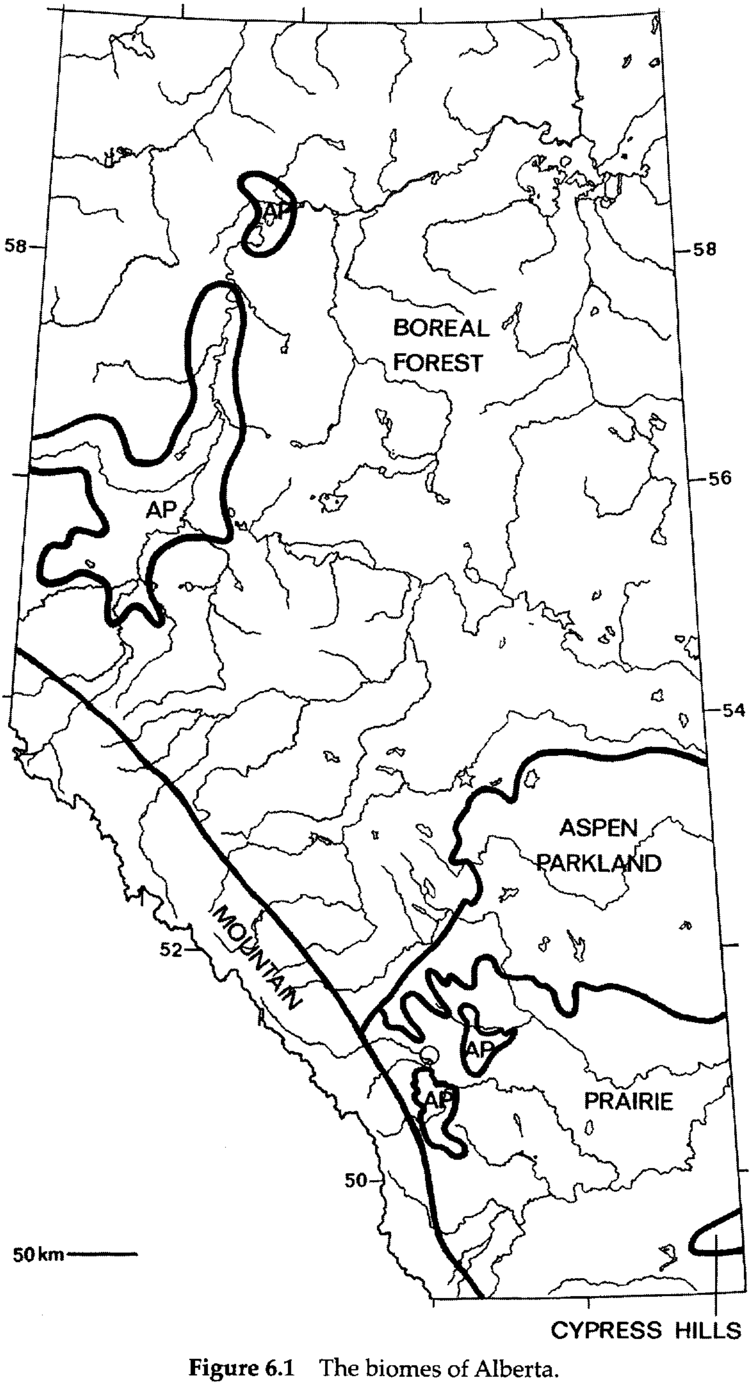


Figure 6.1 The biomes of Alberta.

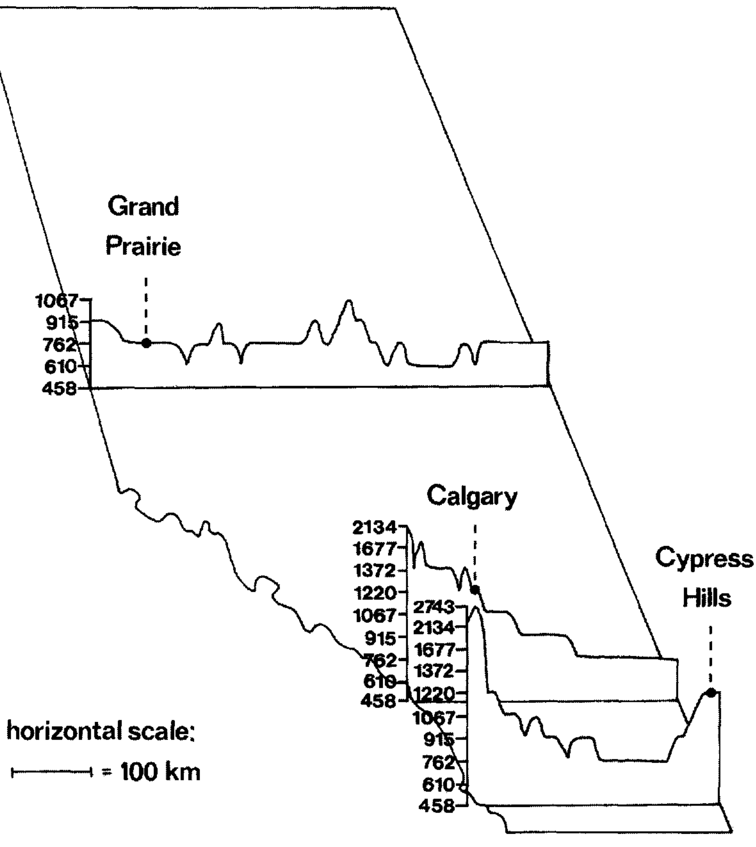


Figure 6.2 Profiles of the elevation of Alberta represented as east-west cross sections through three locations. Vertical scale in metres (above sea level).

To the north of the prairie lies the aspen parkland of Alberta, an ecotone between the prairie and the boreal forest to the north. Small pockets of parkland occur to the south of the main ecotone, to the east and south of Calgary, and to the north along the Peace River. This is a region of mixed grassland and aspen and willow stands occupying 60,000 km^2, chiefly in the eastern part of the province. The region receives 41-46 cm of rainfall per year and has relatively short warm summers and long cold winters, yielding mean annual temperatures of 1-4°C. The parkland, like the prairie, was affected by glaciation, contributing to its relief. This biome covers rolling to hilly land from 720 to 1,640 metres in elevation (Fig. 6.2). The primary river drainage of the aspen parkland is the Battle River, although the Red Deer River also drains portions of the western parkland. Unlike the prairies, the parkland contains many bodies of standing water, including large and small lakes, sloughs and marshes.

The boreal forest (taiga) region covers the vast majority of Alberta, over 400,000 km^2 (more than 60 percent of the entire area). This is a woodland or forested zone, divisible into several components. In the west, at the interface with the Rocky Mountains, transition taiga occurs in the foothills. To the east, in central Alberta, lies the boreal mixed wood zone. In the north of the province lies the boreal subarctic mixed wood zone, flanked east and west by boreal subarctic alluvial lowlands. Each zone is characterized by a different mixture of dominant tree species. In the southern boreal region, the North Saskatchewan drainage flows eastwards into Saskatchewan. The Peace and Athabasca drainages flow north into Lake Athabasca, which itself is drained by the Slave River. The Slave and the Hay River in the northwestern corner of the province flow north to Great Slave Lake. Although elevation rises from 985 to 1,970 metres as the forests enter the foothills, much of the region has low relief (Fig. 6.2), owing to the glacial scouring experienced by northern Alberta. The region is relatively moist (400-600 mm/year) and experiences long cold winters and short cool summers.

The last of the major biomes of Alberta is the Rocky Mountains proper. Reaching a maximum elevation of 3,747 metres at Mt. Columbia, the great elevational range and the associated vagaries of direction of slope face and local microclimate combine to make the mountains a vegetationally diverse region. Only at the highest elevations do coniferous and/or deciduous forests give way to treeless alpine tundra. Many of the major rivers of the province take their origin in the Rockies, most being derived ultimately from snow melt. Typically the headwaters flow eastward to water the other biomes of the province. The climate is cool and winters are exceptionally long (125-155 frost-free days). While some areas may receive reasonable amounts of rain, most moisture is derived from winter precipitation.

In addition to the four major biomes outlined above, a small region of Alberta's southeast, the Cypress Hills, may be classed as a separate biome of its own. The Hills occupy about 900 km^2 in Alberta and an additional 1,680 in Saskatchewan. They are actually a plateau, with its highest point at 1,580 metres at the western edge. Although they lie within the dry prairie belt, the higher elevation of the Cypress Hills yields a cooler temperature and higher rainfall than the surrounding plains. The hills support coniferous and deciduous forest. While only the very summit was not covered by glaciers in the past,

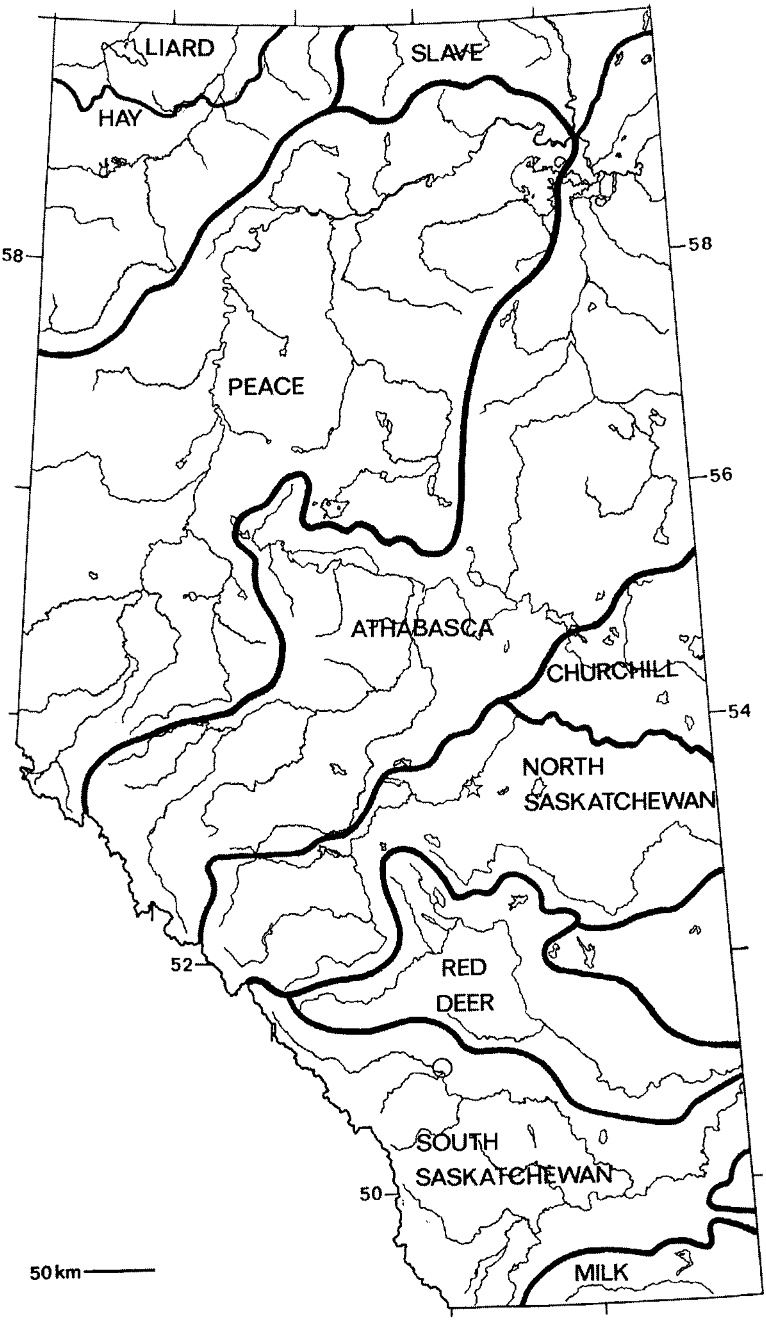


Figure 6.3 Major drainage basins of Alberta.

the Cypress Hills seem to have preserved faunal and floral elements reflecting earlier ties to the Rockies via a now-defunct forest belt.

The divisions between the various biomes are not precise: overlap occurs and pockets of one type may be found within another. The biomes themselves are defined by the vegetation they support but are determined by a combination of existing and historical factors, primarily geological and climatic. The area that is now Alberta was mostly or entirely submerged beneath a series of encroaching embayments and epicontinental seas throughout long periods of its history. During the Devonian (408-360 million years before present—mybp) and Cretaceous (144-65 mybp) very little of the province was emergent. During the latter period, the chief episode of mountain building resulted in the upthrust of the Rocky Mountains, which continue to rise, move and change shape. During the Cretaceous, as for much of its history, Alberta enjoyed a mild or even tropical climate. Under these conditions, the province was able to support the impressive dinosaur fauna that is so familiar to most Albertans. Later, during the Oligocene (37-24 mybp), the Cypress Hills supported a subtropical herpetofauna with relatives of existing species including *Ambystoma* and *Spea*, but also boas, amphisbaenids and crocodylians.

During the late Pleistocene (ca. 35,000 ybp) Alberta became affected by glaciation. A series of glacial and interglacial periods had characterized the preceding 965,000 years, but had not directly impacted upon this region of Western Canada. During the most recent glacial period, all of Alberta, except the higher elevations of the Rocky Mountains and the summit of the Cypress Hills, was covered by ice. The final retreat of the glaciers began approximately 12,000 ybp. Essentially all vegetation in Alberta, and all animals as well, were wiped out or pushed far to the south during the glacial periods. Consequently, present distributions of the biota, including amphibians and reptiles, have been determined only within the relatively short time since the retreat of the ice sheets. For the herpetofauna, the time is shorter still, since most species would not have been able to occupy the newly ice-free environment until after vegetational communities and arthropods had reestablished themselves. Further, lower temperatures near the retreating edges of the glaciers would have left an ever-moving buffer zone not immediately suitable for occupation by poikilothermic (cold-blooded) vertebrates.

The southern and eastern portions of the province have been free of the glaciers longer than the north and the mountains. It is this region, corresponding to the prairie biome, that has the warmest temperatures and lowest rainfall, and it is this region in which amphibians and reptiles are most diverse (Table 6.1). This diversity is expressed to its fullest in the short-grass plains of the southeastern corner of Alberta, and it is here that one finds those species that are typically arid-adapted. The richness of this region is reflective of the herpetofauna of adjacent regions of the United States. The arid and semi-arid states of the Rockies and northern Great Plains are the major source areas for Alberta amphibians and reptiles, and taxa that have reasonably wide tolerances have been able to move as far north as the prairies of the province. Species that occur elsewhere in Alberta tend to be extreme generalists, or cool- / moist- adapted animals that may have moved into Alberta along a western, mountainous corridor or that followed the retreating glaciers northward, remaining in a cooler climatic belt, such as the modern boreal forest.

Of the reptiles, seven of the eight species occur within the prairie region. Three of these, *Chrysemys picta, Phrynosoma hernandesi* and *Heterodon nasicus* are absolutely restricted to this region and the low elevations of the Cypress Hills. In addition, *Pituophis catenifer* and *Crotalus viridis* extend out of the prairies only marginally, and may be considered as typical prairie species. The remaining reptile genus, *Thamnophis* (the garter snakes) is widely distributed throughout the province. Each of the three species, however, is centred in a different region (Fig. 6.4). *Thamnophis radix,* which reaches its western limit in Canada in Alberta, is centred in the prairie region but extends northward to the aspen parkland (it is marginally distributed in other biomes). *T. elegans* is also found chiefly in the south, but is more common than *radix* in the mountainous west. Its distribution in the north is poorly documented, but it seems to be largely absent from the boreal forest, where it is replaced by *Thamnophis sirtalis,* a chiefly northern, cool-adapted form. This last species is the only reptile species in Alberta that is not typical of the prairies. Indeed, most aspects of its biology (see pp. 110-113) are those of an animal specialized for surviving and reproducing in very cold regions with short activity seasons.

Two species of Alberta amphibians are restricted to the prairies only: *Spea bombifrons* and *Bufo cognatus.* Both species require sandy soil for burrowing, intermittent periods of heavy rainfall and high summer temperatures for successful breeding, conditions generally only met in the south of the province. The two remaining species of *Bufo* are generally absent from the prairies but segregate to some extent in the other biomes (Fig. 6.5). The western toad, *B. boreas,* occurs in the aspen parkland, boreal forest and mountain regions. In general, it is most common in the western parts of the province. The Canadian toad, *B. hemiophrys,* is chiefly an eastern species and, like *Thamnophis sirtalis,* is a northern specialist.

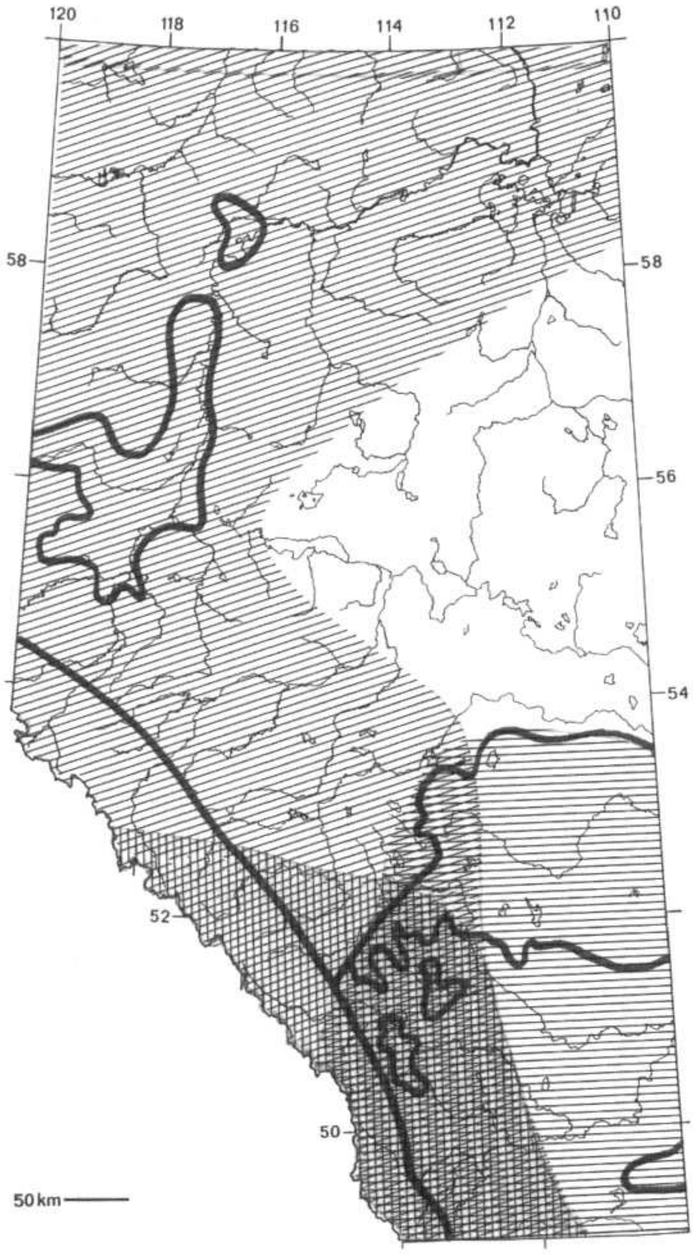


Figure 6.4 Distributional patterns of the three species of garter snake native to Alberta, showing areas of overlap and areas of exclusivity. Diagonal lines: *Thamnophis sirtalis;* vertical lines: *T. elegans;* horizontal lines: *T. radix.* The heavy black lines represent the outlines of the biomes (see Fig. 6.1).

