Chapter 2

Canada’s Grasslands as Habitat for Arthropods

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Abstract. The grasslands of Canada’s prairies provide a wide range of habitats that support innumerable mites, spiders, and insects. This chapter reviews and illustrates the most important of these habitats, starting with an overview of the impact that glaciation has had on the topography of our existing prairie grasslands and of abiotic attributes such as soils and fire. The biology of grasses, which are critical for the survival of all animals found here, are examined with an emphasis on the attributes that make grasses so important in grassland ecosystems. The role that bison once played in the sustainability of grassland biodiversity is also discussed. The chapter concludes with a description of aquatic systems, including rivers, riparian zones, irrigation reservoirs, ponds, sloughs, lakes, and saline lakes and their attributes as they relate to the biodiversity of arthropods.

Résumé. Les prairies canadiennes renferment une vaste gamme d’habitats propices à d’innombrables espèces d’acariens, d’arachnides et d’insectes. Ce chapitre examine et décrit les plus importants de ces habitats. Il propose d’abord un aperçu de l’impact des périodes de glaciation sur la topographie des prairies actuelles, et de certaines caractéristiques abiotiques de cette région—par exemple, les incendies et les sols. Nous examinons la biologie des graminées qui sont essentielles à la survie de tous les animaux présents dans ce milieu, en insistant sur les caractéristiques qui rendent ces espèces végétales si importantes dans les écosystèmes des prairies. Nous nous penchons également sur le rôle que les bisons ont joué autrefois dans le maintien de la biodiversité des prairies. Nous concluons avec une description des systèmes aquatiques—y compris les cours d’eau, les zones riveraines, les réservoirs d’irrigation, les étangs, les marécages, les lacs, les lacs salés et leurs caractéristiques—et de leur incidence sur la biodiversité des arthropodes.

Introduction

The grasslands of Canada’s prairies, at least those remaining in a somewhat natural state, provide habitats for a wide array of arthropod species, with the most dominant being within the mite, spider, and insect taxa. As is the case with arthropods in most other terrestrial habitats on the planet (Wilson 1992), more species of arthropods live on the grasslands than any other species of animal by far, and their populations far outnumber their nearest vertebrate rivals. Arthropods have evolved and adapted to living in all conceivable habitats on the grasslands.

The purpose of this chapter is to provide an overview of the diversity of grassland habitats occupied by arthropods, with an emphasis on the abiotic and biotic attributes that influence their distribution and abundance. The chapter starts with an overview of the impact of glaciation, followed by the role of soils and fire in the formation and maintenance of prairie ecosystems. Some prominent prairie plant life is discussed with an emphasis on grasses, which are an important source of food and shelter for many species of prairie arthropods.
Glaciation and Its Effects on Prairie Grasslands

The physical features we see today on the prairie grasslands of western Canada are the result of a multitude of geophysical events that have occurred over millions of years. The most recent events that shaped the prairies were a series of glacial periods that occurred over the Pleistocene Epoch that lasted from 1.6 million to 11,000 years before present (bp) (Dyke and Prest 1987). Each of the several glacial periods during this epoch covered Canada with a thick mantle of ice. Maximum glaciation occurred during the Wisconsin period, which peaked about 18,000 years ago (Brouillet and Whetstone 1993). Prairie grasslands were covered by the Laurentide ice sheet, whereas grasslands in southern British Columbia were covered by the Cordilleran ice sheet.

The continental ice sheets formed as a result of the planet cooling and the winter snows in northern regions not thawing during the following summers. The accumulated snows turned to ice because of their weight and compaction, and then the ice slowly began to move southward. The advancing ice sheets cooled the planet further, resulting in more snow turning to ice and an increase in the speed of the ice advance. In time, nearly all of Canada was covered by a mantle of ice, with the distributions of all flora and fauna becoming established in what is now the central and southern United States (Pielou 1991).

The planet began to warm about 18,000 years bp and the ice sheets began to melt. The southwestern prairies were the first areas to become ice free as the glaciers receded northward and the displaced flora and fauna slowly began to return (Matthews 1979). Vast amounts of water rushing away from the glaciers scoured out valleys and redistributed coarse-textured outwash. All rivers flowed southward as the receding ice sheets blocked their movement northward. Aquatic fauna used the rivers to disperse northward as the ice receded. Rivers carried silts and clays into large lakes that formed at the snouts of the receding glaciers, resulting in the lacustrine plains we see today as the glacial lakes drained. The retreat of the Laurentide ice sheet was toward the east-northeast. Therefore, postglacial warming and drying began first in the westernmost part of the plains, immediately east of the Rockies, and progressed eastward in the wake of the receding ice. Hence, the oldest prairies are those to the southwest, which became ice-free from 12,000 to 10,000 years bp (Brouillet and Whetstone 1993).

The receding ice sheets left a desolate landscape north of the prairies, with signs everywhere of their destructive power. All soils had been removed, other than those deposited in depressions as the ice sheets advanced, and slowly had to be formed before advanced plants could become re-established. Flowing waters from melting glaciers cut steep-sided ravines (Figs. 1 and 2). Common in southern Alberta and Saskatchewan, these ravines are called “coulees,” from the French verb “couler” (to flow or to run) (Beaty 1975). Snowmelt and rainwater continue to drain into these coulees and often into larger streams and rivers. Because of the moister conditions, the sides of coulees usually support grasses and herbs, with shrubs common on north-facing slopes and coulee bottoms. These sites provide important nesting, feeding, and sheltering areas for birds, mammals, and arthropods. Step-like layers are another feature of coulees. These layers, or “terracettes,” form on the sides of coulees (seen in the upper left of Fig. 1) in response to the slow downslope movement of covering soils or rock debris. Erosion of some coulees has resulted in them becoming very broad (Fig. 3), making them ideal for water storage (Fig. 4) for use in irrigation.

Accumulations of soil and rock formed ridges of debris pushed forward by the face of advancing glaciers. These accumulations, called “moraines,” were left behind when the glaciers receded. The Milk River Ridge (Fig. 5) in southern Alberta is one of the most
prominent of these moraines. Rivers south of this ridge ultimately empty into the Gulf of Mexico. Rivers north of this ridge drain into Hudson Bay. The Milk River Ridge is one of the few areas on the prairies that remained unglaciated.