Ambystoma macrodactylum and *Rana luteiventris* are largely restricted to the mountains, the former species having recently been found at lower elevations in the vicinity of Fairview. In many respects, the environmental conditions here are similar to those of higher elevations further to the south. Their habitat preferences are for cooler waters, and they are representatives of montane groups that occupy high elevations throughout western North America. Within the mountains, several aquatic habitat types, differing in water temperature, depth, permanence and flow rate, occur, and the specific distributions of these and other amphibians that reach the Rockies are determined by these microhabitat differences. Tiger salamanders, *Ambystoma tigrinum*, are chiefly animals of the prairies and aspen parkland. This species reaches the borders of the Rockies and has scattered populations in the boreal forest. Typically, this species occupies burrows, so the soils of the south are particularly suitable for it. Its distribution in the north is confused somewhat by the availability of artificial breeding sites (e.g., dugouts) and the artificial introduction of larvae as bait by fishermen. *Pseudacris maculata* does not occur at high elevations, but is common throughout the rest of the province, from the prairies to Lake Athabasca. It is a widespread species in much of North America and has broad tolerance levels. It appears to be able to utilize ponds or marshes wherever they occur. Northern leopard frogs, *Rana pipiens*, have declined in Alberta, but were formerly common chiefly in the prairie regions and the Cypress Hills. Records, however, are scattered as far north as the border of the Northwest Territories, but the distribution in the north of Alberta is poorly understood and needs to be investigated more thoroughly. Finally, *Rana sylvatica* is a non-prairie form. Like some of the previously mentioned taxa, it is a cool-adapted specialist and is even able to withstand freezing of its body fluids. It occurs in all of the remaining biomes, and its presence in the region of the Cypress Hills illustrates the early post-glacial connection to the west described above.

The species discussed in Chapter 5 as forms which might occur in Alberta would divide into two distributional categories. The snapping turtle and racer both represent southeastern forms, which could only enter the province through the grassland regions of Montana. These would be prairie-restricted species. The tailed frog and rubber boa, however, are western species, whose only corridors into Alberta would be via the Rocky Mountains of British Columbia or western Montana. The requirement for cool, forested regions would most likely limit both to the mountains of the province.

The most important features of the biomes, from the point of view of amphibians and reptiles, are generally the parameters of

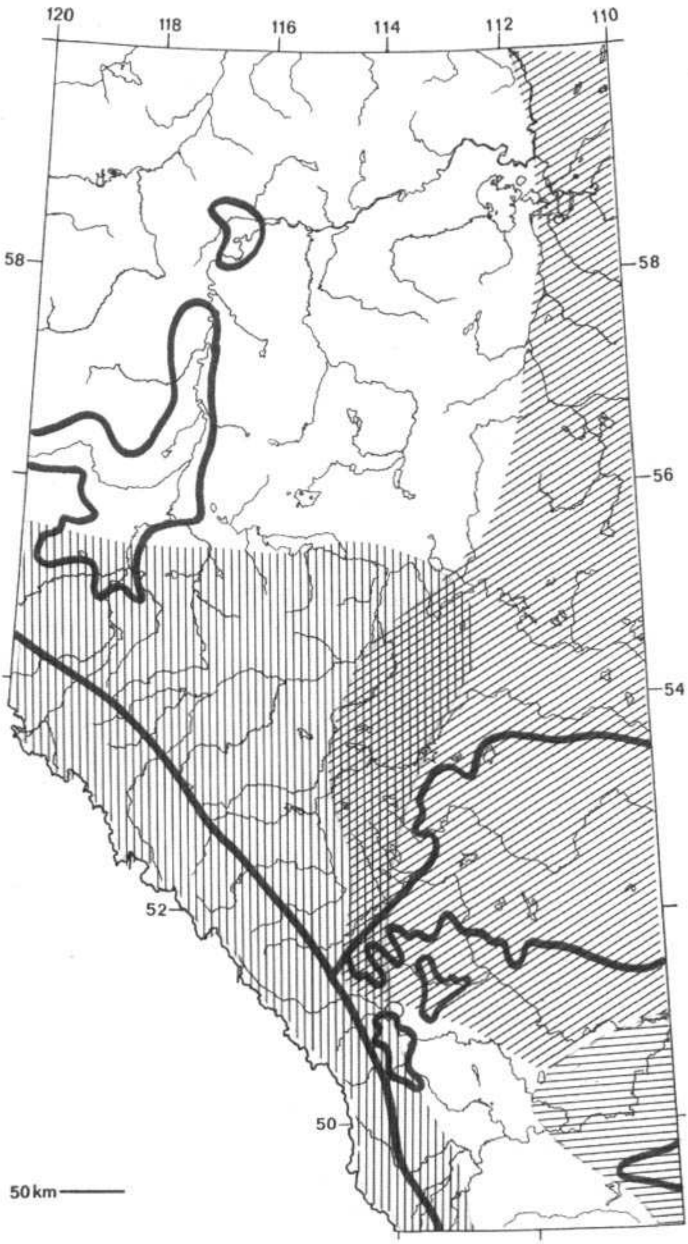


Figure 6.5 Distributional patterns of the three species of true toads native to Alberta, showing areas of overlap and areas of exclusivity. Diagonal lines: *Bufo hemiophrys;* vertical lines: *B. boreas;* horizontal lines: *B. cognatus.* The heavy black lines represent the outlines of the biomes (see Fig. 6.1).

temperature and water availability. These determine the distribution of animals via the stresses they place on their physiology and breeding. Biotic features of the environment, such as food availability and predator density are also important but are secondary rather than primary determinants of distribution, establishing how successfully the animals can cope within the absolute limits established by the abiotic factors. The means by which amphibians and reptiles are able to cope with both the abiotic and biotic demands of their environments are discussed more fully in Chapters 7, 8, and 9.

Significant references: Alberta Energy and Natural Resources, Fish and Wildlife Division 1984; Braithwaite 1970; Brode and Bury 1984; Cook 1964a; Gorham 1957; Hardy 1967; Harper 1931b; Holman 1972; Hovingh 1986; Lewin 1963a; Longley 1972; Minister of Supply and Services, Canada 1986a, b; Russell and Bauer 1991; Savage 1973; Schall and Pianka 1978; Shmida and Wilson 1985; Williams 1946.

TABLE 6.1. DISTRIBUTION OF ALBERTA AMPHIBIANS AND REPTILES BY BIOME.

	Prairie	Aspen Parkland	Boreal Forest	Rocky Mountain	Cypress Hills*
Amphibia					
Ambystoma macrodactylum		P		•	
Ambystoma tigrinum	•	•	P	•	
Spea bombifrons	•				
Bufo boreas	P	•	•	•	
Bufo cognatus	•				
Bufo hemiophrys	P	•	•		
Pseudacris maculata	•	•	•	P	•
Rana pipiens	•	•	•	P	•
Rana luteiventris				•	
Rana sylvatica	P	•	•	•	
Total, *Amphibia*	5	6	5	5	2
Reptilia					
Chrysemys picta	•				
Phrynosoma hernandesi	•				•
Heterodon nasicus	•				•
Pituophis catenifer	•		P		P
Thamnophis elegans	•	P	P	•	
Thamnophis radix	•	•	P	P	P
Thamnophis sirtalis	P	•	•	•	
Crotalus viridis	•	P			P
Total, *Reptilia*	7	2	1	2	2
Overall totals	12	8	6	7	4

• = present;
P = peripheral.

Since the Cypress Hills region is rather small and has not been well-studied, it may be under-represented in terms of the species recorded.

7 Amphibian and Reptile Natural History

REFERENCE TO THE SPECIES accounts in Chapter 5 clearly indicates that amphibians and reptiles interact with a wide variety of vertebrates and invertebrates in relation to trophic dynamics. The herpetofauna thus plays a key role in the food webs of a variety of communities (Fig. 7.1). Indeed, amphibian and reptile consumption of insects and rodents, respectively, may be far greater than generally appreciated. Likewise, amphibians, especially, contribute a significant resource base for both terrestrial and aquatic predators. A single species of amphibian will participate in at least two community trophic relation systems. Tadpoles are generally herbivores and occur in huge numbers, constituting a seasonally significant proportion of the primary consumer biomass. As insectivorous adults, they may participate in either aquatic or terrestrial trophic assemblages, or both. Most reptiles, which generally have fewer offspring and lower mortality than amphibians, are insectivorous or carnivorous and are more significant as secondary or tertiary consumers in food webs. Although reptiles interact primarily in the terrestrial environment, some species, including turtles (which may be partially or entirely herbivorous) and snakes such as *Thamnophis*, may feed in aquatic situations.

Two factors make amphibians and reptiles especially important elements in trophic relation systems in Alberta and elsewhere. First, despite the fact that they are rarely seen, these animals may constitute a huge biomass. In a variety of habitats throughout North America, the total biomass of amphibians per unit area has been shown to exceed that of birds and mammals combined. In Alberta, this may well be true of many of the more mesic (moist) habitats, where every year billions of frog eggs are laid. Reptiles, though less fecund, may also be extremely numerous. This may be demonstrated by reference

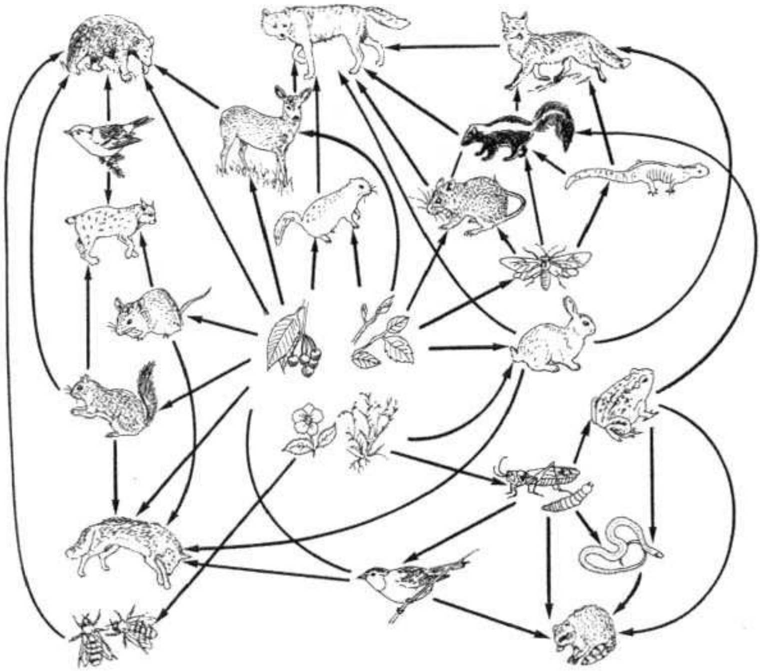


Figure 7.1 Stylised food web of animals of Alberta.

to the dens of *Thamnophis*, where thousands of individuals may congregate to overwinter. Secondly, because they are poikilothermic (see Chapter 8), amphibians and reptiles require far less energy to grow and reproduce than do birds or mammals of equivalent size. Thus, relative to other terrestrial vertebrates, they contribute a disproportionate amount of useable energy to the food web. Food-web maintenance is important in any habitat type. However, disruption of fragile systems—such as deserts, where the number of organisms at any trophic level can be relatively small—may be particularly devastating. The richest herpetofauna in Alberta occurs in the semi-arid southeast, which is in just such a delicate balance. For this reason, the recent decline of certain Alberta species such as the hog-nosed snake and northern leopard frog, is especially disturbing.

The size and general demography of amphibian and reptile populations in Alberta are not well known. In general, populations are dispersed for most of their activity periods and only congregate, if at all, for overwintering or short periods of breeding. This aspect of the herpetofauna makes it especially difficult to study characteristics of population ecology. From what is known from other regions of North America, it would seem that individuals have rather low vagility (capability of dispersing) and the geographic area covered by a population is probably quite small for most species. Gene flow is therefore restricted, and total population size is modest. The extent of genetic exchange between adjacent populations is unknown, but in the case of species such as the short-horned lizard, which occupies a discontinuous habitat, it may be minimal. Many species exhibit periods of "programmed" dispersal which may serve to ensure some genetic interchange between populations, but the extent of this phenomenon among Alberta amphibians and reptiles is unknown. Such dispersals may take place in the juvenile stage or, as in some turtles, may be carried out by females in search of egg-laying sites. The Alberta taxa are typically widely distributed throughout central and / or western North America, suggesting that gene flow sufficient to maintain species cohesiveness does occur. However, the populations in our province are often at the northern edge of their range (only *Rana sylvatica* extends much further north and only *Bufo hemiophrys*, the Canadian toad, is centred around our latitudinal band) and run the risk of losing contact with the main body of the species and becoming peripheral isolates. This may have occurred in the case of the Canadian toad, which has close affinities to *Bufo americanus*, a species typical of eastern North America. It may have speciated quite recently in association with environmental changes and geographic isolation brought about by glacial movements.

For any species, the ability of individuals to recognize conspecifics as potential mates is essential to the maintenance of cohesiveness. Certain features of general ecology, such as habitat preference and activity pattern, serve to segregate species and maximize the chance of mate encounter. Beyond this, however, specific behavioural traits allow specific recognition to be established. In salamanders, such as *Ambystoma*, fertilization is internal, and a complex pattern of species-specific courtship movements must be performed by the male in order to entice the female to accept his spermatophore. Pheromones (hormones that act between individuals) also play a role in salamander courtship, especially in those forms with terrestrial mating. In frogs, specific patterns of vocalization serve as the primary premating isolating mechanisms. Females respond preferentially to the call of conspecific males and may even gather information about age or size, and thus fitness, from these mating calls. Once in proximity, females are grasped by males and held in amplexus (pectoral or pelvic embrace that ensures correct placement of the male and female cloacae for fertilization to occur). In frogs and many other amphibians and reptiles, there may be pronounced sexual dimorphism, with either males or females achieving greater size (Fig. 7.2).

Large female size is often attributed to the greater reproductive output of this sex and the additional space required for gamete production and egg/embryo storage. Larger male size is often related to sexual selection and predominates in species that are territorial or in which competition for mates occurs. Dimorphism may also relate to non-reproductive parameters, such as differences in the diet of males and females. (See species accounts in Chapter 5 for information about dimorphism in Alberta species.)

Fertilization in reptiles is always internal and usually involves copulation. As in salamanders, reproduction in reptiles also involves complex behaviours that maximize the likelihood that only intraspecific matings will occur. *Chrysemys picta* males use their elongate claws in a courtship ritual (Fig. 7.3) and most snakes employ species-specific stereotypical behaviour in conjunction with pheromonal communication in mating. All terrestrial reptiles in Alberta congregate in winter dens or hibernacula. Mating usually occurs early in the active season, just as animals are leaving their winter dens. This timing takes advantage of the proximity of individuals and removes the difficulty faced by solitary individuals in locating a mate. Reptiles at dens and amphibians at ponds have high site-fidelity and are able to use a variety of biotic and abiotic clues to locate these gathering places year after year. Females of some species, including *Thamnophis sirtalis* in Alberta, are able to store sperm and delay fertilization—in the event of a season in which no mating is achieved, successful reproduction could still occur.

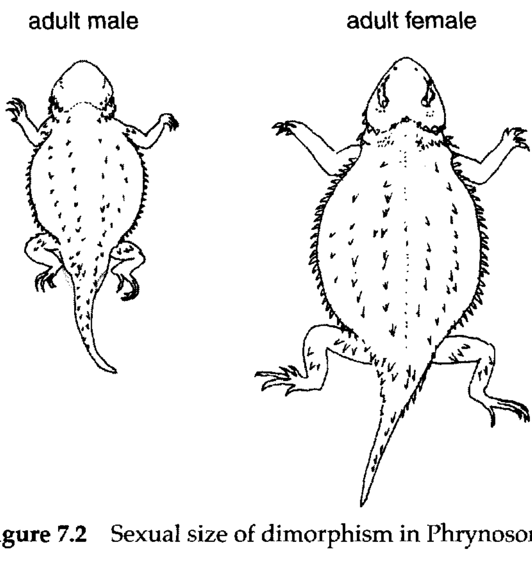


Figure 7.2 Sexual size of dimorphism in Phrynosoma.

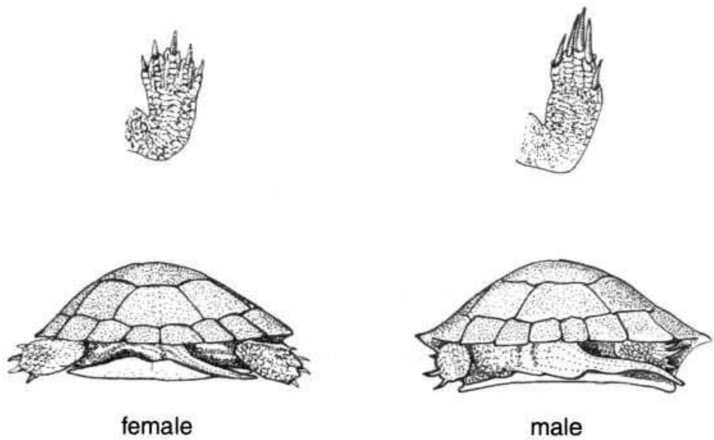


Figure 7.3 Sexual dimorphism in Chrysemys picta.

The ecology of the Alberta herpetofauna cannot be fully understood without giving special consideration to the complex life history of amphibians. Larval amphibians constitute a truly distinctive life form. Their biology is almost wholly separate from that of the adults. Larval amphibians cannot be described as "poor tetrapods," nor likened to fish. Like all larvae, they exist to feed, grow, and accrue the energetic reserves necessary for metamorphosis into the adult form. Most tadpoles (and some salamander larvae) have relatively short pre-metamorphic lives which correspond to a period of high algal or prey productivity. Thus, in Alberta, the warm, rainy early summer is the prime time to find most larval amphibians. The necessity to match the larval period with peak productivity accounts for the early breeding of many species, in some cases even as the snow is beginning to melt. All Alberta amphibians lay eggs in an aquatic environment. These vary from species to species in size, shape and type of gelatinous coating. The eggs themselves may be laid singly or in strings or clusters (see Chapter 5). Because they are not guarded by the parents, eggs run a greater risk of predation and destruction due to environmental fluctuations. Pigmentation of the embryo or its coating may shield it from excessive solar radiation. The shape of the egg mass may promote gas exchange, or in some cases, symbiotic algae resident in the egg may provide oxygen to the developing embryo. Hatching is triggered by temperature, p*H*, and especially oxygen availability. Hypoxia appears to be the proximal signal that initiates the production of enzymes used to break down the vitelline membrane and egg capsule in those species that have been investigated.

Both salamander larvae and frog tadpoles possess large guts, suitable for the processing of copious amounts of food or filtrate (Fig. 7.4). Their mouthparts are specialized for ingestion in the dense aquatic medium. Typically, salamander larvae employ "gape and suck" feeding mechanisms, whereby relatively large prey items are rapidly drawn into the mouth via a complex negative-pressure system. In this type of feeding, a column of water containing the prey is drawn into the pharynx, where gill rakers strain out the solid material, allowing the fluid to pass out of the body via the gill slits. Frog tadpoles tend to employ less spectacular feeding modes. Some types filter large quantities of detritus across their gills, removing tiny particles of digestible material. This is a rather indiscriminate approach to nutrition, with the animal selecting out valuable items only after ingestion. Water taken in with the food is expelled through the spiracle, the common opening of the internal gill chambers. Other tadpoles feed on algae or carrion which is scraped away by their horny teeth. These teeth are unrelated developmentally and evolutionarily to the true adult teeth. Their patterns are typically complex and are used as key features in the identification of larval specimens (see Chapter 5).

Just as the feeding mechanisms of larvae are related to the aquatic medium, so are their modes of locomotion. The chief device for producing thrust in swimming is the tail. In salamander larvae, both the tail and body are thrown into S-shaped undulatory waves which pass posteriorly, generating thrust as the tail fins and lateral surfaces of the animal are pushed against the water. The globular body of frog tadpoles, however, precludes its incorporation into the generation of propulsive waves. Rather, the tail alone sweeps or sculls to move the animal. Salamander larvae, which develop limbs relatively early in ontogeny, are also able to walk on the substrate, but rely on lateral undulation for any rapid locomotion.

All larvae will attempt to swim away from danger, but their speeds are slow when compared to those of many predators, which include fish, aquatic insects, snakes and other amphibians. Many forms have evolved noxious or even poisonous skin toxins to deter predators (see Chapter 10). At least some tadpoles are able to warn their siblings, and in some cases other species, of danger. Larvae that have been wounded by a predator release "Schreckstoff," a chemical alarm substance, into the water. Its effect is to cause the other members of the school to flee. Chemical communication, which is highly effective in water, is also used to regulate coordinated schooling behaviour in tadpoles. Amphibian larvae also obtain information about their surroundings via the lateral line system, a series

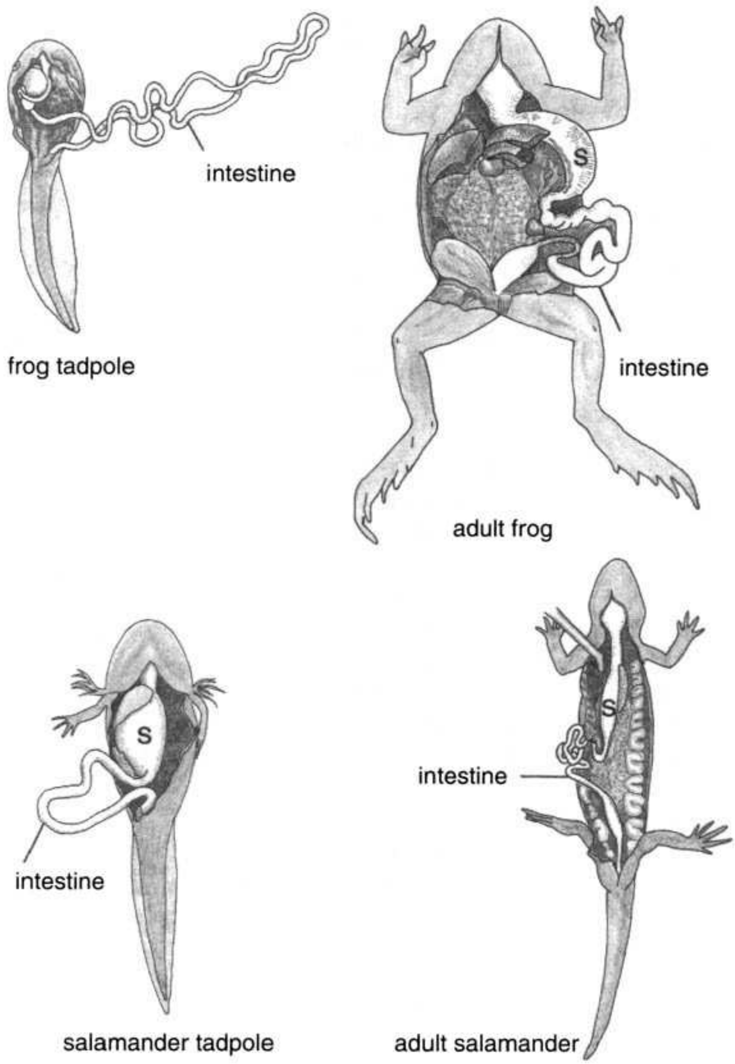


Figure 7.4 Relative length of the gut in tadpoles and adults of Alberta amphibians. S = Stomach.

of mechanoreceptors sensitive to vibration and angular displacement. The system may also have electroreceptive capabilities useful in detecting prey. These receptors are similar in construction to the receptors of the inner ear of all vertebrates. During metamorphosis the lateral line system degenerates, as it cannot function in air, and is therefore unnecessary for the chiefly terrestrial adult amphibian.

Larvae are prone to heavy predation, as their period of activity is also the period of peak predator activity (Fig. 7.5). They also suffer high mortality as vernal ponds dry up or other conditions become unfavourable. Competition and food availability also place constraints on populations. In such unstable environments, where no parental care exists, it is necessary that huge numbers of larvae be produced so that a few may survive. This strategy, typical of most amphibians, is referred to as *r*-selection. Here, relatively few resources are devoted to each egg, and successful reproduction is based on the statistical probability that at least some offspring will survive long enough to reach breeding age themselves. Mortality for most amphibians is high in all stages from egg to metamorphosis. In contrast, in *K*-selection, in which parental care often occurs, few offspring are produced and investment in each is high, yielding low mortality. This strategy is widely employed by birds and mammals and also characterizes some reptiles and salamanders. In some cases *K*-selected reptiles (and some amphibians) give birth to live young (viviparity). In this reproductive mode, parental investment is extremely high. Although little or no care may be given after birth, the retention of the embryos within the female's body provides protection, thermal stability, and in some cases nutrition. This is provided at a cost to the female, whose locomotor abilities may be compromised by the additional burden of the developing young. Viviparity is especially common at high latitudes and elevations. In Alberta, *Phrynosoma hernandesi*, *Crotalus viridis*, and all species of *Thamnophis* are live-bearers.

Some larval habitats, such as the vernal ponds occupied by spadefoot toads or the dugouts in which tiger salamanders may be found, are very poor in food resources and, in the former instance, may be exceptionally short-lived as water bodies. Under these highly stressful conditions, some species, including the two mentioned above, have adopted cannibalism as a strategy for success (Fig. 7.6). In these larval populations, those individuals which begin to grow the fastest inhibit the growth of their siblings and begin to develop modified mouthparts, suitable for the ingestion of vertebrate prey. These cannibal-morphs are thus insured access to a rich food resource and can further speed their own development. In this way, the genetic stock as a whole benefits at the expense of particular individuals. This is a manifestation of the more general phenomenon of density-dependent survivorship, in which larvae maintained at lower densities experience lower mortality than those at high densities.

Alternatively, some amphibian larvae may extend their premetamorphic growth through the phenomenon of paedomorphosis (see

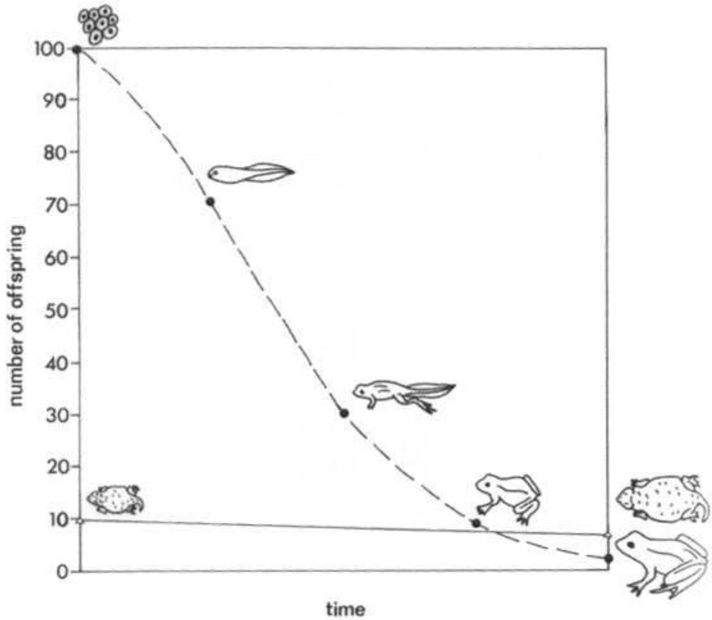


Figure 7.5 Relative survivorship in *r*-selected (frog) and *K*-selected (short-horned lizard) species.

Chapter 2) to take advantage of abundant resources when they are available. This is especially common in salamanders, which may even mature sexually and breed while maintaining the larval body form. In frogs, larval life may be extended over several years, but reproduction as a tadpole is not possible. The extension of larval life to encompass several growing seasons is one way in which amphibians may overcome the barrier to northern colonization imposed by the short productive period of high latitudes. This is but one facet of the plasticity exhibited by larval amphibians with respect to timing and rate of growth and differentiation.

The process of metamorphosis is extremely complex and involves a shift from a period of rapid larval growth to a period of anatomical (Fig. 7.7) and physiological reorganization. It incorporates the regression of larval features, the transformation of larval features into adult and the development *de novo* of certain adult characteristics. In frogs, the most obvious changes involve the reduction of the tail and the growth and differentiation of limbs. The feeding apparatus changes as well, shifting to a lingual prehension mechanism in which the tongue grasps prey items in a non-aquatic medium. Likewise, the gills regress and lungs take over respiratory function in

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Figure 7.6 A large tadpole of a spadefoot toad in a temporary pool, Writing-on-Stone Provincial Park.

conjunction with the highly vascularized skin, which itself changes radically, developing multicellular mucous and poison glands. With the change of respiratory organs come changes in the blood-flow patterns of the major vessels. The gastrointestinal tract becomes shorter as the animal's diet shifts from plant material requiring extensive breakdown, to more easily digestible arthropod prey (Fig. 7.4). Its relative proportion also decreases as gonadal growth is initiated in preparation for the adult's reproductive activities. Physiological changes involve the shift of haemoglobin type and other biochemical shifts in the excretory system to accommodate terrestrial life. Salamander metamorphosis is somewhat less spectacular, as the larvae rather closely resemble adults. Nonetheless, gill regression and changes in morphological and biochemical aspects affect all organ systems.

The changes involved in metamorphosis are tightly integrated and are under hormonal control (Fig. 7.8). The onset of metamorphosis is triggered, via hormonal mechanisms, by environmental factors such as pond drying. Larvae are thus plastic in this regard, but eventual survivorship, adult size and fecundity may be correlated with the time at which metamorphosis occurs. In general, animals that undergo metamorphosis earliest are larger at first reproduction and may have greater genetic fitness. However, fecundity in both amphibians and reptiles is also influenced by latitude, elevation, and

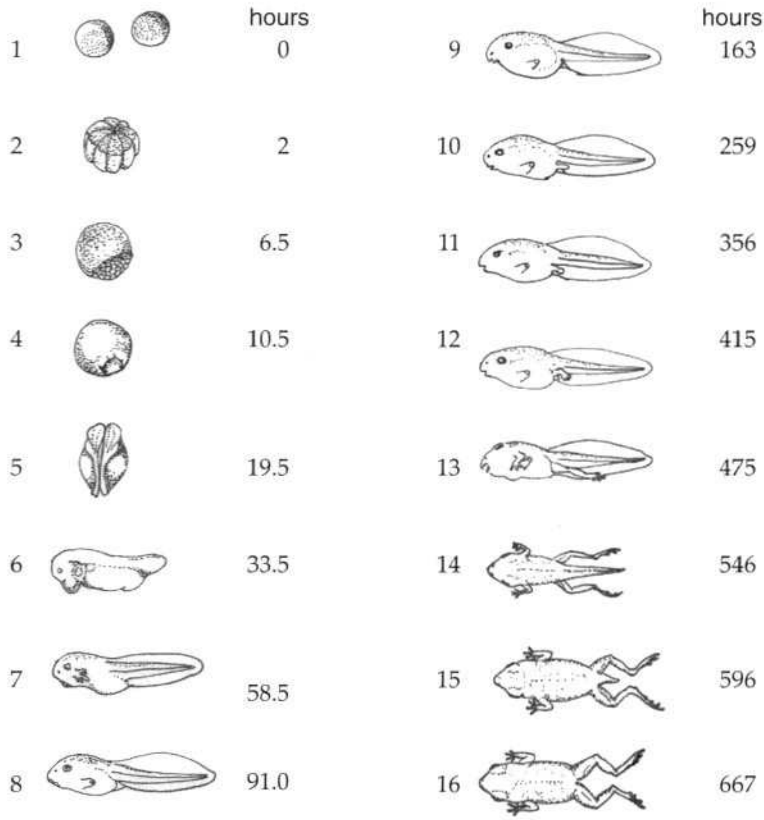

Figure 7.7 Staged metamorphosis of a frog.

nutritional state. The hypothalamus and pituitary ultimately regulate and coordinate all of the hormonal changes that typify metamorphosis. Much of the proximal direction of differentiation is mediated by the thyroid, which produces thyroxin and triiodothyronine. The levels of these hormones rise sharply during metamorphosis, promoting differentiation. Metamorphosis may be considered as consisting of three stages, pre- and pro-metamorphosis and climax metamorphosis. Thyroid hormone levels rise during prometamorphosis and plateau during climax, when most changes in body form and function actually occur.

Metamorphosis is a particularly hazardous time for amphibians as they pass through a period during which they do not function particularly well in either water or on land. At this stage, they are less efficient at avoiding predation than are either larvae or adults. Fortunately, the metamorphic changes occur rapidly and the

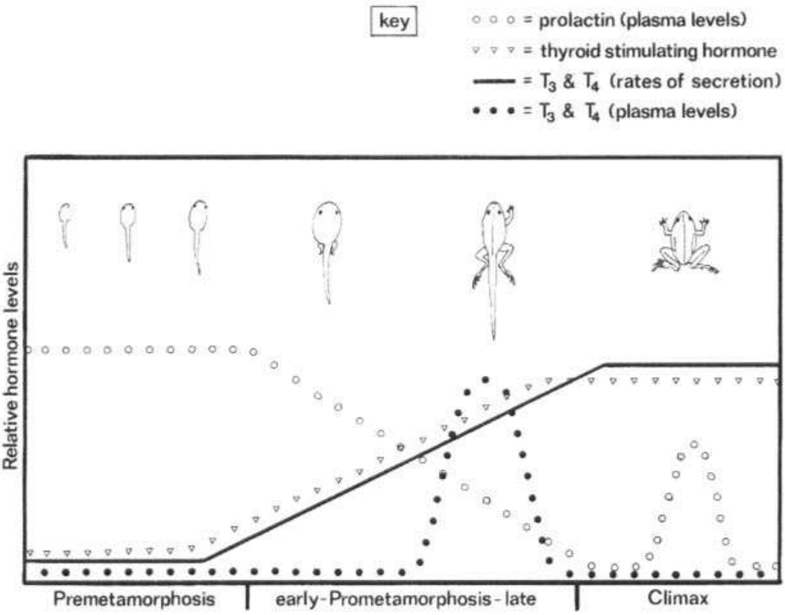

Figure 7.8 The relationship between hormone levels and stages of metamorphosis in a typical amphibian.

animals are able to suspend many activities, such as feeding, until the switch to the adult body form has been accomplished.