Deposits of sand are another legacy of glaciation. Such deposits are called “glacioeolian” material and can be shaped by winds to form dunes. These dunes become stabilized and covered by vegetation. However, blowouts occur in places where the vegetation has been destroyed to allow sand movement. Examples are the Great Sand Hills of Saskatchewan (see Chapter 3) and Spruce Woods Provincial Park in Manitoba. Vegetation growing on dunes differs from that growing on nearby non-dune areas.

Large boulders called erratics were carried southward by advancing glaciers and then remained after the glaciers melted. One erratic alongside the road between Fort Macleod, Alberta, and the Head-Smashed-In Buffalo Jump (Fig. 6) is interesting because it sits in a depression caused by bison as they walked around the rock scraping ticks from their sides.

Meltwater from the Laurentide ice sheet formed large lakes whose waters were trapped between rising land on one side and the ice front on the other (Barnosky et al. 1987). Two of these lakes were Lake Agassiz and Lake McConnell. Lake Agassiz once covered all of southern Manitoba and parts of Saskatchewan and Ontario. The Laurentide ice sheet blocked the drainage of the prairies into what is today Hudson Bay. As a result, the waters of the Saskatchewan and other rivers backed up to form Lake Agassiz, which drained into the Mississippi River and Lake Superior. These same rivers now flow northeast to Hudson Bay. The frequent disruption and rearrangement for drainage systems had interesting biogeographical consequences for river fauna (Lehmkuhl 1980). The fine clay-like silt that accumulated on the bottom of Lake Agassiz is responsible for the fertility of the valleys of the Red and Souris rivers (Rannie et al. 1989).

Soils

Prairie soils are among the deepest and richest in the world and are a key reason that so much of the area has been converted to agriculture. They comprise minerals, organic matter, liquids, and gases stratified into layers called “horizons.” Each horizon, from the surface down to the underlying geological material, differs in vertical cross-section from adjacent horizons in properties such as colour, structure, and texture, and in chemical, biological, or mineral composition. These horizons reflect the formation of soil from the original parent material, which involves the physical breakdown or weathering of rock by water and changes in temperature, as well as biological activities, including the growth of plants, the decomposition of plant material, and the production of humus (soil organic matter) by the work of micro- and macro-organisms in the soil (Clayton et al. 1977). Parent material is the unconsolidated material from which soils develop and was deposited through the actions of ice, wind, water, or gravity. Materials deposited by glacial ice are referred to as “glacial till,” whereas gravels, sands, and silts deposited by moving water are referred to as “fluvial” deposits. Sands or silts deposited by wind are eolian deposits. Materials moved by water and deposited in lakes are referred to as lacustrine deposits.

The succession of layers or horizons extending from the surface down to the unaltered parent material is referred to as a soil profile (Clayton et al. 1977). Different horizons, referred to as A, B, or C, develop as a result of additions (e.g., organic matter from plants and animals; water), transfers within the soil profile (e.g., leaching; loss of nutrients; movement of materials such as clay, organic compounds, or minerals) and transformations (e.g., through chemical and biological reactions). The A horizon is at or near the surface
and usually has the most organic (e.g., humus) matter accumulation and contains the most invertebrates. This is the layer where most of the plowing occurs in cultivated soils, having a depth of around 10–15 cm. The B horizon usually has an enrichment or alteration of some materials, such as clay, and has more structure than the A horizon. The C horizon, closest to the parent material, is relatively unaffected by soil-forming processes.

Prairie soils consist of innumerable aggregations of organic and inorganic matter interspersed with an equally innumerable number of small pores. Life in the soil occurs on a
micro scale, and these small pores are large habitable spaces to the organisms that use them. Temperature in prairie soils is fairly constant, much more so than the air above. The humidity, which is crucial to many organisms, is high and much more constant than on the surface.

Classification of soils in Canada is based on the kinds, degree of development, and sequence of soil horizons recognizable in a soil profile (Clayton et al. 1977). The dominant soil in the grasslands is classified as Chernozemic. These soils have dark surface horizons that are high in organic matter and result from the slow decomposition of the roots of grasses under dry conditions. Much of the plant biomass that dies off each year is added to the soil through decomposition. Most Chernozemic soils in Canada are frozen during the winter and dry at some period each summer.

The three basic types of Chernozemic soils are referred to as Black, Dark Brown, and Brown. Black Chernozemic soils are found at the southern boundary of the aspen parkland and in the fescue grasslands (see Chapter 3). Dark Brown Chernozemic soils are found in an arc that stretches from southwestern Alberta across Saskatchewan to southwestern Manitoba. Brown Chernozemic soils are found in the driest parts of southeastern Alberta and southwestern Saskatchewan. These soils have a brownish upper horizon and are associated with xerophytic and mesophytic grasses, forbs, and shrubs (Fig. 7). In undisturbed areas, the upper horizon is usually darkest at the surface and becomes progressively lighter in colour with depth. Where the climate is drier, such as the southern Okanagan Valley, the soils may be a much lighter brown and commonly thicker than soils of the Brown Chernozemic and Dark Brown Chernozemic. Chernozemic soils are also found in the southern Okanagan Valley in British Columbia.

Solonetzic or “alkali” soils have high levels of salts and occur in parts of the dry southern prairies. Natural deposits of salts occur below the root zone in glacial till and underground deposits and are transported upward by both surface and groundwater (Hammer et al. 1975; Hammer and Haynes 1978). Salts are deposited on the surface when the salty water evaporates into the atmosphere.

An extensive literature describes the role of invertebrates below ground and in the decomposition processes that take place in grassland and other soils (Curry 1979, 1994; Swift et al. 1979; Petersen and Luxton 1982; Lussenhop 1992; Blossey and Hunt-Joshi 2003; Whiles and Charlton 2006; Nardi 2007). Much of the organic matter is incorporated into the soil in temperate climes by earthworms (Swift et al. 1979; Curry 1994), but the breakdown of material is done by fungi and bacteria (Swift et al. 1979; Petersen and Luxton 1982). However, arthropods are important in decomposition through indirect action as agents of comminution and propagule dispersal and as grazers of microflora, particularly fungi (e.g., Macfadyen 1978; Swift et al. 1979; Petersen and Luxton 1982; Seastedt 1984; Curry 1994). Acari and Collembola are considered the most important soil microarthropods (Wood 1966; Wallwork 1970; Swift et al. 1979; Curry 1994) (see Chapter 7). Seastedt (1984) found that the Acari and Collembola usually account for 95% of the soil arthropod fauna. Many species of beetles, flies, grasshoppers, and moths lay their eggs in the soil, and the immatures of many species live there as well. Many species of bees and wasps make their nests in the soil.