Significant references: Ariizumi and Asashima 1995; Aleksiuk 1976b; Allen 1938; Altig and Christensen 1976; Altig and Johnston 1986; Altig and Tohoefener 1980; Anderson and Graham 1967; Anderson et al. 1971; Angelini and Ghiara 1984; Arnold 1976, 1977a, 1980; Arnold and Houck 1982; Arnold and Wassersug 1978; Bachmann et al. 1986; Bellis 1961; Bauerle 1972; Bogert 1960; Boisseau and Joly 1973; Brode and Bury 1984; Brown and Taylor 1995; Bruce et al. 1994; Brunkow and Collins 1996; Burggren and Infantino 1994; Burton and Lickens 1975; Bury et al. 1991; Cagle 1944, 1953, 1956; Carpenter 1952b, 1956; Clark and Gibbons 1969; Cocroft and Ryan 1995; Congdon and Gibbons 1987; Congdon et al. 1982, 1986; Cook 1987; Cortwright 1988; Delidow 1989; Dodd and Dodd 1976; Duellman 1985; Dupree and Petranka 1985; Feder 1981; Feder and Lynch 1982; Feder et al. 1982; Fitch 1970; Formanowicz and Brodie 1982; Gerhardt et al. 1989; Gibbons 1976, 1982, 1987; Gibbons and Semlitsch 1982; Gibbons and Smith 1968; Gibbons and Tinkle 1969; Goin and Goin 1962; Gosner 1960; Greene 1983; Gregory et al. 1987; Gross and Shine 1981; Heyer 1976; Hoff et al. 1985, 1989; Holomuzki 1989; Holomuzki and Collins 1987; Huey and Kingsolver

1989; Jameson 1955; Jones et al. 1999; Keen et al. 1983; Kenny 1969; Kephart and Arnold 1982; Lannoo 1986; Lannoo et al. 1989; Lauder 1985; Lawler 1989; Licht and Bogart 1989a, b; Malvin and Heisler 1988; Marchisin and Anderson 1978; Morin 1983; Naitoh et al. 1989; Noble 1927; Noble and Schmidt 1937; Nussbaum 1985; Nussbaum and Schultz 1989; Obarrd and Brooks 1979, 1981; Orton 1953; Packard et al. 1977, 1981; Petranka 1989; Petranka et al. 1982; Philips 1987; Salthe 1967; Salthe and Mecham 1974; Scadding 1977, 1981; Schiebe 1987; Scott 1990; Seigel et al. 1987; Semlitsch 1987a, b, c; Semlitsch and Gibbons 1988; Semlitsch et al. 1988; Sherbrooke and Montanucci 1988; Shine 1978, 1979; Shine and Bull 1979; Smith 1976; Stangel and Semlitsch 1986; Starrett 1973; Stebbins and Eakin 1958; Steimwascher 1979; Sternberg 1930; Stewart 1965; Taigen 1983; Taigen and Pough 1981; Taigen et al. 1982; Taylor et al. 1988; Tilley 1980; Tinkle et al. 1970; Turner 1962; Twitty 1961; Wake and Morowitz 1990; Walls and Jaeger 1987; Wassersug 1973, 1975, 1976, 1989; Wassersug and Arnold 1976; Wassersug and Hoff 1979, 1985; Wassersug and Rosenberg 1979; Wells 1977; Werschkul 1982; Whitford and Whitford 1973; Wilbur and Collins 1973; Wilbur et al. 1983.

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8 Coping with the Cold

THE MOST NOTABLE FEATURE of amphibian and reptile distributions worldwide is the exclusion of these groups from most high latitude and high elevation areas. This is a general illustration of the restrictions for dealing with the cold placed upon these animals by their physiology, morphology and behaviour. Alberta lies at the northern extent of the ranges of most of the amphibian and reptile species that occur in the province (see the range maps in Chapter 5). Many more species drop out well to the south in the northern Great Plains and Rocky Mountains of the United States. Alberta's latitude alone, however, is not the only factor contributing to the province's inhospitability to amphibians and reptiles. In the west, the high elevations of the Rockies experience extremely long winters, and mean summer temperatures remain much lower than those on the prairie. Even the prairie, aspen parkland and boreal forests of Alberta are at relatively high elevation in comparison with much of eastern Canada at similar latitudes. Temperature changes relatively more rapidly with elevation (approximately 6°C per 1,000 m) than with latitude (approximately 1°C per 3° of latitude).

In addition to these simple geographic factors, the actual location of the land that makes up the province is of great significance. Being land-locked, Alberta does not benefit from the ameliorating effects of a maritime climate. Coastal regions of northern British Columbia and the panhandle of Alaska, which are moderated by the ocean, in general experience less extreme expressions of heat and cold than do areas of Alberta at comparable latitudes. For amphibians and reptiles, the key limitation is the length of the winter and the severity of temperature depression. The combined effects that elevation, latitude and geographic location have on overall climate, and therefore on the overall suitability of a region for the existence of amphibians and reptiles, can be seen by comparing Edmonton with Anchorage, Alaska. While Anchorage is about 7° north of Edmonton, the mean January and July temperatures are about the same, and rainfall, another limiting factor, especially for amphibians, is greater in Anchorage. While the herpetofauna of Edmonton is more extensive than that of Anchorage, this is not explainable primarily on climatic grounds and is related to historical factors. To the south and east, Alberta has a vast herpetofauna from which to draw its representatives, with no major physical barriers standing in the way. This is not the case for Alaska, however, where repeating series of mountain ranges act as formidable barriers against range expansion.

The chief reason why cold is a limiting factor for amphibians and reptiles is that their physiological strategy is directly linked to environmental temperature. Unlike birds and mammals, which are homeothermic (having a constant body temperature) and endothermic (producing their body heat by way of their own physiological activities), reptiles and amphibians are poikilothermic (their body temperature changing with that of their surroundings) and ectothermic (obtaining their body heat, from their surroundings). This type of strategy has both advantages and disadvantages for its users. Its advantages are that energy does not have to be devoted to producing body heat, and therefore a given area can support a greater biomass (the total amount of living material) of poikilothermic ectotherms than it can of homeothermic endotherms. For an individual, this means that less energy (= food) is needed to fuel the needs of basal metabolic rate, and more of the available resources can be devoted to growth and reproduction. On the other hand, the inability to physiologically regulate body temperature severely limits the conditions under which such animals can remain active. Most biochemical reactions in the body have temperature-dependent rates, with their optimal rates occurring in the range of 30-40°C. Thus, as body temperature drops, the efficiency of the metabolic machinery declines, affecting digestion, locomotion and indeed all aspects of the animal's biology.

This is not to say that amphibians and reptiles are entirely incapable of temperature regulation. Indeed, during their periods of activity, they may be able to maintain a nearly constant body temperature. This is accomplished, however, primarily through behavioural means, the animals shuttling between warmer and cooler areas in order to provide an appropriate stable thermal environment for their metabolic processes (Fig. 2.7). Ultimately, however, to be successful at achieving this, environmental conditions must present suitably high temperatures to allow for the required heating of the body to occur. In a seasonal environment, such conditions are not available throughout the year, and thus poikilothermic ectotherms are forced to become dormant when they can no longer raise their body temperatures to levels at which metabolic processes can support continuous activity. In addition, growth and reproduction require a certain minimal critical level of energy input in an active season, not only for allowing survival during times of activity but also for providing sufficient resources to permit existence from one active season to the next. To draw a comparison: the warmest summer days in Alberta are comparable to those much further south, but the number of them is far fewer. Thus, corn grows in Calgary but does not receive enough energy input to ripen and set seed. Its survival from one year to the next, were it not cultivated, would be greatly compromised by this, and the ability to survive the winter would be the true test of suitability to withstand the rigours of the climate. Furthermore, the food resources utilized by many amphibians and reptiles, such as insects, arachnids and other amphibians and reptiles, are themselves poikilothermic and limited by climatic conditions, and are hence not available as energy sources throughout the winter (Fig. 7.1).

The amphibians and reptiles that occur in Alberta are a subset of those characteristic of prairie and montane regions to the south. Most are extremely wide-ranging and several extend as far south as Mexico (see range maps in Chapter 5). Clearly, environmental factors throughout the ranges of these species vary considerably. Those populations occurring in Alberta are generally at one end of the spectrum of physiological tolerance and plasticity exhibited by the species as a whole. Most species that occur in Alberta are at the edges of their ranges, and thus are interesting for this fact alone, as they exemplify an extreme in terms of survival ability.

The mechanisms for dealing with the cold are varied, but can be loosely categorized as either behavioural or physiological. Behavioural responses may be viewed as short-term adjustments to changing conditions, while physiological responses equip the animals for longer bouts of depressed temperatures. While the winter, with its almost constant depressed temperatures, may be viewed as the most obvious aspect of the cold that reptiles and amphibians must deal with, it should also be noted that the spring and fall, with fluctuant and often unpredictable temperatures, may have a significant influence on how species can adjust to cold temperatures and remain active at critical periods in what appear to be suboptimal conditions. Thus, the aspects of behavioural and physiological adjustment to cold temperatures are complexly interwoven and interact with each other to enable survival. Beyond those individual modifications, most species also exhibit patterns of life history that have evolved in tune with the yearly temperature cycles and the limitations that these impose on their environment. Such life history parameters tend to show clinal variation (gradual change across an environmental gradient). These behavioural, physiological and evolutionary strategies may be viewed in light of three major aspects of the animal's biology: daily maintenance, overwintering and reproduction.

The chief mode of behaviourally increasing temperature is basking (Fig. 8.1). Basking is employed by most reptiles and some amphibians in order to raise body temperature during times of the day and parts of the season when ambient air temperature may be too low to support normal activity. Basking takes advantage of direct solar radiation. Animals may also pick up heat from reflected radiation or through conductance from surfaces with which they are in contact (Fig. 2.7). While basking, animals are often exposed and may be subject to cooling from wind convection or, if the substrate is cooler than body temperature, from conduction to the substrate. The rate of heat flux is also moderated by postural changes assumed by the thermoregulator. Exposing maximal surface area to the sun's rays and/or pressing flat against a warm substrate promotes uptake from radiation and conductance and minimizes exposure to wind convection. Conversely, once a suitable temperature has been attained, overheating may be prevented by shuttling into shade or water. *Bufo hemiophrys*, which lives in forested areas, retreats to the shade of vegetation, whereas *Bufo cognatus*, which occupies a more open habitat, burrows in response to heat stress.

Because cold amphibians and reptiles may be sluggish and prone to predation at the onset of basking, it is common that an animal will begin basking from a protected site, such as a burrow or a crevice, exposing only a small portion of its body, moving into full sunlight only after reaching some minimum temperature that will allow effective defence or escape. Each species has what is known as a "preferred body temperature" and behavioural thermoregulation attempts to ensure that body temperature tracks this modal value throughout the active portion of the day. In the spring and fall and on cool summer days, available solar radiation and reflection may be insufficient to allow this preferred body temperature to be reached, and the animal may thus remain relatively dormant as a result. At both ends of the active season, the ability to thermoregulate effectively will play an important role in determining when normal activities may begin and when they must cease for the winter. While not

Figure 8.1 A chuckwalla basking on rocks in California.

all of the factors controlling behavioural thermoregulation are fully understood, it is known that centres in the brain, such as the pineal body, integrate information and provide the cues for appropriate behaviour patterns.

For amphibians which rely, at least in part, upon water, the aquatic habitat may provide both food and refuge. However, although the water is more thermally stable than air, average temperatures during daylight hours are lower and usually not sufficiently high to support all maintenance activities. At higher elevations in Alberta, *Bufo boreas* (and perhaps other amphibians) routinely basks while partially submerged. This practice is particularly striking in juvenile toads, which may effectively increase body temperature 10-15°C above ambient water temperature.

One of the reasons that amphibians are more successful (in numbers of species and individuals) than reptiles in Alberta is that their preferred body temperatures are generally lower than those of reptiles, and the range of temperatures over which most maintenance functions can be continued is greater. Unlike amphibians, which risk desiccation in their efforts to raise body temperature (see Chapter 9), most reptiles require very high temperatures. Because of their generally larger size and lower surface-area-to-volume ratio, reptiles also take longer to heat up, and typically do not appear until many weeks after most frogs and salamanders have begun their activities. Most of the reptiles of the province are in fact likely to be encountered only during basking periods. For turtles, basking sites are usually logs or river banks. The limited number of suitable basking sites may result in intense agonistic behaviour between individuals as they vie for the most favourable spots. Rocky outcrops and coulee rims are favoured basking spots for short-horned lizards and snakes.

Maintenance activities are physiologically adjusted to changing environmental temperatures throughout the active season by the process of acclimation. Certain metabolic functions may be reasonably plastic and adequate even at quite low temperatures, although maximal performance will not be attained. This is particularly true of amphibians, which are able to escape from predators at temperatures lower than 10°C. Other functions, such as prey acquisition and calling in male frogs, require higher temperatures for maximal efficiency, but may still be carried out under the conditions experienced in Alberta in early to mid-spring. Digestive assimilation is also plastic, and lower temperatures induce slower feeding rates concomitant with the limits of enzymatic activity at any given temperature. At temperatures below 5°C, enzymatic activity approaches zero, and amphibians typically cease to feed. Similarly, garter snakes employ different suites of enzymes at different acclimation temperatures and thus maintain digestive activity at a range of body temperatures as the active season progresses. Although acclimation of this sort has not yet been experimentally demonstrated under laboratory conditions for short-horned lizards, field observations strongly suggest such adjustment as individuals have been observed to be active, in sheltered situations, at ambient temperatures as low as freezing.

The foregoing account of daily maintenance represents situations that, to a greater or lesser extent, must be faced by all non-tropical amphibians and reptiles. At higher latitudes and altitudes, however, the problem of overwintering manifests itself as a severe challenge to survival and calls forth approaches not seen in species inhabiting more temperate environments. The basic strategy is to hide from the severe conditions of winter. This may be achieved in a variety of ways.

All amphibians and reptiles in Alberta spend the winter below the surface. Amphibians and turtles typically pass the winter singly in protected terrestrial habitats (*Rana sylvatica, Pseudacris maculata*), in subterranean burrows (*Ambystoma tigrinum, Spea bombifrons, Bufo cognatus*), or in mud at the bottom of standing or slow-flowing water (*Rana luteiventris, Chrysemys picta*). *Phrynosoma* uses shallow burrows and an insulating layer of snow and may also employ naturally occurring sink-holes and crevices that take it below frost line.

The snake species typically overwinter in dens or hibernacula and may aggregate there in vast numbers (Fig. 8.2). Hibernacula may be naturally occurring pits or crevices in rocky outcrops or karst topography (Fig. 8.3), burrows co-opted from small or medium-sized mammals, or may be excavated by the snakes themselves, as in *Pituophis catenifer.* When fall temperatures approach those that no longer permit sustained activity, snakes begin to converge on den sites, possibly using chemical cues to locate their whereabouts and the whereabouts of den mates. Temperatures within the hibernacula remain above freezing and further insulation may be provided by the snow cover above and the bodies of the snakes themselves, which in the case of *Thamnophis* may number in the thousands. In the hibernacula, activity does not necessarily completely cease. Snakes are able to follow thermal gradients within the den and, if disturbed, retain the ability to initiate defensive behaviours even though body temperature may be only a few degrees above freezing. Some dens may be occupied by more than one species. For example, *Crotalus, Pituophis* and *Thamnophis* are known to den communally near the Milk River. In spring, a combination of increasing day length and rising temperatures cues emergence. These factors also initiate sexual behaviour, and mating takes place before the snakes disperse from the den site for the summer. Overwinter mortality is poorly known, but may be significant, especially for the young of the year

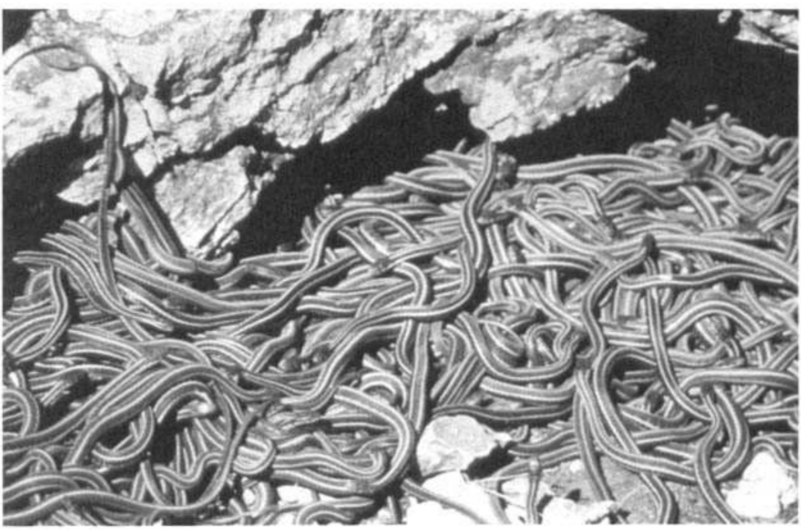

Figure 8.2 Part of a massive accumulation of garter snakes emerging from a den in the spring in the Interlakes region of Manitoba.

and females that have given birth late in the summer and have not had an opportunity to accrue sufficient resources to allow them to successfully pass the winter.

Most snakes in hibernacula are in situations where body temperature is maintained just above freezing. Metabolic activities thus drop to a very low level, but no special physiological mechanisms are required to maintain life. *Thamnophis sirtalis* preferentially overwinters in dens with available free water, and in far northern Alberta this may be crucial to survival. By submerging themselves, they avoid dehydration but risk entrapment should the water freeze. Some individuals have survived such freezing, suggesting the most extreme example of cold tolerance yet known in snakes. Amphibians and turtles, on the other hand, may be unable to avoid sub-zero temperatures and have developed physiological mechanisms to allow these otherwise lethal temperatures to be withstood. Turtles may be able to escape freezing by burrowing into muddy river bottoms where they are able to withstand anoxic (lack of oxygen) conditions for several months. They are able to utilize stored glycogen to fuel their minimal metabolic needs and withstand acidosis (acidification of the blood and tissue fluids) as a result of the high buffering capacity of their blood. However, some turtles, and hatchlings overwintering in the nest in particular, may experience sub-zero

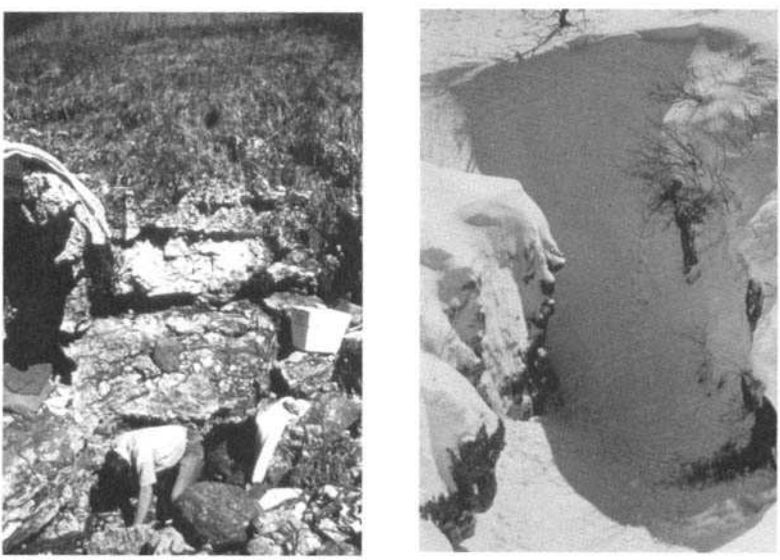

Figure 8.3 A sink-hole in the Karst country of the Interlakes region of Manitoba. The picture on the left is taken in summer, that on the right in winter.

temperatures and are able to supercool (to lower the temperature of the blood and tissue fluids without ice crystals forming) to as low as −13°C, the lowest known temperature that has been survived by any amniote. Choice of type of substrate appears to be critical. Freeze tolerance involves a cryoprotectant in the tissues. Often nucleation of ice is promoted by inoculation by environmental ice, but bacteria and other agents may also play a role.