Fire

Prairie fires were a major force that shaped and sustained prairie grasslands before the arrival of Europeans (Rowe 1969). However, fires rarely occur naturally today because of changes in vegetation, roads, and human intervention. In the past, periodic fires increased
the primary productivity of grasslands above that of unburned sites (Blair 1997; Coppedge et al. 1998). Fire removes accumulated litter, speeds nutrient cycling, and can kill woody plant species, preventing or slowing their growth or invasion into grasslands (Daubenmire 1968; Wright and Bailey 1982; Gibson 1988; Collins and Steinauer 1998). Intermittent fires mediate plant competition and produce higher species richness. Grasses that appear after

Fig. 7. Profile of Brown Chernozemic soil in the dry prairies of southern Alberta. Note the thick layer of organic soil under the short grasses and sagebrush. Photograph by the author.
the surface is burned are nutritionally improved and grow more vigorously (Daubenmire 1968) and are therefore of greater benefit to both invertebrate and vertebrate herbivores.

**Prairie Plants**

Although Canada’s prairie flora is dominated by grasses adapted to dry conditions, the many types of open, semi-arid-to-mesic landscapes contain a rich diversity of other plants. Primitive species such as algae, lichens, and mosses inhabit the soil surface, as do many species of forbs and shrubs. Only a few of the more common prairie species will be mentioned here. The term “forbs” is used for broad-leaved herbs other than grasses, with little or no woody tissues, especially those growing in open prairie or meadows. Shrubs are woody plants of relatively low height, having several stems arising from the base. In contrast, trees are perennial woody plants of considerable size (usually over 6 m in height) with a single trunk and a distinct crown. Most species of shrubs and trees are found in the bottom of coulees and river valleys and around the margins of sloughs and lakes. The vertical stratification of the vegetation in grasslands creates a myriad of microhabitats for arthropods. All species of shrubs and trees of the grasslands of Canada have large arthropod loads (Ives and Wong 1988; Johnson and Lyon 1991).

The surface of soils, whether in the driest areas of grasslands on the prairies or in British Columbia, is host to complex microbial communities. In many areas, soils form a surface layer called a “cryptogamic crust” (Johansen 1993). These biological soil crusts comprise cyanobacteria, lichens, mosses, liverworts, green algae, microfungi, and bacteria and form over unvegetated areas between shrubs, grasses, and flowering plants in undisturbed sites. Cryptogamic crusts help stabilize the soil, prevent wind and water erosion, absorb moisture, and provide nitrogen and other nutrients for plant growth (Johansen 1993). In addition, they contribute to the water relations of soil-inhabiting insects.

Lichens grow on surfaces that are too harsh or limited for other organisms, such as the surface of rocks, the most common type being crustose lichens, and on the branches of shrubs and trees. Particularly noticeable on glacial erratics (Fig. 8), lichens are tolerant of heat, cold, and drought on the prairies and in southern British Columbia. About 800 species of lichens live on the grasslands of Canada (Brodo et al. 2001). Many species of invertebrates live on and among lichens, using them for concealment, shelter, or food (Gerson and Seaward 1977). Some ants build their nests beneath mats of lichens and are known to disperse lichen propagules (Bailey 1970).

Grasslands of the prairies and those of southern British Columbia are host to a multitude of more advanced plants with fascinating adaptations to dry habitats and close associations with specialized arthropods. For example, the prairie crocus (*Anemone patens* (L.)) is one of the first plants to flower in the spring. Its large, showy blooms often push up through the cold ground before the snow has melted and are a key source of food for bumble bees and other early pollinators. The buffalo bean, or golden bean (*Thermopsis rhombifolia* (Pursh) Richardson), a member of the pea family, occurs in dense patches throughout the prairies in dry open fields and on the sides of coulees (Fig. 9). It is also an important source of pollen and nectar for spring insects.

Perhaps no other group of plants better epitomizes the dry prairies than cacti (Stelfox and Vriend 1977). Three species of cacti are found in bare fields and on south-facing hills and coulees across the southern part of the three prairie provinces: the plains prickly pear *Opuntia polyacantha* Haw. (Fig. 10), the purple ball cactus or pincushion cactus *Escobaria vivipara* (Nutt.) Buxb (Fig. 11), and the pygmy prickly pear *Opuntia fragilis* (Nutt.) (Houston
All species are well adapted to survive the freezing temperatures prevalent during the long Canadian prairie winters. *Opuntia fragilis* also is found in the Peace River area of Alberta, which makes it the world’s northernmost cactus. Flowers of *O. polyacantha* attract many insect pollinators, especially beetles and bees (Osborn et al. 1988). It is found on dry open prairie, particularly south-facing slopes. Pincushion cactus is a perennial, leafless plant whose fleshy stems carry out photosynthesis. Both *O. fragilis* and *O. polyacantha* are found on the grasslands of southern British Columbia.

Most shrubs are found in the moister coulee bottoms or river valleys; however, some thrive in the driest of prairie habitats. Some of the more common shrubs include Saskatoon or western serviceberry (*Amelanchier alnifolia* (Nutt.)), which is common west of Manitoba along streams, prairie ravines, hillsides, and forested edges. Pin cherry (*Prunus pensylvanica* L.) is common to most forested areas of Canada and occurs on the river valleys of the grasslands and throughout southern Manitoba. Chokecherry (*Prunus virginiana* L.) is found across all of the prairies and southern British Columbia in protected, shaded areas. Wolf willow, or silverberry (*Elaeagnus commutata* Bernh.), is found on moist plains, ravines, slopes, coulees, and stream banks and can tolerate dry conditions on gravelly or light soil. Similarly, sagebrush (*Artemisia cana* Pursh) is found on dry hillsides, badlands, and coulees on light, well-drained soils. Prickly rose (*Rosa acicularis* Lindl.) is found on riverbanks in the south and at the edge of aspen forests to the north and in the Cypress Hills, whereas the common Woods’ rose (*Rosa woodsii* Lindl.) is widespread throughout the province in coulees, open areas, dry slopes, and river banks (see Chapter 12).
Native prairie trees typically grow on the flood plains of river bottoms, near sloughs and lakes, and where planted by humans (e.g., urban sites and around farms). Common species of trees in river valleys in southern Saskatchewan and Manitoba include Manitoba maple (Acer negundo L.) and green ash (Fraxinus pennsylvanica Marsh.). Bur oak (Quercus macrocarpa Michx.) is a characteristic species of the remaining tallgrass prairie and grows along the eastern edge of Saskatchewan. Trembling or aspen poplar (Populus tremuloides Michx.) occurs throughout the forested regions of Canada. It grows in the Cypress Hills and throughout the aspen parkland to the north of the grasslands in Alberta and Saskatchewan and all of Manitoba. The distribution of white birch (Betula papyrifera Marsh.) is similar to that of aspens. Balsam poplar (Populus balsamifera L.) co-occurs with aspen and white birch, but also grows in the river valleys of the south. Plains cottonwood (Populus deltoides Bartr. ex Marsh) occurs in river valleys of southern Alberta and Saskatchewan and across southern Manitoba (see Chapter 13). Narrow-leaf cottonwood (Populus angustifolia James) is found in a few river valleys in southern Alberta. Bebb or beaked willow (Salix bebbiana Sarg.), the most common tree-sized willow native to Canada, grows throughout the prairies. It forms thickets in flood plains of southern river valleys and around margins of sloughs.

Grasses

Grasses comprise one of the world’s four largest families of flowering plants, with approximately 600 genera and 7,500 species, and are the dominant flora on Canada’s grasslands (Gould and Shaw 1983). Grasses are a key source of food for thousands of species of animals ranging from mites to bison and are ideally adapted to the climatic conditions of the prairies, southern British Columbia, and a few other regions of Canada. Grasses are members of the family Poaceae within the monocotyledons and are thought to be of recent evolutionary origin (Owen 1980).

Grasses also have been arbitrarily placed into three groups based on their height (Coupland 1961, 1979; Looman 1963, 1982). Species of 15 to 60 cm in height at maturity are commonly referred to as short grasses, those from 60 to 120 cm as midgrasses, and those that exceed 120 cm as tallgrasses. Short grasses are most common in the driest regions of southern Alberta and Saskatchewan (e.g., in the rain shadow of the Rocky Mountains). Grasses of mid-height are found in the northern part of the prairies and near the aspen parkland, where moisture deficits are less severe. Tallgrasses are found in southern Manitoba, where there is more moisture than in grassland regions to the west. Tallgrass prairies are considered to be among the most productive vegetation types in the world (Kline 1997). They are dependent on fire and grazing for their perpetuation (Collins and Steinauer 1998; Knapp et al. 1999).

Although prairie grasses typically account for only about 20% of the total plant species, they account for about 90% of the biomass at any site (Coupland 1979). Most grasses are long-lived perennials with extensive root systems. Their architecture is simple compared with most forbs, shrubs, and trees, comprising four main parts: the roots, the stem (the culm), the leaves, and the flower head or inflorescence (Best et al. 1982; Zomlefer 1994). Each part has diagnostic features that help in identification (Looman 1982; Gould and Shaw 1983).

Leaves of grasses are narrow and designed to maximize photosynthesis while exposing little surface area to the sun’s drying rays (Younger and McKell 1972). Waxy coatings on the leaves reduce water loss from evaporation. The blades of some species curve inward to capture raindrops and direct moisture to the centre of the plant, where it can be absorbed by
the roots. The leaves of other species curl up in hot weather and when water is scarce, turning brown to minimize exposure to sun and wind and to slow their metabolic processes.

Most grasses have deep fibrous root systems, sometimes extending 1–2 m (Kline 1997). Grasses have fibrous secondary roots (the primary root disappears early in development) and can be annual or perennial.

Flowers of grasses are inconspicuous and are pollinated by the wind. Grasses have a characteristic fruit called a caryopsis (commonly called a grain, seed, or kernel) that consists of the ovary with one or more of the floret bracts attached. They are most often small, hard cylinders, sometimes with a long, thread-like “awn” on the end.

Grasses exhibit a variety of traits that allow them to tolerate both drought and fire, including intercalary meristems protected at the base of the leaves, below-ground nutrient reserves, and rapid growth (Younger and McKell 1972; Coughenour 1985; Reichman 1987). Grasses have their apical meristems about 2–3 cm below the surface of the ground such that grazing by ungulates does not prevent the regrowth of stems and leaves. Removal of the older upper aerial portions of the plant is thought to stimulate meristematic proliferation and the production of tillers, which increases plant fecundity (Owen 1980). Grasses are remarkably palatable and can sustain higher levels of herbivory than can other terrestrial plants (Wiegert and Owen 1971).

Vertebrate Herbivores and Their Interaction with Prairie Arthropods

The vegetation of prairie grasslands reflects adaptations to a long history of pressure by grazers, both large ungulates and invertebrates (Savage 2004; Anderson 2006). McNaughton (1984) suggested that grasslands and ungulates may have coevolved because grazing was such an integral part of the prairie ecosystem. In the past, grazing increased the diversity of plants, especially forbs, in response to selective feeding on grasses (Joern 2005). Even today, grazed sites have plants with higher nutritional quality and increased nutrient cycling compared with non-grazed sites (Frank and Evans 1997; Johnson and Matchett 2001). Heterogeneity in vegetation structure was also increased (Fuhlendorf and Eagle 2001), which would have benefited arthropods.

Many prairie forbs respond to grazing or pruning by growing into bushier plants, as do shrubs such as roses, which sprout new adventitious shoots when the above-ground parts are removed. Grazing also prevented trees from overtaking the grasslands because tree seedlings are destroyed when their tips are eaten (Campbell et al. 1994). In addition, grazing by ungulates recycles nitrogen through urine and feces, and the trampling opened up habitat for plant species that prefer disturbed sites. Grazers often preferentially eat the dominant grasses, thus releasing subdominant species such as forbs. All of these factors increased plant diversity (Collins and Steinauer 1998; Fuhlendorf and Eagle 2001).