Overwintering frogs are unable to lower metabolic rates to the same extent as turtles and cannot withstand the extreme anoxia of subaqueous burial. As a result, most frogs must overwinter in less thermally buffered situations and may therefore be exposed to freezing temperatures. Some frogs undergo supercooling, but others, including *Rana sylvatica* and *Pseudacris maculata,* are freeze-tolerant and actually are able to withstand the formation of ice in up to two thirds of the body's water content at temperatures as low as −6°C. Freezing takes place in the extracellular fluids, but the cells and tissues themselves are buffered from the ravages of freezing by cryoprotectants (low-molecular-weight carbohydrates which act to lower the freezing point). In *Rana sylvatica,* the cryoprotectant is glucose, which is mobilized only after ice crystals begin to form. Other frogs may use glycerol in this same capacity. The ability to utilize cryoprotectants to allow freezing seems to be seasonally variable, peaking in the late fall when glucose levels of frozen individuals may be an order of magnitude higher than in spring. Freeze-tolerance is not a long-term solution. Animals may be able to survive days or weeks in a frozen state, but cannot endure a constantly frozen state throughout the winter. Again, they must rely upon the thermal buffering of their immediate environment to ensure that permanent freezing does not occur.

Cold temperatures and a short active season are particularly restrictive with respect to amphibian and reptile reproduction. For most species, it is necessary that young be produced early enough to be able to accrue sufficient resources to tide them over their first winter. In the case of amphibians, metamorphosis may also take place in the narrow window of time before the onset of winter. Amphibians such as *Rana sylvatica* and *Ambystoma macrodactylum* breed at the earliest possible opportunity to ensure sufficient time for larval growth and differentiation. In some cases, larvae must overwinter or, like *Ascaphus,* pass two to three years as tadpoles before metamorphosing. Frogs and toads of the prairie must capitalize on the limited water availability and may miss breeding opportunities if favourable temperatures do not coincide with the availability of breeding sites.

While some proximal mechanisms for ensuring reproductive success exist (depositing eggs below the water surface to prevent damage from surface freezing), most of the strategies employed by Alberta amphibians and reptiles are evolutionary solutions acting through life-history parameters. Maturation for almost all Alberta amphibians and reptiles is delayed relative to populations of conspecifics or congeners to the south (see individual species accounts, above). Short growing seasons permit energy input of smaller animals into growth or reproduction, but not both. Since egg size and fecundity are related to female body size in many amphibians, delayed maturation may be viewed as a strategy to maximize gamete output within the limitations of a short activity season.

Reptiles, too, must accommodate reproductive cycles to the limited availability of resources. For example, rattlesnakes, which breed every other year to the south, may give birth only every third or fourth year in the prairies of Canada. Rattlesnakes give birth to large young, and gravid females normally do not feed. Consequently, a great deal of stored energy must be accumulated in non-reproductive years. Only when sufficient resources have been sequestered can a new reproductive cycle begin. In turtles, both individual egg mass and total clutch mass may be affected by latitude. Below certain temperatures, fewer and/or less-viable offspring may be produced. This may be a more important factor in determining the northern limits of oviparous reptiles than is any aspect of adult biology.

Since resources are widely dispersed, opportunities for mating may be restricted to early spring and/or late fall aggregations at breeding ponds or dens. While these times may be appropriate for mating, they may not be so for development of young. Thus, in some instances, sperm are stored in the reproductive tracts of the female and remain viable until fertilization can proceed. The cue for this resides in whether or not sufficient resources have been acquired by the female to permit successful production of yolk or other reserves to fuel development. Alternatively, fertilization may occur normally, but subsequent development may be delayed. In the case of *Chrysemys picta,* hatchlings may remain in the nest over winter, avoiding risk of predation until such time as availability of food makes emergence an acceptable risk.

All three species of *Thamnophis,* as well as *Crotalus* and *Phrynosoma* exhibit viviparity (live birth) (Fig. 8.4). This too appears to be a strategy for life in the cold, since the developing embryos receive not only protection but also the benefits of the thermoregulatory behaviour of the mother. In both *Thamnophis sirtalis* and *T. elegans,* gravid females prefer areas that provide both protection from predation and higher temperatures for the developing young. In *Phrynosoma,* and perhaps in the other species, birth may be more or less synchronous for all pregnant females within the population, exemplifying the rather uniform conditions that the developing young experience.

The conditions of climate and geography that prevail in Alberta restrict productivity to a short spring and summer period. Amphibians and reptiles, like other organisms, capitalize upon this short period by accruing large amounts of energy and / or converting large amounts of energy into reproductive output. Because maintenance requirements for these animals are low, the province in this brief productive period is capable of supporting huge populations of those few species that can endure its harsh winters and are equipped to cope with the cold.

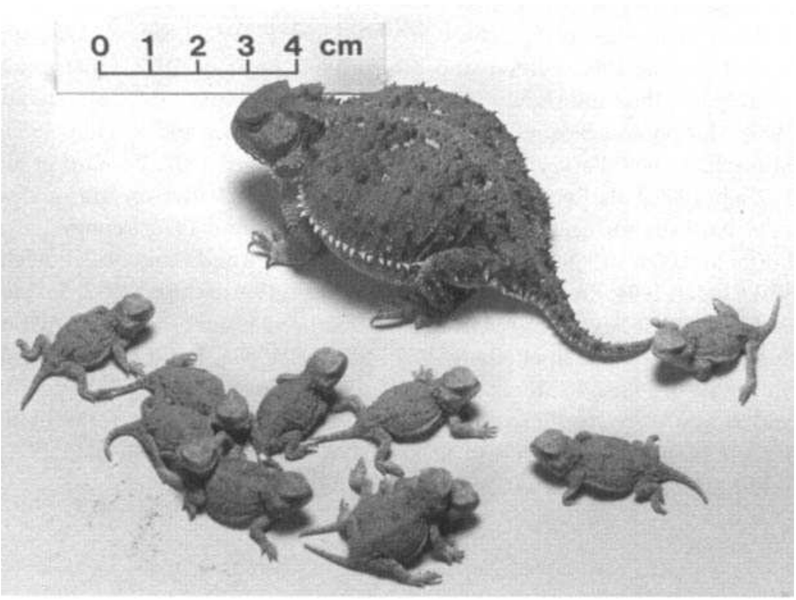

Figure 8.4 An Albertan female short-horned lizard and her litter of ten young, one day after birth.

Significant references: Aleksiuk 1970, 1971a, b, 1976a, b; Aleksiuk and Gregory 1974; Aleksiuk and Stewart 1971; Anderson 1968a; Andrews and Pough 1985; Attaway et al. 1998; Avery 1979, 1982, 1984; Avery and D'Eath 1986; Ballinger and McKinney 1966; Bartholomew 1959, 1982; Beall and Privatera 1973; Belkin 1963; Bennett 1980; Bennett and Dawson 1976; Bobyn and Brooks 1994; Black and Black 1969; Bogert 1949, 1959; Boyer 1965; Bradford 1983; Brattstrom 1963, 1965; Breckenridge and Tester 1961; Breitenbach et al. 1984; Browder and Davison 1964; Brown, W.S. et al. 1974; Carpenter 1953; Charland and Gregory 1995; Cloudsley-Thompson 1968, 1971; Costanzo 1985, 1986, 1988, 1989a, b, c; Costanzo and Claussen 1988; Costanzo and Lee 1995, 1996; Costanzo et al. 1992, 1993, 1995, 1997, 1998; Cunjak 1986; Else and Bennett 1987; Dunlap 1980; Emery et al. 1972; Feder et al. 1982; Fitzpatrick and Atebara 1974; Fraser et al. 1993; Funk and Milsom 1987; Gatten 1985, 1987a; Gillingham and Carpenter 1978; Gregory 1975, 1976, 1977, 1982, 1984b; Hartweg 1946; Heath, J.E. 1975; Herreid and Kinney 1966; Hodge 1971, 1976; Hoskins and Aleksiuk 1973; Huey 1982; Huey and Slatkin 1976; Huey et al. 1989; Iverson et al. 1993; Jackson and Ultsch 1982; Joy and Crews 1986; Kling et al. 1994; Kuyt 1991; Layne, 1992, 1995; Layne and Lee 1986, 1989, 1995; Licht, L.E. 1991; Licht, P. 1972; Lee and Costanzo 1993; Lee et al. 1992; Lefevre and Brooks 1995; Lotshaw 1977; Lowe et al. 1971; MacArthur and Dandy 1982; Macartney and Gregory 1988; Marchand 1987; Marion and Sexton 1981; Mayhew 1965b; Miller and Zoghby 1985; Musacchia 1959; Packard 1997; Packard and Packard 1997; Packard et al. 1997a,b, 1999; Paladino 1985; Parker and Brown 1974; Patterson and Davies 1978; Paukstis and Shuman 1989; Pearson and Bradford 1976; Penney 1987; Porter and Gates 1969; Porter and Tracy 1974; Pough and Gans 1982; Powell and Russell 1994; Preest and Pough 1989; Rosen 1991; Schmid 1982; Sexton and Hunt 1980; Sexton and Marion 1981; Sherbrooke and Frost 1989; Snyder and Weathers 1975; Spellerberg 1976; Stevens 1988a, b; Storey, J.M. and Storey 1984, 1985a, b; Storey, K.B. 1984, 1985, 1986, 1987, 1988; Storey, K.B. and Storey 1986a, b, 1987, 1988; Tattersall and Boutilier, 1999; Tester et al. 1965; Ultsch 1988; Ultsch and Jackson 1982; White and Lasiewski 1971; Whitford and Massey 1970; Woolmuth et al. 1987.

9 The Challenge of Aridity

ALBERTA IS UNIQUE IN Canada in possessing an extensive truly arid (non-polar) biome: the badlands and short-grass prairie of the southeastern corner. Similar habitats occur in adjacent southwestern Saskatchewan and in some of the interior valleys of southern British Columbia. These areas are really continuations of the desert and semi-desert systems of Mexico and the United States, and it is from these that the local fauna is derived. In particular, the arid regions of Alberta may be viewed as incorporating life forms more typical of the Sonoran desert, such as *Yucca*, cactus, scorpions, solpugids and reptiles such as the short-horned lizard.

The total annual precipitation for this area is only 30-40 cm, with much of the region being in the low end of this range. Summer rainfall accounts for only half of this and is not evenly spread throughout the active season. Thus, the lack of availability of free water becomes a severe limiting factor in determining what species can persist in this area. Nonetheless, while such limiting factors apply, overall this region provides a set of conditions that permits the survival of more species of amphibians and reptiles than anywhere else in the province (see Table 6.1). While it is the driest region, it is also the warmest, and the relatively hot, dry climate permits the persistence of species that have not been able to extend their ranges further north and west. The transition from short-grass prairie to aspen parkland is, of course, rather gradual, but the physical conditions that demarcate the two are rather finely balanced. As was seen in the 1930s, a relatively slight shift in patterns of precipitation over a period of a few years resulted in many of the conditions we associate with the arid prairie extending into the parkland areas. While this shift did not persist long enough to bring about changes in the patterns of biotic distribution, it does serve to illustrate how the borders of biomes are marked out and maintained when conditions remain relatively stable for long periods of time.

Dryness imposes challenges that must be faced in addition to those of the cold. These consist primarily of desiccation, exposure to overheating and limitations imposed by the patchiness of food resources and breeding sites. While amphibians fare better than reptiles in Alberta as a whole (ten species versus eight species), in the arid southeast, the reverse is true (five species versus seven species). Most of the reptiles are generalists, occurring elsewhere in their ranges in a number of habitat types. The occurrence of these species in Alberta is only made possible by the greater number of sunshine days and higher average temperatures, which happen to be coincident with the aridity of the region. Outside the arid southeast, the only reptiles encountered in Alberta are the garter snakes. Three of the amphibian species have enormous species ranges (*Ambystoma tigrinum, Pseudacris maculata* and *Rana pipiens*), while the remaining two (*Bufo cognatus* and *Spea bombifrons*) are more or less arid specialists. Five additional species of amphibian occur elsewhere in the province.

One of the main factors accounting for the differential success of amphibians and reptiles is the structure of the skin (Figs. 9.1 and 9.2). Amphibians typically use their skin as a gas exchange organ (Fig. 9.1). As such, it must remain moist and in so doing cannot be exposed for more than brief periods to desiccating environments. Indeed, the skin is more or less completely permeable to water in both directions and amphibians must, therefore, precisely regulate their behaviour with respect to water balance if they are to survive in arid areas. They thus tend to be nocturnal, emerging when ambient temperature is relatively low and humidity relatively high, or are sporadic in their appearance, with their periods of activity being closely tied to episodes of heavy rainfall. The amphibian species that are not arid specialists (for example, leopard frogs and chorus frogs) are found in the arid southeast only where permanent water persists, such as around the margins of ponds and lakes and along streams and rivers. Tiger salamanders, which are poor behavioural thermoregulators, are nocturnal and retreat to burrows when temperatures are high or humidity low. The two arid specialist species (*Bufo cognatus* and *Spea bombifrons*), both burrowers, take advantage of skin permeability by absorbing water when it is available through the so-called "seat patch" (a region of especially permeable skin on the belly between the hind limbs). Further, hormones may act to enhance this permeability when appropriate conditions occur. These species are active further away from permanent water than the non-specialist

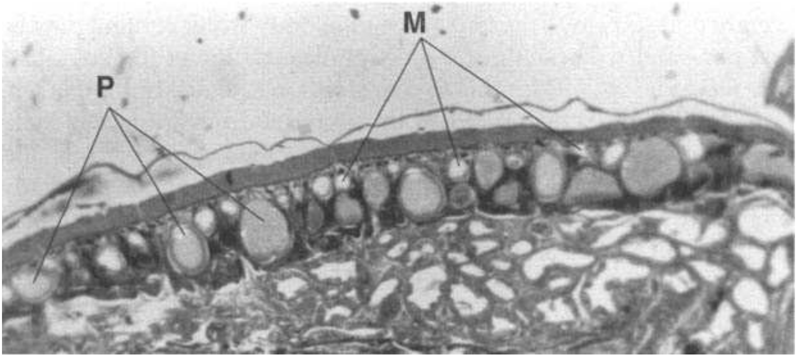

Figure 9.1 A section through the glandular skin of a frog. Note the numerous mucus (M) and poison (P) glands sunken into the outer layers of the dermis.

amphibian species, but may be active for only a limited portion of the spring and summer when they are able to tolerate the prevailing conditions. When conditions are unfavourable these animals dig backwards into the soil assisted by tubercles on the metatarsus which, in *Spea*, are modified to form a spade-like prominence (Fig. 5.2).

Regardless of specialization, all amphibians deprived of water suffer from dehydration resulting from evaporative water loss. Paradoxically, the higher temperatures of the prairie which are beneficial for growth and reproduction may also be detrimental, as they induce evaporative cooling and hence water stress. The nocturnal habits of arid amphibians are a strategy for minimizing this type of water loss. Aside from escaping desiccation by burrowing or hiding, amphibians incorporate a number of physiological mechanisms to cope with such stresses.

Amphibians are unable to form hypertonic urine (urine that is more concentrated than the body fluids), but they are able to cease urine production in response to dehydration. This saves water but may result in rising concentrations of salts and nitrogenous waste in the blood. The ability to tolerate these high concentrations is crucial to the water-balance strategy of amphibians in general. Urine, once produced, may be retained in the bladder, which acts as a reservoir from which water may later be withdrawn. In some frogs, up to fifty percent of the body weight may be stored as water in the bladder. These various physiological mechanisms are tightly regulated hormonally by the pituitary (a region of the brain). When water loss is unavoidable, amphibians are able to cope with severe desiccation stress. In more arid-adapted forms, up to fifty percent of the body weight and sixty-two percent of the total body water content may be lost non-fatally. These figures are significantly lower in generalists like *Rana pipiens.* Under this severe stress, resistance in the peripheral circulation increases. While this may retard evaporation, leakage of plasma into the tissues makes the blood more viscous and thus harder to pump. The resulting cardiac stress, along with greatly increased salt concentrations in the blood, tests the physiological limits of the animal and cannot be tolerated for long.

During extended periods of inactivity, such as overwintering or aestivation (summer dormancy), some frogs, including *Spea,* encapsulate themselves with partially ecdysed (shed) skin which serves to significantly retard water loss through evaporation within the burrow, which normally maintains a higher humidity than the surface.

Reptiles are buffered from desiccation and the physiological stresses it induces because their skin is largely impermeable to water flux (Fig. 9.2). They are thus able to be freely active for much longer periods in arid situations and may typically be active during the day as well as at night. At least part of the impermeability of the reptilian integument is related to the keratinized epidermis, which is extremely complex in structure. Essentially, reptiles are largely freed from the behavioural aspects of maintaining an appropriate water balance with their environment and are much more effective physiological regulators. They are, however, still constrained to some degree by their reliance upon behavioural thermoregulation.

In addition to a reduction in cutaneous water loss, reptiles also show a reduction in pulmonary water loss when compared to amphibians. Within certain limits, the rates of water loss in reptiles may be adjusted to local environmental conditions. The low rates of water turnover in reptiles are also in part due to their ability to produce concentrated urine in the form of uric acid. This is largely crystalline rather than liquid. Among Alberta reptiles, the only exception to this is seen in *Chrysemys picta.* Since this species lives in and around water, it may be able to utilize this medium to void nitrogenous wastes in a less metabolically expensive fashion. When severe water stress does occur, most reptiles, like amphibians, are capable of tolerating high concentrations of solutes in their body fluids. Prolonged dehydration, however, may be fatal, as the ability to maintain homeostasis is decreased under conditions of water stress.