Until the 1870s, prairie “oases” near the middle of southern Saskatchewan (e.g., Moose Mountain, Wood Mountain, Old Wives Lake, Cypress Hills, and Bears Paw Mountains) and areas to the west in Alberta (e.g., Porcupine Hills, Milk River Ridge, and drainages of the Oldman, Belly, Waterton, and St. Mary’s rivers) were rich with ungulates such as bison, moose, antelope, elk, and deer and with predators such as wolves, grizzly bears, and coyotes (Huck and Whiteway 1998). These mammalian species would have supported blood-feeding insects such as black flies, mosquitoes, horse flies, and deer flies, as well as other insects feeding on dung and carrion.

The most dominant grazer until the mid- to late 1800s was the plains bison (*Bison bison* L.) or “buffalo” (Fig. 12). An estimated 30–60 million bison roamed the plains of North
America prior to the arrival of Europeans (Roe 1970; Foster et al. 1992), but bison were nearly exterminated from the continent by 1879 (Potyondi 1995). Bison were a keystone species that had many ecological effects on prairie grasslands, which would have also influenced arthropods (Foster et al. 1992; Knapp et al. 1999). Grazing by bison altered the characteristics of habitats that were beneficial to grasshoppers and other insect herbivores (Vinton et al. 1993; Hartnett et al. 1996). There is evidence that grazing results in larger populations of grasshoppers than does fire (Joern 2005), even though fire also increases the nutritional quality of plants fed upon by grasshoppers (Blair 1997). From an ecological perspective, cattle may be equivalent to bison on grasslands because both feed primarily on graminoid species and disturb terrestrial communities (Fritz et al. 1999). However, cattle forage on a higher percentage of forbs and woody vegetation and feed on more species than did bison (Hartnett et al. 1996).

Natural fertilization provided by bison dung was probably an important factor in maintaining the Canadian prairies (Soper 1941). When the first European explorers arrived on the Canadian plains, they likely saw vast amounts of dung (Fig. 13), referred to as “buffalo chips,” before they confronted any animals. Early European visitors would have faced hazardous footing and fouled waterholes. Dung-feeding beetles and flies must have been among the most numerous insects on the prairies. Grasshoppers today feed on and thermoregulate within cavities of the dried dung of cattle and horses (O’Neill 1994) and likely did the same with bison dung.

Eyewitness accounts by early European travellers relate the impacts of huge herds of bison trampling and churning the soil (England and De Vos 1969), as still happens today on lands restocked with bison (Fig. 14). Excessive trampling when conditions were dry reduced the size of soil aggregates and broke up plant litter (Goudie 1993). Bison often walked in lines, leaving “highways” of packed earth that would have led to erosion. In river valleys and at the southern edge of the aspen parkland, bison uprooted trees (Fig. 15) by rubbing against them. The depression around the glacial erratic shown in Fig. 6 was caused by bison. They churned and fouled the water of lakes and sloughs (Fig. 16), which would have altered the suitability of these waters for aquatic invertebrates. Bison would have had a minimal impact on macroinvertebrate communities in streams because they crossed in single file (Fritz et al. 1999). In contrast, cattle cause more disturbance to streams because they spend more time in the water than did bison (Fritz et al. 1999) and consume woody vegetation along the banks (Hartnett et al. 1996).

Bison also made countless wallows that likely affected grassland arthropods. Wallows are circular depressions in the ground (Fig. 17) up to 30 cm in depth and 2–4 m across. They were made by bison rolling repeatedly on their sides to dust-bathe, shed their winter coats, gain relief from biting insects, and remove ticks and lice (Coppedge et al. 1999; McMillan et al. 2000). Bison wallows were once a widespread soil disturbance across the Great Plains and their vegetation often differed strikingly from that of the surrounding prairie (Trager et al. 2004). At some sites, the dark, pulverized soils in the wallows were used by grasshoppers for egg laying and thermoregulation. Many wallows filled with water in the spring and became ephemeral habitats for aquatic insects (Gerlanc and Kaufman 2003).

Many smaller species of grassland mammals consume insects as an important part of their diet (Pattie and Fisher 1999), including the common shrew (Sorex cinereus Kerr), the prairie shrew (Sorex haydeni Baird), and the striped skunk (Mephitis mephitis (Schreber)). Seven species of bats are found on the prairies and all are insectivores. The little brown bat (Myotis lucifugus (LeConte)) eats midges and mosquitoes over bodies of water. The hoary bat (Lasiurus cinereus (Palisot de Beauvois)) and the big brown bat (Eptesicus
fuscus Palisot de Beauvois) eat beetles and moths above fields, trees, water, and other open spaces.

Numerous species of insectivorous birds inhabit the grasslands (Fisher and Acorn 1998), such as the western bluebird (Sialia mexicana Swainson), the grasshopper sparrow (Ammodramus savannarum Gmelin), and the western meadowlark (Sturnella neglecta Audubon). Some insectivorous birds such as the burrowing owl (Athene cunicularia Molina) are now threatened because of habitat fragmentation and insecticides. Birds are also host to many species of mites (Knee and Proctor 1996), lice, and ticks (Galloway 2006).
Aquatic Habitats for Grassland Arthropods

Aquatic habitats on the prairies include large rivers, streams, lakes, wetlands (potholes and sloughs), and man-made reservoirs for irrigation. All of these have diverse assemblages of aquatic invertebrates. Some aquatic habitats such as saline lakes have unique characteristics and are more numerous on the prairies than anywhere else in the world.

There are at least 11 common orders of insects throughout the prairies that live part of their lives in or on water. These orders include Collembola (springtails), Ephemeroptera (mayflies), Odonata (dragonflies and damselflies), Plecoptera (stoneflies), Hemiptera (true bugs) (see Chapter 14), Coleoptera (beetles), Trichoptera (caddisflies), Lepidoptera (moths), Megaloptera (dobsonflies), Diptera (midges and flies), and Hymenoptera (wasps). Insects are important components of aquatic ecosystems, where they recycle much of the decaying plant and animal material back into the food web and are themselves food for fish and waterfowl. Adults are also food for insectivorous birds. Many of the familiar biting insects (mosquitoes, black flies, horse flies, deer flies, and no-see-ums) start their life cycles in lakes, ponds, rivers, and streams.

The greatest diversity is to be found with the macroinvertebrates, which are mostly aquatic stages of insects but also include clams and worms (Clifford 1991). Benthic invertebrates, usually the immatures of aquatic insects, live in or on the bottom mud, on aquatic plants, on or under rocks, on sunken or floating trees, and among the debris on the bottoms of lakes or streams. These animals eat almost all forms of organic material, such as bacteria, small algae, filamentous algae, large aquatic plants, decaying plant material, microscopic animals, other macroinvertebrates, or large dead animals.

Much has been written on the aquatic insects of North America and there is good coverage in the scientific literature of insects found in the aquatic habitats on Canada’s prairies. Examples of general works include Lehmkuhl (1979), Vinson and Hawkins (1998), Resh and Rosenberg (1984), Merritt and Cummins (1996), and Clifford (1991). Treatises on select taxa include Wiggins (1977; caddisflies), McAlpine et al. (1981, 1987; Diptera), Larson et al. (2000; dytiscid beetles), and Adler et al. (2004; black flies). Collecting and studying macroinvertebrates also provides an understanding of the biological health of aquatic ecosystems (Rosenberg and Resh 1993).

The aquatic insect fauna present on the prairies today is the result of immigration into the area after the Wisconsin glaciation (100,000–17,000 years bp) (Lehmkuhl 1980). Periods of glacial advance and retreat severed and re-established links between the prairie region and the southern refugia, Beringia, and the eastern Canadian refugia (Christiansen 1979).

Rivers

The most prominent aquatic habitats on the prairies are rivers and streams. Prairie rivers flow across the surface of the land in channels and are characterized by their one-directional downhill movement, variable levels of discharge, and associated parameters such as current velocity, depth, width, and turbidity; continual turbulence and mixing of water layers; and instability of bottom sediments. Each of these properties influences the diversity of insect fauna (Lehmkuhl 1979). The major rivers of the prairie grasslands begin as streams carrying meltwater from snowpack or glaciers in the eastern slopes of the Rocky Mountains. Streams then flow eastward through the foothills with their volume supplemented by tributaries bearing runoff from local snowmelt, rainfall within the river basin, and groundwater. However, the plains usually contribute less than 10% of the river’s volume (De Jong and Kachanoski 1987).
Two of the most interesting rivers in southern Alberta are the Milk River (Fig. 18) and the South Saskatchewan River (Fig. 19). The Milk River is in the smallest of Alberta’s river basins, encompassing an area of about 6,500 km². It enters Alberta from Montana and flows eastward through the southern portion of the province prior to looping back to Montana. The Milk River gets its name from particles called “natural rock flour” deposited upstream by glaciers and carried downstream via meltwater streams, where the particles of quartz and feldspar travel in suspension. All other rivers in southern Alberta are part of the South Saskatchewan River Basin, which includes the sub-basins of the Bow, Red Deer, Oldman, and South Saskatchewan rivers. The combined watershed of this basin is 121,095 km². The South Saskatchewan is the largest river in the southern prairies (Fig. 19). This broad river cuts deeply into the prairies with the banks along much of its route lined with stands of cottonwood (Populus spp.) trees. This river originates at the confluence of the Bow and Oldman rivers near Grassy Lake, Alberta, and flows through Medicine Hat into Lake Diefenbaker in Saskatchewan, the reservoir created by the construction of the Gardiner and Qu’Appelle River dams. Downstream from the dam, the river flows north through Saskatoon and joins the North Saskatchewan River east of Prince Albert, forming the Saskatchewan River.

The North Saskatchewan River Basin, to the north of the South Saskatchewan Basin, covers about 80,000 km² of Alberta. This basin begins in the ice fields of the Rocky Mountains and generally flows in an eastward direction to the Alberta–Saskatchewan border. The North Saskatchewan River joins the South Saskatchewan River near Prince Alberta, Saskatchewan, to form the Saskatchewan River, which enters Cedar Lake and Lake Winnipeg in Manitoba. They in turn drain into Hudson Bay via the Nelson River.

The Qu’Appelle River in southeastern Saskatchewan originates near Lake Diefenbaker and flows eastward to join the Assiniboine River, making it one of the few prairie rivers that does not originate in the Rocky Mountains. The Assiniboine River is a typical meandering river with a single main channel embanked within a flat, shallow valley. This river flows southeast from its source in eastern Saskatchewan and then into the Red River in Winnipeg. The Assiniboine River flows through an area of sandy parent material deposited by glacial meltwater that flowed into glacial Lake Agassiz. The Souris River originates in the southeastern corner of Saskatchewan and flows into North Dakota for a stretch before re-entering Manitoba and flowing into the Red River. The Red River arises in North Dakota and flows northward to Winnipeg across the flat former bottom of ancient glacial Lake Agassiz through what was once tallgrass prairie, where it joins with the Assiniboine River. The Red River then enters Lake Winnipeg and drains into Hudson Bay through the Nelson River. The Pembina River originates north of La Riviè re, Manitoba, flows southeast, entering the United States northeast of Langdon, North Dakota, and empties into the Red River. Significant areas of south-central Alberta and Saskatchewan are closed basins where waters flow into depressions that have no outflow (see Fig. 4 in Chapter 3). Such waters are saline.

The riparian zones of most prairie rivers have extensive stands of shrubs and trees along much of their length (Figs. 18–20). This unique band of vegetation is found between the river channel and that portion of the terrestrial landscape from the high-water mark toward the uplands, where vegetation may be influenced by elevated water tables (Naiman and Décamps 1997). Most riparian zones of prairie rivers are narrow, often less than 100 m wide. The microhabitats of riparian areas differ sharply from those of the nearby uplands (Fig. 20) by having more humidity, a higher rate of transpiration, and more shade, which in turn provides more opportunities for insects (Fitch and Adams 1998).
The flood plains of prairie rivers are sometimes close to the river’s edge (Figs. 18 and 19) and sometimes much farther away (Fig. 20). These riparian habitats often have grassy plains growing among the trees. More species of mammals (Fig. 20), birds, and insects are associated with the vegetation here than on the prairies above the river valleys.

Flood plains of prairie rivers are often physically complex with lateral channel migration and the formation of oxbow lakes in old river channels. Flood plains are often harsh environments for the establishment of plants and animals because they are subject to floods, erosion, abrasion by ice flows at spring break up, summer and winter droughts, and soil deposition (Wikum and Wali 1974). As a result, riparian plant communities are composed of disturbance-adapted species (Naiman and Décamp 1997). Trees such as cottonwoods and willows on the flood plains form stands called “gallery forests” (Kindscher and Holah 1998).