Overheating, which may be a risk for both amphibians and reptiles on hot days in the treeless prairie, is primarily dealt with behaviourally. Nocturnality, burrowing and aestivation (prolonged periods of inactivity during hot weather) are all responses that help

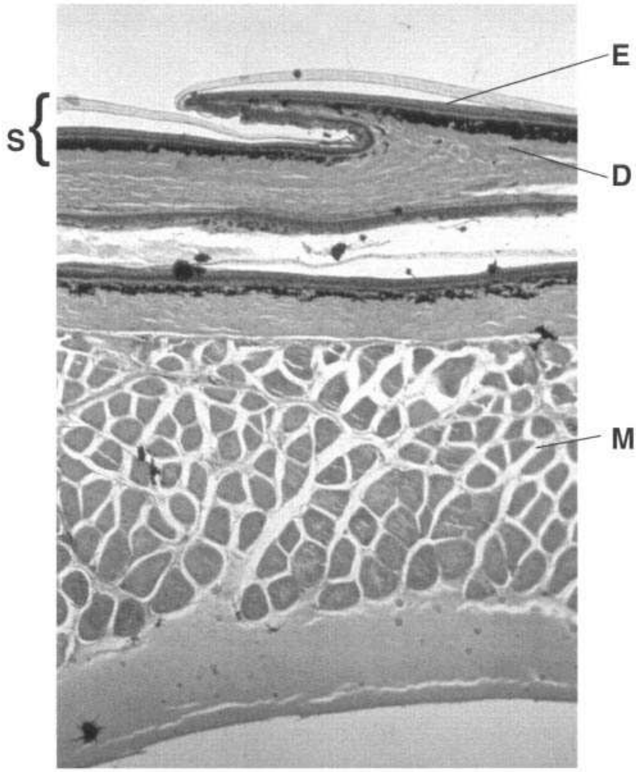

Figure 9.2 A section through the skin of a lizard showing the scales (S) covered by the thin but desiccation-resident epidermis (E), the thickened dermis (D) and the subcutaneous muscle (M). This skin is not glandular (compare with Fig. 9.1) but is very resistant to water loss.

animals to cope with thermal stress. A number of morphological features of Alberta amphibians and reptiles may be associated with nocturnality, such as those enabling foraging at night. *Crotalus,* which as adults feed on warm-blooded prey, locates suitable food items by infra-red heat detection. Pit organs on the sides of the face between the eyes and nostrils are sensitive to heat and enable the snake to pick out mammals from their background by discriminating between different intensities of heat radiation (Fig. 9.3). Both the rattlesnake and the spadefoot toad (Fig. 5.2) have vertical pupils which close down to slits in high levels of light intensity, but which are well designed for night vision by being able to open up widely to make maximal use of the available light.

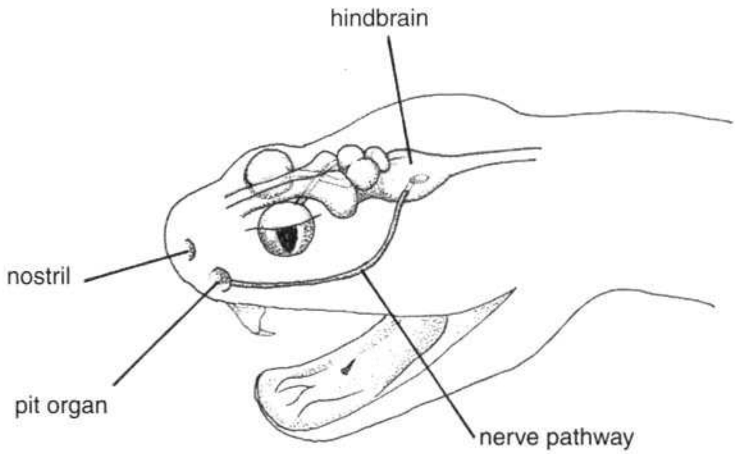

Figure 9.3 A schematic representation of the nervous connections between the heat-sensitive pit organs and the hindbrain in a rattlesnake.

The limited availability of free water is a major obstacle that arid region amphibians must overcome. All Alberta species of amphibians lay their eggs in water and have aquatic larvae. Most naturally occurring permanent water in the southeast corner is associated with rivers and streams, which are generally unsuitable for amphibian reproduction. Ponds, ditches and sloughs, although appropriate for breeding, are often ephemeral, drying up during the summer. Thus, for those amphibian species that are not arid-environment specialists, the limited availability of suitable breeding sites restricts their distribution within the southeastern corner of the province. The arid-environment specialists, *Spea* and *Bufo cognatus*, as well as being behaviourally and physiologically more suited to the exploitation of such areas, also exhibit reproductive modifications that allow them to be generally more widespread. Their emergence in the spring is tightly correlated with rainfall. If this does not provide sufficient water for breeding or comes at the wrong time, breeding for that year will be forsaken. In extreme cases, these animals may fail to emerge entirely and remain dormant until the next year. In truly desert-dwelling forms, this strategy is quite common. These species typically breed in temporary water bodies and have larval stages that persist for very short periods of time before metamorphosis. The egg masses of the species are small and are frequently spread out across the surface in order to maximize heat uptake to promote development and minimize the risk of oxygen deprivation in the shallow, oxygen-poor ephemeral habitats.

For many amphibians, larval growth and development is density-dependent. This is especially so for temporary ponds, since, as these ponds begin to dry up, larval density increases, leading to overcrowding. One solution to this stress, and to problems of limited food resources, is to permit the larval population to regulate itself. In *Spea,* this is accomplished by some tadpoles being cannibal morphs (Fig. 7.6). These grow more rapidly than non-cannibal siblings, secrete substances to control the growth of the latter, and use them as a food resource. In this way, the proteins required for growth and metamorphosis can be rapidly built up within the population, and sufficient resources for metamorphosis accrued before the pond dries. Development time for *Spea* is among the most rapid for amphibians anywhere. Cannibalism is one of the most extreme cases of altruism known in the animal kingdom. Such strategies are also employed by *Ambystoma tigrinum,* although cannibal morph larvae have not yet been identified in Alberta. Cannibalism may also be employed to provide adults with sufficient resources in energy-poor high altitude and high latitude ponds—adult *Rana luteiventris* have been observed to consume conspecific tadpoles in such habitats.

Since reptilian reproduction is not dependent upon free water, little in the way of breeding specializations occur that are particularly pertinent to arid prairie conditions. Nonetheless, viviparity, which may have evolved in response to the stressful thermal regime, may likewise be beneficial with respect to aridity—ensuring that embryonic development is not compromised by egg dehydration. *Heterodon,* which lays eggs, is very particular in its microhabitat choice for egg deposition. One of the possible limitations affecting this snake is the need for suitably humid sites for nesting.

In summary, we can state that the arid southeast of Alberta is a relatively unstable region in terms of climatic and associated conditions. It is these that present particular challenges to the amphibians and reptiles that live there. Distribution of resources is patchy and the availability of certain necessities, such as sufficient rainfall, is unpredictable. For amphibians, this results in prolific production of new recruits to the population whenever this is climatically or energetically feasible, but may mean several seasons of low or no recruitment between such episodes. Reptiles are able to reproduce more regularly by providing parental investment in the form of large yolk supplies which are distributed among relatively few offspring.

Significant references: Adolph 1933; Andrews and Pough 1985; Avery 1984; Avery and D'Eath 1986; Ballinger and McKinney 1966; Bani et al. 1985; Bartholomew 1959; Bennett 1980; Bennett and Licht 1975; Bentley 1966, 1971; Bentley and Schmidt-Nielsen 1966; Bradshaw 1988; Campbell et al. 1987; Christensen 1974; Cloudsley-Thompson 1968, 1971, 1972; Cowles and Bogert 1944; deCock Buning 1983; deCock Buning et al. 1981; Delson and Whitford 1973; Emerson 1976; Fowler 1934; Fraser and Grigg 1983; Gatten 1987b; Goin 1960; Heath 1964; Hillman 1980, 1987; Hoffman and Katz 1989; Licht and Bennett 1972; Lillywhite and Maderson 1982; Maderson 1965; Maderson et al. 1969, 1978; Mayhew 1965a, 1968; McClanahan 1967, 1972; McClanahan and Baldwin 1969; Minnich 1982; Mullen and Alvarado 1976; Nagy 1982; Newman 1988a, b, 1989; Norris 1967; Pianka 1986; Pilliod 1999; Porter 1967; Porter and Gates 1969; Ricklefs et al. 1981; Preest and Pough 1989; Schmid 1965; Shoemaker 1975; Shoemaker and Nagy 1977; Spight 1967a, b, 1968; Spotila 1972; Tinkle and Gibbons 1977; Walker and Whitford 1970; Zweifel 1968.

10 Defence and Venoms

MOST AMPHIBIANS AND REPTILES are relatively small by vertebrate standards, and as such are prone to predation attempts by a variety of animals, ranging from insect larvae to bears. As a consequence, most species have evolved one or more anti-predator mechanisms. All species exhibit some behavioural traits that are used to attempt to deter predators, and in some these are augmented by biochemical mechanisms that may be regarded as either toxins or venoms. In some instances, the biochemical materials can also be employed as agents that assist in predation as well as in defence.

All Alberta amphibians and reptiles will attempt to flee, or in some instances "freeze," as an initial response to perceived danger. In the case of amphibians and garter snakes, which occupy both terrestrial and aquatic habitats, it is common to move rapidly from land to water in order to avoid terrestrial predators. Tadpoles, turtles and some frogs will sink or dive to the bottom of water bodies to avoid avian predators. Further, amphibian larvae that occur in waters that also harbour predatory fish may alter their behaviour and become primarily benthic to avoid detection.

If such relatively simple strategies fail, then more elaborate species-specific defensive behaviours are invoked. Salamanders, upon capture, rely chiefly upon unpalatability as a means of defence. Poison or granular glands are present in the skin and may be aggregated in areas most likely to be attacked—chiefly the head and tail. The two species of *Ambystoma* occurring in Alberta are only mildly noxious in this regard. Extremely potent toxins characterize newts (family Salamandridae), including those of coastal British Columbia. Frogs and toads may respond to attack by uttering alarm or release calls that serve to startle the aggressor. If handled, they may rapidly empty their bladders, both disconcerting the aggressor and shedding additional body weight to facilitate a more rapid escape should this response induce release. In addition, toads may exhibit bluff behaviour, inflating their bodies and rising high on their legs to increase their apparent size. The head is often depressed, with the parotoid glands (Fig. 5.1) turned towards the aggressor. These large glandular concentrations behind the eyes exude a viscous, milky substance which contains a mixture of noxious toxins and irritants. Certain predators of toads selectively avoid eating the head and back because of the presence of these defensive secretions. For unwary or inexperienced predators, the defensive secretions can cause severe discomfort as they irritate the eyes and the mucous membranes of the mouth. This will result in the captured toad being dropped. Such defensive mechanisms play an important role in conditioning potential predators to avoid such encounters on future occasions. Although the skins of Alberta frogs may be somewhat distasteful, they contain little in the way of toxic substances. Elsewhere, however, cutaneous toxins of frogs may be extremely potent and may result in the death of the aggressor due to severe physiological disruption induced by the defensive secretions. Such is the case with the arrow-poison frogs (family Dendrobatidae) of South and Central America.

Larval anurans, because of their very different morphology and mode of existence, must employ other defensive tactics. Like the adults, they may be somewhat unpalatable, but in addition to toxic secretions they may also produce chemical alarm substances ("Schreckstoff"). These pheromones are released by traumatized individuals and warn conspecifics of impending danger. This strategy is known in Alberta for tadpoles of *Bufo boreas,* which occur in large schools that are likely to be made up of siblings.

Turtles rely primarily upon their strong carapace and plastron (Figs. 2.8, 3.1, 5.3) to protect them from putative predators. They may also attempt to bite with their powerful jaws and scratch with their formidable claws (Fig. 7.3). *Chrysemys picta* is able to retract the head and limbs into the shell, making itself more or less impregnable to any carnivores it might encounter. *Chelydra,* on the other hand, with its reduced plastron, cannot withdraw its appendages and relies upon aggressive biting and odoriferous musk from cloacal glands to repel potential predators.

Phrynosoma hernandesi relies chiefly upon seclusion to avoid predators. If encountered, its chief defence is to inflate its body and posture so as to render itself difficult to ingest. Other horned toads occurring in the United States and Mexico often have much larger horns on the head and spines along the sides of the body that enhance the awkwardness of prehension by a predator. Some of these species also startle potential predators by squirting blood from the region of the eyes. Another common defensive tactic used by lizards in general is caudal autotomy (casting off of the entire tail or a portion thereof to distract a potential predator). This tactic is not employed by *Phrynosoma,* and the tail in this genus is rather reduced in size (Fig. 3.1).

The widest array of defensive tactics is exhibited by snakes. When handled, all species of snakes will bite as well as defecate and writhe to spread the faeces over their body and onto the aggressor. In addition, smelly secretions from the cloaca are mixed with the faeces in garter snakes, adding a further degree of repulsiveness to the encounter. *Pituophis, Heterodon* and *Crotalus* may hiss, inflate their bodies and strike. In the hog-nosed snake, death-feigning (Fig. 10.1) may occur, in which the animal rolls onto its back, lolls out the tongue and remains motionless.

Both *Heterodon* and the garter snake species also possess a venom- injecting apparatus (Fig. 10.2a,b) which is used primarily in subduing prey and assisting in digestion. This venom, which is produced in Duvernoy's gland, is extremely mild and generally does not produce a reaction in humans (although in exceptional cases the bite of a hog-nosed snake may be unpleasant to those with a particular sensitivity). Rattlesnakes, of course, rattle to warn of their presence. They possess a complex venom-delivery system, the products of which are primarily used for subduing prey but which also become a significant factor in the defensive armory of *Crotalus.*

From the foregoing, it can be seen that chemical defences are widespread among amphibians and reptiles. Toxins proper are chemical

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Figure 10.1 A hog-nosed snake feigning death.

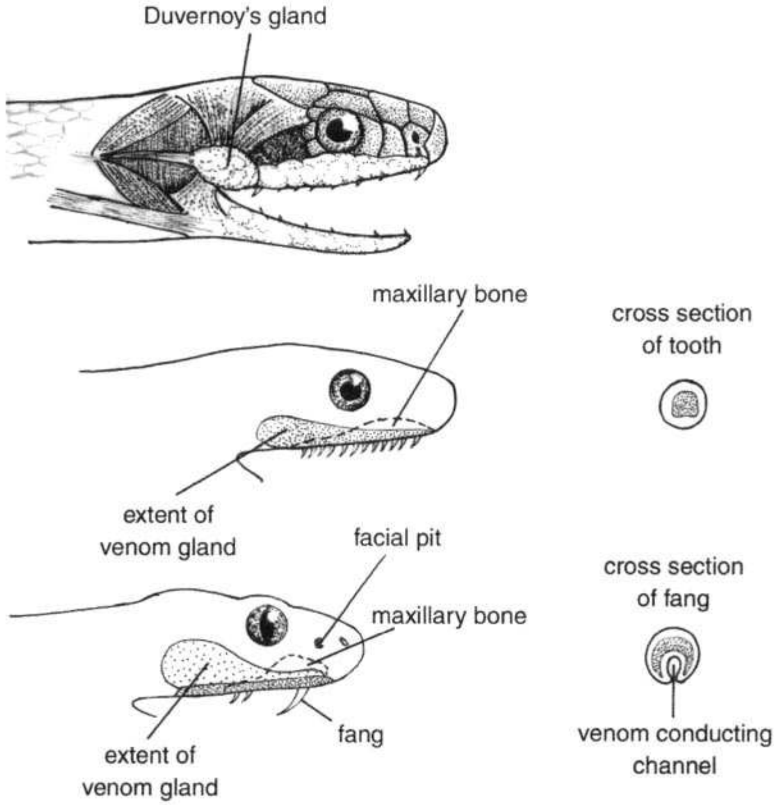

Figure 10.2 Schematic representation of the venom apparatus of Alberta snakes. In (a) and (b) the rear-fanged mechanism of a garter snake is depicted, while in (c) the front-fanged arrangement of the rattlesnake is shown.

substances that are used primarily in defence and generally require contact by the aggressor for their release and transference. Venoms, on the other hand, are chemical compounds that are employed primarily in food acquisition, and are associated with some sort of venom-delivery mechanism and a precise set of actions on behalf of the envenomator for transference.

Skin toxins in amphibians may be derived from a large number of different compounds of several classes. Alkaloids and steroids are among the more commonly occurring building blocks of salamander and frog poisons. Two of the most potent toxins are tarichotoxin and batrachotoxin. These are actually collective terms for a number of very similar compounds. The former is found chiefly in newts and the latter in the arrow-poison frogs. Their effects on would-be predators include paralysis and cardiac arrest. These result from the actions of the toxins on nervous tissue at the cellular level and reflect a disruption of the electrical potentials of the cell membranes necessary for normal function. These toxins are generally extremely rapid in their actions and thus become additionally problematic when humans are involved. The toxins of some arrow-poison frogs are so powerful that one one-ten-thousandth of a gram is sufficient to kill an adult human. The effect of most amphibian toxins is somewhat less dramatic. These typically act as irritants, causing nausea, inflammation and inconvenience rather than death of the recipient. It should be noted that the more lethal toxins are generally associated with aposematic (warning) coloration patterns that, by association, are sufficient to deter most would-be predators.

Venoms are characteristic of a number of snake families (Elapidae, Hydrophiidae, Viperidae and some Colubridae) and one lizard family (Helodermatidae). The venom apparatus generally consists of a venom gland and associated muscles, one or more ducts and an injection mechanism derived from the teeth. In snakes, the venom apparatus is always present in the upper jaw, while in the venomous lizards, it is associated with the lower jaw. Venom glands appear to be derived from salivary-like dental glands and may have evolved several times within snakes. Many colubrids possess a Duvernoy's gland (Fig. 10.2a) which produces mildly to highly potent venom. In these snakes, there is generally no musculature associated with the gland and venom is delivered via enlarged teeth at the posterior end of the maxillary bone (the largest bone of the upper jaw). These teeth may or may not have grooves for directing the venom towards the site of injection (Fig. 10.2b). Venom secretion is not copious and these so-called "rear-fanged" colubrids must often grip prey for extended periods to ensure adequate envenomation. Such a venom apparatus characterizes *Thamnophis* and *Heterodon.*

The venom gland in elapids and sea snakes is somewhat similar to the Duvernoy's gland of colubrids, but venom is injected, with the aid of muscles, by enlarged, grooved or hollow fangs at the front of the mouth (Fig. 10.2c). The most elaborate system is that seen in viperids, including pit vipers like the prairie rattlesnake. The venom glands are large and can store copious amounts of secretion, and the large, hollow fangs are erected during the strike as part of the complex kinetic movements of the skull.