Periodic flood disturbances of various intensities are critical for maintaining riparian communities. All rivers in the South and North Saskatchewan River basins are subject to spring flooding, especially in years when heavy snowpack in the mountains melts quickly. These floods cover much of the flood plain, and the fast-moving waters, often with heavy chunks of ice, uproot trees and wash them downstream. Silts, sands, and clays are deposited along the banks and on shallow areas within the rivers. Piles of logs and branches are common along the valleys following floods (Fig. 21). They serve as ideal habitat for...
xylophagous species such as long-horned beetles of the family Cerambycidae and hornet wasps of the family Siricidae. Spring floods are much less severe today as a result of waters being stored in irrigation reservoirs.

Most organic matter in prairie streams and rivers comes from erosion of the banks (Naiman and Décamps 1997) and from leaves and branches that are deposited into the rivers. Organic matter from riparian vegetation is the main source of nourishment for aquatic organisms. Indeed, the presence or absence of riparian trees may be a key factor in sustaining the diversity of aquatic macroinvertebrates (Naiman and Décamps 1997).

Because many macroinvertebrates live in the stream year-round and sometimes over multiple years, their presence or absence provides valuable information about a river’s health (Rosenberg and Resh 1993). Macroinvertebrates are used to determine the impact of developments such as roads and urban sprawl and to assess the effects of contaminants such as pesticides, sewer effluent, and agricultural fertilizers. Aquatic insects are used in this role because they are diverse, they respond quickly, they are relatively sedentary and therefore cannot effectively leave the contaminated area, and each species reacts to pollutants in a characteristic manner.

**Irrigation Reservoirs**

Irrigation of crops is common in southern Alberta and parts of southern Saskatchewan. Because no major natural lakes are present from which to withdraw water for agriculture, the solution has been to store water behind dams in artificial lakes called irrigation reservoirs. Water diversion is developed and controlled within an irrigation district that is responsible for maintaining water supply to farmers.

Land-filled dams constructed across river valleys with wide and deep flood plains are used to irrigate crops in southern Alberta (Fig. 22). Water is held behind the dam (Fig. 23) to be diverted into an irrigation canal (Fig. 24) that directs water into a series of smaller ditches (Fig. 25), ultimately to be used by farmers to water their crops. The normal pattern in drainage basins is for waterways to develop in a dendritic manner, with small tributaries joining to form progressively larger, but fewer, streams in a downstream direction. Irrigating practitioners have reversed these drainage “trees” so that large dams divert water from the original river into irrigation systems that start from a main channel and then branch progressively into smaller and smaller channels before disappearing into fields. The flow pattern is also reversed, as most water from dams flows in the summer during dry periods and the channels lie dry the rest of the year. Irrigation does not follow a pattern to which most of the biota is adapted and may leave a highly skewed ecosystem in its wake. Much remains to be learned about arthropod biodiversity in these seasonal, artificial streams.

Most of the major river systems in the North and South Saskatchewan River basins have been dammed with large reservoirs formed behind them, with a total surface area of about 1,000 km² (De Jong and Kachanoski 1987). Especially large reservoirs are found on the St. Mary’s, Waterton, Oldman, South Saskatchewan, and Saskatchewan rivers (see Fig. 4 in Chapter 3). For example, Lake Diefenbaker is the reservoir formed behind the dam on the South Saskatchewan River near Outlook in southern Saskatchewan, and Tobin Lake was formed behind the E. B. Campbell Dam on the Saskatchewan River east of Prince Albert for producing electricity.

Although construction of irrigation reservoirs and water distribution systems has increased agricultural productivity on the prairies, large dams are detrimental to aquatic and downstream habitats because these dams reduce water flow, sediment flow, the size of flood plains and riparian zones, and overall ecosystem services (Dynesius and Nilsson...
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Changes in the thermal regime downstream from deep-release reservoirs such as Lake Diefenbaker in Saskatchewan, where warm waters are discharged in the winter and cold waters in the summer, alter the phenology of mayflies such that they can no longer survive (Lehmkuhl 1972). River mayflies depend on key temperatures to trigger embryological development, egg hatch, and the rate of development to synchronize the emergence of adults. They can no longer survive when these triggers disappear. Most mayflies and other members of the food chain have been eliminated in the South Saskatchewan River for up to 70 km downstream from the dam (Lehmkuhl 1972). Other studies have shown that reductions in flood magnitude, frequency, and sedimentation caused by dams on prairie rivers reduces the density of plains cottonwoods (Bradley and Smith 1986).

**Ponds and Lakes**

Potholes and sloughs are both types of ponds that occur on the prairies. They are scattered across an area of about 715,000 km² extending from north-central Iowa to central Alberta that is referred to as the prairie pothole region (De Jong and Kachanoski 1987). Most of these ponds are nutrient-rich with low acidity and they contain standing water seasonally to a maximum depth of 2 m. These prairie wetlands are systems where standing water or saturated soil is a dominant feature, at least seasonally, and hydrophytes (water-adapted plants) are the...
Figs. 26 and 27. Small water bodies in the southern prairies. Fig. 26. Steep-sided pothole in southern Saskatchewan. Fig. 27. Shallow prairie slough near Lethbridge, Alberta. Photographs by the author.
predominant rooted macrophytes (Whillans 1987). These ponds frequently contain cattails
(Typha spp.), bulrushes (Scirpus spp.), and reeds (Phragmites spp.) and shrubs such as
willows are frequently found around the edges (De Jong and Kachanoski 1987).

Potholes are often steep sided (Fig. 26) and form in depressions formed thousands of
years ago when chunks of ice that were left beneath glacial sediments melted, causing
the ground to slump. Water in these kettle-lake potholes is supplied by precipitation on the land
surface, basin runoff, or seepage inflow of groundwater. Sloughs are in gentle depressions
with wide shorelines (Fig. 27) on the surface of lacustrine deposits. Both potholes and
sloughs are shallow enough to support rooted plants across their width, and both vary in
size and may be temporary, seasonal, or permanent. Up to 26 potholes per km² occur in
some areas with glacial till, and up to 14 sloughs per km² occur on lacustrine deposits (De
Jong and Kachanoski 1987).