Venoms are generally colourless-to-amber liquids containing approximately twenty to seventy percent protein. Although a large number of proteins and polypeptides have been characterized from snake venoms, the most important group is polypeptide neurotoxins. These act to block nerve transmission and are most common in the elapids and sea snakes. Envenomations by these snakes frequently result in paralysis, loss of motor control and ultimately death by asphyxiation. Other components of the venom may act directly on cardiac tissue.

A variety of enzymes in snake venom may cause thrombosis or destroy clotting factors of the blood and cause haemorrhaging, and may also contribute to the breakdown of skeletal muscle. Haemorrhaging is particularly symptomatic of bites of the dangerously venomous rear-fanged colubrids (none of which occur in North America). These enzymatic functions, which may be generally termed "haemolytic," may occur in concert with neurotoxic effects to produce a variety of severe symptoms typical of envenomation. The enzymatic effects are related to the original digestive function of the oral secretions and cause tissue breakdown, while the neurotoxic effects are involved with immobilization of the prey. Viperids seem to have evolved their particular venom system as a means of subduing the relatively large animals that they typically prey upon (Fig. 10.3). When the venom is employed as a defence rather than as a means of prey acquisition, the effects are the same, and the victim's suffering allows the snake to escape. Like vipers in general, the venom of *Crotalus viridis* is primarily haemolytic in its actions. Bites of this species are usually associated with intense pain, nausea and extensive tissue damage in the area of the wound. Without treatment, systemic effects such as kidney failure and shock may also ensue. The potency of prairie rattlesnake venom is comparable to that of most other North American viperids, but because of the relatively small size of this species, mechanical damage and venom dosage are likely to be reduced in comparison with other, larger species of rattlesnake with equally potent venom.

Snake bite worldwide is a relatively serious health threat. As many as one million people may be bitten annually. Of these, perhaps 40,000 die as a result. Numbers for North America are much lower. In the United States, there are approximately 45,000 snake bites reported annually, of which only 7-8,000 are caused by venomous species. The number of deaths is generally fewer than fifteen per year. Although published figures are not available for Alberta, incidence of envenomation in Montana (where prairie rattlesnakes are much more widespread) is five to sixty-three per 100,000 population. We know of no fatalities due to rattlesnake bite in Alberta.

In Alberta, snake bite is most likely to occur in the rural areas of the southeastern corner. North of Trochu and west of High River rattlesnakes do not occur, and all bites may be assumed to be attributable

Figure 10.3 A rattlesnake subduing a rodent.

to harmless species. Within the range of *Crotalus* both *Heterodon* and *Pituophis* may be mistaken for rattlesnakes, and in fact *Pituophis,* which may be quite aggressive, may be the most likely snake to bite in this region.

Snake bite is most likely to occur between May and September, when snakes are active, and will almost certainly be associated with chance encounters. The extremities, and particularly the lower leg, are most likely to be bitten. In most cases, the victim inadvertently disturbs the snake, or accidentally steps on or touches a concealed snake. Some bites, however, are due to overt provocation after encountering a snake. Given these circumstances the risk of snake bite can be minimized by:

- Avoiding placing hands and feet into burrows, crevices or other places where a snake may be concealed;
- Refraining from purposely disturbing snakes, attempting to capture or to kill them;
- Avoiding touching or handling apparently dead snakes;
- Wearing long, loose-fitting pants and high-top leather boots while walking in snake country;
- Avoiding walking in tall grass or other areas where a snake on the ground may be concealed.

Before rattlesnakes strike, they do not always (contrary to popular belief) rattle a warning. In a strike, the snake may extend up to two thirds of its body length. Bluff strikes may occur with the mouth open or closed. Strikes that reach their target may not always result in penetration or envenomation. Actual envenomation may vary greatly in its severity, since the snake can control how much venom is released during a bite. Should there be any signs at all of penetration, the following precautions and actions should be taken immediately:

- Remain calm (remember that most prairie rattlesnake bites do not result in lasting damage if treated).
- Avoid excessive movement as the spread of venom may be promoted by muscular activity. If possible, immobilize the bitten area and maintain it below heart level. A pressure bandage may be applied to the wound.
- Arrange transportation to a hospital as soon as possible (all areas of Alberta in which prairie rattlesnakes occur are within a maximum of three hours travelling time from a hospital).

DO NOT make incisions in the area of the wound or apply a tourniquet. These actions may be beneficial under some circumstances if performed correctly, but may in fact exacerbate the effects of the envenomation itself. Do not attempt to kill or capture the offending snake in order to make an identification as this may result in being bitten a second time.

The following hospitals in southeastern Alberta and north central Montana maintain a supply of antivenin:

Milk River	(403) 647-3500
Medicine Hat	(403) 529-8000
Lethbridge	(403) 382-6111
Brooks	(403) 362-3456
Foothills Hospital, Calgary	(403) 670-1110
Havre, Montana,	(406) 265-2211
Shelby, Montana	(406) 434-5536
Great Falls, Montana	(406) 761-1200

It should be noted that antivenin is not always necessary and its use carries a certain risk because of possible allergic reactions. Symptoms of envenomation may be highly variable, but the following account of an incidence of prairie rattlesnake bite is illustrative. This episode took place in the summer of 1988 in Writing-on-Stone Provincial Park; the victim was a field biologist.

On one occasion I was handling a medium sized rattler (approx. 50 cm in length) and accidentally loosened my grip on it enough for it to twist around and bite me on the index finger. The bite itself was not painful, considerably less so than a bee sting, and happened so quickly that I barely realized what had happened. The bite bled for a short time. My finger began to swell immediately, and after five minutes I was unable to bend it because of the swelling. The swelling continued to progress up to the base of my finger and across the other knuckles and within ten minutes began to move up my arm. It did not affect the other fingers on my hand. With the swelling came a numb feeling.

After about 30 minutes, I began to have a tingling sensation in my mouth, lips and tongue. An hour after receiving the bite my forearm was swollen. At about this time I noticed a licorice taste in my mouth, and the arm and afflicted hand began to tingle with a sensation similar to that of a hand or foot being "asleep." It felt as if my forearm muscles were vibrating, but no actual movement was noticeable. At the same time I also experienced this sensation in the opposite hand, which had not been bitten and was not swollen. The spread of the swelling seemed to stop by about three to four hours after the bite, and it did not progress beyond my elbow, although my armpit was painful when touched.

Once in the hospital the bite was disinfected and anti-venin was administered. In my case anti-venin was used since I showed no reaction to the preliminary test. (Depending upon the amount of anti-venin administered, a secondary allergic reaction a week to ten days afterwards may be experienced.) Exactly a week after I received the anti-venin my body broke out in a painful rash and was only soothed with anti-histamines over a period of four to five days.

Significant references: Aird and Kaiser 1985; Aird et al. 1985; Arnold and Bennett 1984; Buckley and Porges 1956; Daly et al. 1978; Dowling et al. 1968; Gans 1978; Gennaro et al. 1961; Greene 1985; Hardy 1988a, b, 1989; Herzog and Bailey 1987; Herzog and Burghardt 1986; Jansen and Foehring 1983; Kardong 1979, 1983; Klauber 1972; Kochva 1978a, b, 1987; Kochva et al. 1983; McKinstry 1978; Mebs 1978, 1985; Ohsaka et al. 1976; Parrish 1957, 1966; Rosenberg et al. 1985a, b; Rosenberg, 1978; Rosenfeld et al. 1968; Russell 1966, 1969, 1980, 1984; Russell and Michaelis 1960; Russell et al. 1962; Savitsky 1980; Schaeffer et al. 1972, 1978; Stanic 1956; Strydom 1977; Swaroup and Grab 1954; Thomas and Pough 1979; Van Meirop 1976; Wagner and Prescott 1966; Watt 1978; Zwisler 1966.

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11 Amphibians, Reptiles and People

ALTHOUGH THE SCIENTIFIC STUDY of amphibians and reptiles is a relatively new field, man has long interacted with these animals at other levels. Many of the modern beliefs, perceptions and misconceptions regarding these animals stem from the earliest periods of Western civilization. The most obvious of these is the symbolizing of Satan by the snake. This representation of the snake as the embodiment of evil, as codified in the Bible, has persisted to the present day and must certainly contribute to the revulsion experienced by many in response to these reptiles. The Greco-Roman tradition has also contributed to modern thoughts about the herpetofauna. The Aesculapian emblem of the medical profession (two snakes intertwined) is a positive representation of serpents recognizable to most people. The association of turtles with wisdom is also derived from the earliest periods of Western history. Some beliefs were based on direct observation or inference from observed phenomena, as, for example, in the works of Aristotle. Others were purely fanciful, perhaps developed entirely for allegorical purposes and subsequently carried on through oral and written tradition, as in Aesop's fables.

In non-Western societies, amphibians and reptiles have often played important roles in religion and social custom. This was and is especially true in tropical and subtropical regions where these animals are both more abundant and more likely to be encountered in daily routine. Cultures from Egypt to India to Central America have worshipped snakes, crocodiles and turtles as gods. The Egyptians mummified the Nile crocodile, *Crocodylus niloticus,* in association with its role in their pantheon. Quetzalcoatl, one of the primary deities of the Aztecs, was at least in part based on a snake. Similar traditions exist today; indeed, the softshell turtle *Aspideretes nigricans* is known only from a single temple pond in Bangladesh where it is revered because of its supposed relationship to a holy man of the eighteenth century.

In North America, aboriginal peoples also incorporated the herpetofauna into their religion and folklore. Perhaps the best known examples are those of Indians of the American southwest, especially the Hopis, who incorporated rattlesnakes into their "snake dances." The Seminoles of Florida likewise involved *Alligator mississippiensis* in their rituals. Closer to Alberta, the Indians of the Pacific coast represented frogs along with other animals in their totem poles and had specific beliefs about the sometimes supernatural attributes of these animals. As in many cultures, frogs were associated with rain because of their sudden appearance at the onset of wet weather.

Today, there are hundreds of folk tales concerning reptiles and amphibians. Most arose as the result of ignorance—unexplained phenomena were often attributed to animals, frequently via some supernatural link. For example, salamanders in Europe were believed to be "born of fire" because they appeared crawling from logs thrown into a fire. Observers were unaware that these animals frequently retire to hollows or crevices in moist logs and did not recognize their issuing from the flames as the dash for escape that it was. Other beliefs, such as those of "milk snakes" and "hoop snakes," or that toads cause warts, are similarly based on misinterpretations but through tradition are established as credible, despite the fact that no observer has ever actually witnessed the phenomenon.

Reptiles even play a role in religious and social practices in the United States today. Certain cults advocate the handling of venomous snakes as a test of their faith. Such practices receive undue attention and serve to further reinforce the abhorrence that the general populace has for these maligned creatures.

Amphibians and reptiles have also traditionally played an important role in the practical life of man. Larger species, especially turtles, boid snakes and monitor lizards, have been used by man as food, and the skins and shells of these animals have served to produce clothing, containers, and a variety of other implements of daily use. In our society today, snake, crocodilian, and lizard skins are used to produce shoes, wallets, handbags, belts and other items of self-adornment. Tortoise shell is used as decorative inlay and for other ornamental purposes. Turtles, frogs, and to a lesser extent other amphibians and reptiles are harvested commercially for human consumption and for use in biological laboratories. Such practices may place severe pressure on their populations. In combination with traditional beliefs, which have assigned a very low level of appreciation for these animals as living things, commercial harvesting of the herpetofauna has, until quite recently, resulted in the thoughtless slaughter of large numbers of many taxa.

However, the direct commercial exploitation of amphibians and reptiles is probably only highly significant for relatively few species, such as crocodilians and sea turtles. Indirect effects of human activity are much more significant and much more indiscriminate, and impact upon a much wider array of species. It is these effects that are most directly pertinent to the herpetofauna of Alberta. Unfortunately, most processes involved in human growth and expansion are in some way detrimental to wildlife in general and amphibians and reptiles in particular. The most extreme example is the process of urbanization. It replaces usable habitat with unusable, and typically results in the local extinction of populations and the fragmentation of once-continuous ranges. Agriculture, as well, has a significant impact on the herpetofauna. While rangeland appears to be relatively undisturbed at a gross level, the intervention of humans and cattle changes its vegetational composition and physically disturbs the local environment in such a way as to render the habitat unsuitable or suboptimal for many species. This restricts populations to isolated pockets of remaining habitat and affects the possibility of gene flow between them. In crop land, the application of pesticides and herbicides and the substrate disturbance by farm machinery may kill animals directly, or prevent successful breeding. These processes occur worldwide and the current emphasis on the conservation of tropical biodiversity should not blind us to the fact that the same destruction affecting the Third World today has already left its mark on North America and Europe.

Nonetheless, habitat changes do not affect all species to the same extent. Some taxa are able to live and even thrive in disturbed habitats, occupying vacant lots in cities or using cattle tanks and dugouts as breeding sites. Still others are sensitive to even the smallest perturbations. Pollution in the form of acid rain, perhaps generated hundreds of kilometres away, may change the habitat in ways that are not immediately visible, but may be significant enough to inhibit or totally suppress breeding in amphibians. At least some lakes containing long-toed salamanders are known to have undergone significant decrease in pH over the last twenty-five years, perhaps contributing to decreased survival in some populations. Changes in the acidity of the soil may likewise have detrimental effects on the adults of burrowing amphibians. Water pollution or other factors may impact directly on the herpetofauna or may have their effect on other components in the food web (Fig. 7.1), disrupting the flow of energy through the ecosystem. Another indirect effect is the introduction of potential predators or competitors into the environment, as is the case for declines in *Ambystoma tigrinum* induced by the introduction of predatory fish.

The above factors are of worldwide import, and, while they may appear to be more significant in other regions, each can be illustrated by examples from Alberta. Historical records indicate that urbanization has had a significant impact on the persistence of amphibians and reptiles in what are now urban centres in Alberta. For example, tiger salamanders and leopard frogs were once common in areas of Calgary that are now developed. The University of Calgary, which was, at the time of its founding, on the northwest periphery of the city and adjacent to prime amphibian habitat, is now in a fully urban setting. Amphibian species common on the campus in the 1960s cannot now be found within ten kilometres of this location. Traffic flow in the expanding city has also had its impact on habitat destruction. A case in point is the intersection at Highways 2 and 22X in the southern extremity of Calgary. Prior to these major roadworks being undertaken, several ponds existed immediately to the west of Highway 2. These ponds harboured abundant populations of tiger salamanders, chorus frogs, wood frogs, and boreal toads (as well as their garter snake predators), which since construction have been extirpated with the destruction of the ponds. Horned lizards have never been widespread in the province and the northern extent of their recorded range is in the vicinity of Medicine Hat. Along the banks of the South Saskatchewan River, within the city limits of Medicine Hat, are known localities of horned lizards that have not yielded records or sightings of specimens for several decades. While the habitat of these animals has not been subjected directly to construction, the increased pressures brought on these areas by an expanding urban population and their vehicular traffic have probably resulted in their disappearance.

Over the last hundred years, the short-grass prairie and aspen parkland regions of the province have come under extensive agricultural use. Some species of amphibians and reptiles have been rather sensitive to this mode of disturbance, and their numbers and ranges appear to have declined drastically. In the far southeastern corner of the province, the hog-nosed snake appears not to have adapted well to this change in land use. Rattlesnakes, too, have declined in range and abundance over this period. Records from as far north as Trochu and as far west as High River greatly exceed the apparent current boundaries of the species. These snakes, which may be limited by the availability of overwintering hibernacula as well as appropriate habitat, also suffer from direct persecution by humans because of their venomous properties. Agricultural practices may also have had a negative impact on amphibians, especially the burrowing species (spadefoot toad and Great Plains toad) through soil compaction and water diversion. In this case, however, irrigation and the availability of artificial ponds and cattle tanks may have compensated to some extent. In the boreal forest and the Rocky Mountains, logging poses a similar threat to the herpetofauna. Species such as *Rana luteiventris* and *Ambystoma macrodactylum*, which require cool, clean water for breeding, may be locally threatened by the results of practices that tend to raise temperatures through exposure and introduce pollutants generated by pulping. Two species that may yet be found in Alberta—the tailed frog, *Ascaphus truei*, and the rubber boa, *Charina bottae*—also occur in mountainous areas and could be affected by such activities. Fortunately, much of the rather fragile forested habitat of Alberta is encompassed within the boundaries of three national parks and has been further enhanced by the setting aside by the provincial government of protected areas, such as Kananaskis Country.

Since the late 1970s, there has been a drastic decline in the populations of the leopard frog in Alberta. This species once ranged across the majority of the province but is now only rarely encountered. Other species, such as *Rana sylvatica*, are doing well, however. At present, the reason for this decline of some species is unknown, but it is possible that direct or indirect effects of pollution may be responsible. Drought has almost certainly affected species in some parts of the province, as it has in the Yosemite region of California. Amphibians are generally sensitive bioindicators, and their decline around the world during the last decade may be taken as evidence of changing global conditions.

Beginning in the 1980s scientists around the world began to note the disappearance or reduction in population size of many amphibian species. The species affected were distributed from the tropics to the temperate zones, at a variety of elevations, and occurred from pristine to severely degraded habitats. The apparent ubiquity of amphibian declines led many people to the conclusion that one or more causal agents, acting at a global level, might be at work. Among the suggested causes of amphibian decline are global changes associated with the thinning of the ozone layer and subsequent penetration of ultraviolet light to the earth's surface; global warming as a result of "greenhouse gas" accumulation; biomagnification (the concentration of pollutants and harmful chemicals at higher trophic levels in the food web); and the disruption of reproductive cycles and cell growth and differentiation by man-made chemicals that mimic or interfere with the actions of hormones.