Arthropods of freshwater wetlands on the prairies and elsewhere in Canada are poorly
studied, with existing information limited and scattered (Rosenberg and Danks 1987). The
impetus for most past research on arthropods in this habitat came from studies of their dietary
value to waterfowl during the breeding season (Bartonek and Hickey 1969). However,
arthropods also provide critical food chain support for a wide variety of other organisms and
are important in nutrient cycling and overall wetland productivity (Murkin and Batt 1987).

Low arthropod diversity in prairie potholes likely reflects adverse conditions of the
region, including extremely harsh winters and fluctuating hydrology and chemistry. Prairie
potholes periodically go dry, freeze solid in winter, or exhibit steep salinity gradients. These
habitats have been referred to as “aestival ponds” (Daborn and Clifford 1974) because
they are effectively winter-dry habitats. They differ from other temporary aquatic habitats,
because the dry phase is a function of temperature rather than water supply; all biological
activity is restricted to the summer period (Rosenberg and Danks 1987). Many wetland
arthropods avoid the risk of freezing by flying to habitats that do not freeze completely,
whereas others are able to tolerate cold (Danks 1978). Some coenagrionid damselflies
become encased in ice but do not freeze (Sawchyn and Gillott 1975). Most Hemiptera and
Coleoptera overwinter as adults, and many migrate from shallow habitats to deeper ponds
and lakes (Danks 1978).

During extreme drought, distributions of wetland arthropods undergo severe spatial
reduction. As a result, most such species are specialists (e.g., chironomids) with extremely
short life cycles (Danks 1971) and/or are adapted to survive in highly saline waters
(Scudder 1987). For example, most adult Coleoptera and Hemiptera can withstand a wide
range in salinity and also are capable of flight to exploit the spatial and temporal dynamics
of prairie wetlands.

Recolonization and dispersal mechanisms for prairie pothole arthropods are poorly
studied. Flying insects can rapidly disperse into temporary and seasonal wetlands following
normal seasonal flooding. Flightless life stages of arthropods (e.g., eggs, larvae, and pupae)
must either survive in dry potholes in a resting state or recolonize previously dry wetlands
by using mechanisms such as eggs resistant to drying and freezing, diapause, aestivation,
waterproof secretions, burrowing, and the use of invertebrate and vertebrate wildlife to
transport them (Murkin and Batt 1987). Wiggins et al. (1980) outlined a temporal sequence
that is strongly influenced by climatic conditions, in which various taxa invade newly
flooded habitats. The early colonizing community is structurally simple and comprises
mostly r-selected detritivorous invertebrates. The community later becomes more complex
with the establishment of diverse plant species and the addition of predators and other
functional groups.
In contrast to ponds, lakes are larger, deeper, and more permanent bodies. However, the prairies have few lakes compared with other regions of Canada and most prairie lakes are small. Even so, many are deep enough (greater than 2 m) to contain water for long periods and to sustain fish during the winter. Prairie lakes vary greatly in size, with some, such as Pelican Lake (Fig. 28) near Mortlach, Saskatchewan, being larger than a slough but with shallow shorelines and high productivity. On the prairies in drier parts of Alberta, the larger lakes include Pakowki, Sullivan, Dowling, and Gough. In Saskatchewan, large lakes include Old Wives, Last Mountain, Chaplin, Crane, and Big Muddy. The largest lakes in the aspen parkland in Alberta are Wabamun, Cooking, Beaverhill, Sylvan, Pigeon, Gull, and Buffalo. In Saskatchewan, large lakes of the aspen parkland include Big Quill, Jackfish, Manito, and Lenore. In Manitoba, such lakes include Oak, Whitewater, and Pelican, as well as the southern extents of Lake Manitoba and Lake Winnipeg. Thousands of small lakes are present in the aspen parklands (Fig. 29) and many are inhabited by beavers and are highly productive.

Most permanent lakes on the prairies are saline, with freshwater lakes confined to uplands, drainage ways, or aspen parklands (Hammer 1984). Saline lakes are common across southern and central Alberta and Saskatchewan in closed basins (Last and Ginn 2005). These lakes are fed principally by surface inflow from runoff and small streams and are associated with dry climates, where evaporation exceeds precipitation (Hammer 1986).
No other area in the world can match the density and diversity of saline lakes found in this region of Canada and in the adjoining regions of the United States (Last and Ginn 2005). Estimates of the number of saline ponds and lakes vary from about 1 million to more than 10 million. Little Manitou Lake near Watrous, Saskatchewan, has a salinity greater than that of the Dead Sea. Big Quill and Old Wives lakes are among the six largest inland saline water bodies on the continent. Even Lake Manitoba, North America’s 13th largest lake, is a saline lake (Last and Ginn 2005).

Salt concentrations in these wetlands range from 3 to 370 parts per thousand (ppt) and are caused by one or more sodium, magnesium, and sulfate ions (Hammer et al. 1975). Because evaporation rates are high and precipitation is variable, both salinity and the size of a lake can change seasonally. When shallow saline lakes and ponds completely dry up, their bottoms become covered with salt crusts (Fig. 30). For other lakes, such as Chaplin Lake (Fig. 31) west of Moose Jaw, the shorelines are shallow and the mud flats are extensive with high concentrations of salts. Other lakes such as Ingebrigt Lake north of Maple Creek, Saskatchewan, have deposits of salts about 43 m thick (Last and Ginn 2005).

The most important factor in controlling the vegetation and animal life in saline lakes is the concentration of ions (Rawson and Moore 1944). Lakes with low salinity (2–10 ppt) usually have vegetation patterns similar to freshwater lakes. However, as salinity increases, the biodiversity declines. Lakes with high salinity are dominated by salt-tolerant organisms such as brine shrimp (Rawson and Moore 1944). The only common vascular vegetation is widgeon-grass (Ruppia spp.) and sago pondweed (Potamogeton pectinatus L.) (Hammer et al. 1975). These species become less abundant until the salinity increases to 50 ppt, and then no vascular vegetation can survive.

Hammer et al. (1975) and Timms and Hammer (1988) found that certain species of flies and beetles occur over the widest salinity range and had the greatest diversity. Some of the more common Odonata, Coleoptera, Hemiptera, and Diptera found in saline waters are listed by Williams (1979). Several species of Hemiptera are tolerant of salinity and are common in these water bodies (Scudder 1987; see Chapter 14).

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