It has been demonstrated that exposure to excessive ultraviolet radiation can be damaging or lethal to amphibians. The susceptibility to this source of damage, however, is both life-stage and species specific. Eggs and larvae are especially at risk. Increased ultraviolet radiation may also promote the growth of fungi or bacteria, which can proliferate and cause fatal infections in amphibians. In particular, the bacterium *Aeromonas hydrophila* has been implicated in the disappearance of entire populations of *Bufo boreas* in the mountains of Colorado. Although this bacterium is naturally occurring and typically not a cause of mortality, its impact may be devastating for amphibians experiencing high levels of stress. Such stress suppresses immune system function and leaves frogs and salamanders open to microbial attack. The stress itself may be the result of acid precipitation, habitat degradation, chemical pollutants or hormone mimics. The complex interplay of all of these factors has made the identification of causal agents in amphibian decline particularly difficult. Further, the fact that baseline data on amphibian populations prior to the period of supposed decline are generally lacking makes it nearly impossible to distinguish between global effects and the results of localized habitat loss or degradation. It is noteworthy that the three amphibian species that have been determined to be the most susceptible to ultraviolet radiation—*Bufo boreas, Bufo hemiophrys* and *Rana luteiventris*—all occur in Alberta.

Regardless of the causes of amphibian decline, the loss of local populations may have catastrophic effects for species as a whole. Many amphibians exhibit low levels of physiological tolerance, low mobility, and high fidelity for breeding sites. Taken together, these characteristics tend to reduce the likelihood of successful recolonization following local extirpation. As a result, a number of amphibian species, especially frogs, around the world have apparently become extinct within the last two decades. Luckily, the amphibians of Alberta are generally highly tolerant of at least some environmental extremes, and most have widespread and continuous distributions. Nonetheless, some Alberta amphibians (e.g., *Rana pipiens*) have suffered huge population declines, and we must not become complacent with respect to the fate of our native herpetofauna.

In Alberta, amphibians have also been affected by a number of introductions. Most notable has been the stocking of ponds and lakes with game fish. Many of these are predators upon amphibian larvae and adults and thus constitute an additional challenge to the stability of populations. Although highly productive and spatio-temporally complex lakes may be able to support the larvae of amphibians, such as *Ambystoma macrodactylum,* as well as fish populations, under other circumstances, fish predation on eggs and larvae may result in local extirpations of the native amphibians. The intentional or accidental transportation of salamander larvae (water dogs) may also be a problem. These animals, which are used as bait, are often moved between water bodies. This may extend the natural species' range and almost certainly disrupts existing geographically based genetic patterns. The same is true of painted turtles, which have been introduced (usually as released pets) from non-Alberta stocks into lakes and rivers as far north as Edmonton. In the long run, this could have negative consequences for the species. Finally, at least one species of introduced reptile, the snapping turtle, has been found at isolated localities in the province. While most non-native amphibians and reptiles are unable to cope with Alberta's harsh climate, some might be able to establish themselves, perturbing existing trophic webs.

Compounding the problems faced by amphibians and reptiles in the face of changing environments is the fact that humans, at least until very recently, have not been sympathetic, or even aware, of their plight. Mammals and birds are generally conspicuous and appealing to the general public. In addition, they, like many fish, are of considerable economic importance. Thus, conservation and management efforts have focussed largely on these vertebrates. Amphibians and reptiles, on the other hand, are typically inconspicuous, have little public appeal and are not a direct source of revenue to individuals or governments. Their role in food webs and community structure is enormous, and they are as integral a part of the balance of nature in Alberta, as they are elsewhere.

In more practical terms, amphibians and reptiles are generally beneficial to agriculture, consuming large numbers of potentially destructive insect and rodent pests. Likewise, mosquitos and other insects are also kept in check to some degree by these animals by way of predation on aquatic larvae as well as adult stages. Snake venoms are used in the development and manufacture of numerous beneficial drugs, and amphibians were extensively used in pregnancy testing before the advent of other assay techniques. They are even employed in earthquake prediction!

Today, amphibians and reptiles do receive the official protection of the government. In national parks, all species are absolutely protected. Further, the trade in these animals is strictly regulated. CITES (Convention on International Trade of Endangered Species) dictates rules that govern the movement of protected species between countries. Alberta has no endemic (occurring only in the province) species of amphibians or reptiles. Some of the species that are uncommon in Alberta, such as the short-horned lizard, are very common elsewhere, while the Canadian toad, which is common in much of Alberta, is less frequently encountered to the south. The status of a species is therefore determined relative to a specific geographic area. In Canada, COSEWIC (Committee on the Status of Endangered Wildlife in Canada) has established definitions for several status categories. "Endangered" animals are those whose existence in Canada is threatened with immediate extinction throughout all or most of its range, owing to the action of man. "Threatened" species include any animals that are likely to become endangered in Canada if the factors affecting their vulnerability are not attenuated or eliminated. "Rare" species are those that because of their biological characteristics, or because they occur at the fringe of their range, or for some other reason, exist in low numbers or in very restricted areas in Canada but are not threatened species. Thus, by these definitions, *Chrysemys picta* and *Heterodon nasicus* are endangered in Alberta, occurring only in the Milk River and along the Saskatchewan border, respectively. Another peripheral species, *Phrynosoma hernandesi,* is considered threatened, and *Ambystoma macrodactylum* is viewed as rare. The other species in the province do not fall into these categories, but some, like *Rana pipiens,* may be vulnerable if numbers continue to decline and no cause for their disappearance is found. The Alberta Fish and Wildlife Division has begun to monitor some of these species and has developed a poster campaign in order to try to solicit information about sightings from the public. Information about this public awareness programme can be obtained from the Alberta Fish and Wildlife Division, 7th floor O. S. Longman Building, 6909 116 Street, Edmonton T6H 4P2, or from any Alberta Fish and Wildlife office.

The reptiles for which Alberta is most famous are those which are extinct. Paradoxically, most people seem to find those animals that are irretrievably gone more intriguing than those that are still with us. While efforts to save rare and endangered taxa are laudable, it is, in the long run, equally if not more important to make efforts to maintain those species that still have healthy populations. In so doing, we not only protect individual species, but also entire ecosystems. This is the key to preserving biodiversity. To do this effectively, it is necessary that conservation and management programs take into account amphibians and reptiles and other important, though inconspicuous, animal and plant groups. In this way we can guarantee the survival of the Alberta herpetofauna, with all of its practical and aesthetic value to man, and prevent these animals from following too closely in the footsteps of the dinosaurs.

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Glossary

We provide here a very short list of technical terms and their explanations. For those wishing to know more, we recommend that one of several available dictionaries of the life sciences or zoology be consulted. Especially helpful is J.E. Peters' *Dictionary of Herpetology* (New York: Hafner, 1964).

Actinopterygians: One of the major groupings of bony fishes, characterized by their flexible paired fins supported by fan-like skeletal rays. These fishes include among their ranks all familiar bony fishes, such as trout, salmon, pike, tuna and sole.

Allantois: A sac-like outgrowth of the ventral side of the hind gut in the embryos of amniote vertebrates (reptiles, birds and mammals). Excretory products of the embryo are stored in the allantoic cavity, and the surface of the allantois participates in embryonic gas exchange (see Fig. 2.6).

Amnion: The fluid-filled sac in which the embryos of amniote vertebrates (reptiles, birds and mammals) develop (see Fig. 2.6).

Amplexus: Sexual embrace of amphibians, whereby the male grasps the female's body with his forelimbs from a dorsal position. There are two principal types of grip—pectoral, in which the grip is just behind the forelimbs, and inguinal, where the female is grasped just anterior to her hind limbs.

Anthracosaurs: A group of Palaeozoic amphibians. Certain features of their skull and vertebral column suggest that among their ranks lies the ancestry of the amniote vertebrates (reptiles, birds and mammals) (see Fig. 2.1).

Anura: A group of amphibians consisting of the frogs and toads. The name refers to the typical absence of a tail.

Aposematic coloration: Colour patterns that warn a potential aggressor of potentially unpleasant consequences if molested. The familiar yellow and black coloration of wasps serves as an aposematic device.

Archosauromorphs: One of the two great branches of the diapsid reptiles. The archosauromorphs include the crocodylians, dinosaurs, pterosaurs, birds and a variety of other extinct groups (see Fig. 2.1).

Autotomy: Self-amputation of part of the body, typically the tail. The lost part is usually regenerated.

Basal metabolic rate: A measure of the energy required to maintain life processes while at complete rest. At a given temperatures this can be measured as the amount of oxygen consumed in a given time by a given mass of body tissue.

Biodiversity: The total array of life forms that exist in a given area, be it a forest ecosystem or the entire earth. A measure of species richness.

Biomass: Any quantitative estimate of the total mass of organisms comprising all or part of a population or any other specified unit, or within a given area at a given time.

Biome: A biogeographical region or formation; a major regional ecological community characterized by distinctive life forms and principal plant (terrestrial) or animal (marine) species.

Biota: The total flora and fauna of a given area.

Caecilians: Members of the Gymnophiona (see below).

Carapace: The dorsal component of the shell in turtles (see Figs. 3.1, 5.3).

Caudata: The group of living amphibians consisting of the salamanders and their close relatives.

Chin shields: Paired, elongated scales on the lower jaw of snakes between the lower ends of the labials (see below). They are usually present in two pairs, one anterior, one posterior.

Chorion: An embryonic membrane of amniote vertebrates (reptiles, birds and mammals) that encompasses the entire embryo and the other embryonic membranes, and participates in embryonic gas exchange (see Fig. 2.6).

Cladogram: A branching diagram representing the relationships between species or higher levels of organization (see Fig. 2.1).

Cleidoic egg: Egg of an amniote vertebrate (reptile, bird or [primitively] mammal) enclosed within a protective shell, which largely isolates it from its surroundings and permits only gas exchange and a limited amount of water exchange.

Cloaca: A terminal chamber at the end of the gut of most tetrapod vertebrates into which the digestive tract, reproductive system and urinary system open. A single opening connects the chamber with the outside.

Coelacanth: A living representative of a group of fleshy-finned bony fishes, the Actinistia (see Fig. 2.1), discovered off the coast of South Africa in 1938.

Costal grooves: Deep vertical grooves on the flanks of salamanders indicating the positions of ribs (see Fig. 3.1).

Cryoprotectants: Low molecular weight carbohydrates released into the blood and tissue fluids of anurans (see above) to lower the freezing point.

Demography: The study of populations, especially their growth rates and age structure.

Diapsida: One of the major groups of reptiles, characterized by having two temporal openings (two openings in the skull behind the eye). All living reptiles except the turtles are diapsids (see Fig. 2.1).

Diurnality: Being active by day.

Ectothermy: A strategy by which an organism attains its body temperature chiefly by way of external sources of heat (see Fig. 2.7).

Endothermy: A strategy by which an organism employs its own metabolic processes to provide its operating body temperature.

Environmental sex determination: A phenomenon in which an environmental factor, such as temperature, interacts with the developing embryo to determine the sex of that particular individual.

Extirpated: Locally extinct—refers to the elimination of a species from a portion of its range.

Fecundity: The potential reproductive capacity of an organism or population.

Gastralia: V-shaped, splint-like skeletal structures found in the muscles of the body wall along the belly of certain reptiles, such as crocodiles. They form an armor between the shoulder and hip girdles.

Gill rakers: Finger-like processes on the gill arches of larval amphibians that, as a group, function to prevent solid objects being passed through the gill clefts (see Fig. 5.8).

Gravid: Condition referring to egg- or embryo-containing females.

Gymnophiona: A group of amphibians consisting of the caecilians. They typically lack limbs and have a slender, elongate, snake-like body (see Fig. 2.3).

Heliothermy: A strategy employed by some poikilothermic (see below), ectothermic (see above) vertebrates whereby environmentally derived heat is picked up directly from the sun. Heliothermic animals typically bask (see Figs. 2.7 and 8.1).

Helminth: A member of one of several worm-like groups of invertebrates, some of which are parasitic and may occur in organs of amphibians and reptiles.

Hemipenes: Paired, eversible copulatory organs of male snakes and lizards. When retracted, they are held laterally in cavities at the base of the tail. They are everted by fluid pressure and are retracted by special muscles.

Herpetofauna: The entire amphibian and reptile fauna of a given area.

Herpetology: The scientific study of amphibians and reptiles.

Hibernaculum: The domicile in which an animal or group of animals overwinter.

Homeothermy: A physiologically based temperature-regulation strategy whereby the body temperature is maintained at a constant level independent of environmental temperature. This approach is energetically expensive but ensures the ability to be active at all times.

Internal fertilization: A means of fertilization in which the male and female gametes (sperm and egg) combine their genetic material within the female reproductive tract. This normally takes place with the assistance of copulation, but this is not necessarily so (see spermatophore, below).

Karst topography: Limestone terrain that has been severely eroded by the action of water. A distinctive type of country results, in which caves and underground river channels may be produced, and into which the surface drainage sinks by rifts and swallow holes. The resulting land is usually dry and relatively barren (see Fig. 8.3).

Keratinization: The addition of the hard, tough, fibrous, non-soluble protein keratin to the epidermis. This process provides the skin with its resistance to water loss, which is very evident in reptiles, and forms the basis for such epidermal elaborations as horns, claws and spines (see Fig. 9.2).

Labial scales: The scales that border the mouth in reptiles. They form the "lips" and are present on the upper and lower jaws (see Fig. 5.6).

Larva: The post-embryonic and preadult stage of metamorphosing species of amphibian. The term is more inclusive than "tadpole," which specifically describes the larva of anurans (see above).

Lepidosauromorpha: One of the two great branches of the diapsid reptiles. The lepidosauromorphs include the tuatara, lizards and snakes, and a variety of other extinct groups (see Fig. 2.1).

Lissamphibia: The collective term for the three groups of living amphibians—the Anura, Caudata and Gymnophiona. There is still some debate as to whether or not this is a natural grouping (see Fig. 2.1).

Mental glands: Glands producing sexually stimulating exudates that are located beneath the skin of the chin in certain male salamanders. The secretions are rubbed onto the body of the female.

Metamorphosis: The transformation from the larval (see above) to the adult condition in amphibians. External changes are used as indicators of the degree of completeness of the transformation (see Figs. 7.7, 7.8).

Neoteny: Paedomorphosis (see below) produced by retardation of somatic development, so that sexual maturity is attained in an organism retaining juvenile characters.

Nictitating membrane: A thin, transparent fold of conjunctival tissue in the inner angle of the eye, which can be drawn across the eyeball and can protect the eye without obscuring vision. Also known as the third eyelid.

Nocturnality: Being active by night.

Nuptial pads: Dark, usually roughened areas on the hands and other regions of male frogs. Those on the hands assist in gripping the female during amplexus (see above). Nuptial pads are associated with the breeding cycle and disappear when the animals are sexually inactive.

Ontogeny: The course of growth and development to maturity of an individual.

Osteoderms: Bony deposits in the form of plates or scales found in the dermal layers of the skin. They constitute a form of armor plating. Gastralia (see above) are often considered to be derivatives of osteoderms.

Oviparity: The production of young by means of eggs that are released from the ovary, fertilized, provided with enveloping membranes and/or a shell, and expelled from the body almost immediately to undergo further development.

Paedomorphosis: The retention of juvenile characters of ancestral forms by adults. One means by which this is achieved is the process of neoteny (see above).

Parotoid glands: In anuran amphibians, large, swollen areas lying behind the eye on the head, and in some species extending well onto the neck and shoulder region. Prominently developed in bufonids (see Fig. 5.1).

Pentadactyl: Descriptive of a limb with five digits (fingers or toes).

Plastron: The ventral part of the turtle shell (see Fig. 5.3).

Poikilothermy: A behaviourally based temperature, regulation strategy in which body temperature varies with that of the immediate surroundings. Regulatory mechanisms are associated with ectothermy (see above), heliothermy (see above), and thigmothermy (see below) (see Fig. 2.7).

Rhipidistians: Fleshy-finned bony fishes of the Paleozoic era that are thought to be the closest relatives of tetrapods (see below) (see Fig. 2.1).

Sarcopterygians: One of the major groupings of bony fishes, characterized by their fleshy paired fins. These fishes include among their ranks the coelacanths (see above), lungfishes, and rhipidistians (see above), and it is from within their ranks that tetrapods (see below) are believed to have originated (see Fig. 2.1).

Spermatophore: A gelatinous mass consisting of a cone of jelly with a sperm cap on top, deposited by male salamanders during mating and picked up by the cloacal (see above) lips of the female (see Internal fertilization, above).

Squamata: A subgroup of the Lepidosauromorpha (see above) consisting of the lizards and snakes. The body is covered with horny scales of a specific structure (see Fig. 2.1).

Streptostyly: A condition found in lizards and snakes in which the quadrate bone of the skull is hinged at both ends. The lower jaw articulates with the lower end of the quadrate, forming one hinge, and the upper end of the quadrate is able to move on the braincase.

Supercooling: A process that permits the cooling of body fluids to below 0°C without the formation of ice crystals in the tissues. This is used by some amphibians and reptiles as an overwintering strategy.

Synapsida: One of the major groups of reptiles, characterized by having one temporal opening (one opening in the skull behind the eye). There are no living reptilian representatives, but the mammals are believed to be descended from synapsid reptilian ancestors (see Fig. 2.1).

Tadpole: The larva (see above) of an amphibian. This term is most frequently applied to the Anura.

Temnospondyls: A group of Palaeozoic amphibians. Certain features of their skull and vertebral column suggest that they show a close affinity to the Lissamphibia (see above), the living amphibians (see Fig. 2.1).

Temporal fenestrae: Any gap between the bones of the cheek region of the reptilian skull. The position of these openings in relation to the skull bones has been used in classification (see Diapsida and Synapsida, above).

Tetrapods: A clustering of all vertebrates (amphibians, reptiles, birds, and mammals) that bear paired limbs (primitively pentadactyl—see above) rather than paired fins.

Thigmothermy: A strategy employed by some poikilothermic (see above), ectothermic (see above) vertebrates, whereby environmentally derived heat is picked up from the substrate rather than directly from the sun (see Fig. 2.7).

Torpor: A dormant state.

Urostyle: The elongate, tapered posterior end of the vertebral column of anuran (see above) amphibians. It is composed of a number of fused vertebrae (see Fig. 2.5).

Vagility: The tendency of an organism or population to change its location or distribution with time.

Viviparity: The production of young by means of eggs that are released from the ovary, fertilized and then allowed to remain in the female reproductive tract to undergo further development. Such development may occur by eggs being incubated in the reproductive tract and hatching there (ovoviviparity) or by an association between maternal and fetal tissues permitting an exchange of nutrients and waste products (true viviparity). In neither case do eggs become deposited in the environment to incubate there.

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Note: Boldface numbers refer to definitions of terms, provided in the Glossary.

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