Chapter 13
Black Flies (Diptera: Simuliidae)
of the Prairie Grasslands of Canada

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Mating pair of *Cnephia dacotensis*, the only obligatorily autogenous species of black fly from the Prairies Ecozone of Canada. Photo courtesy of Stephen A. Marshall.
**Abstract.** Only 18 of Canada’s 165 species of black flies are considered residents of the prairie grasslands. Topography and climate influence the quality and quantity of breeding sites, but host availability may also play a role in influencing species richness. Most species that dwell on the prairies are widely distributed, occurring in two or more ecozones. Only *Simulium johannseni* and *Simulium meridionale*, whose distributions fall largely within the Great Plains region, could be considered prairie-adapted species. Outbreaks of prairie black flies today tend to be localized and episodic, causing occasional discomfort to humans and domesticated animals. In general, the nuisance factor is minor compared with that in northern woodland areas. The role of prairie black flies in the transmission of disease agents, especially to wildlife, is not well understood.

**Résumé.** Seules 18 des 165 espèces de mouches noires (simulies) qui existent au Canada sont réputées être des espèces résidentes des prairies. La topographie et le climat influent sur la qualité et sur le nombre des sites de reproduction, mais la disponibilité des hôtes influence aussi probablement la diversité des espèces. La plupart des espèces qui vivent dans les prairies sont largement réparties, occupant au moins deux écozones. Seuls *Simulium johannseni* et *Simulium meridionale*, dont l’aire de répartition coïncide largement avec la région des Grandes Plaines, peuvent être considérés comme des espèces adaptées aux prairies. Les pullulations de mouches noires dans les prairies ont aujourd’hui tendance à être localisées et épisodiques, devenant à l’occasion une source d’inconfort pour les humains et les animaux domestiques. En règle générale, le facteur de nuisance est mineur si on le compare à celui qui existe dans les zones boisées du nord. Le rôle des mouches noires des prairies dans la transmission d’agents pathogènes — en particulier aux animaux sauvages — reste mal connu.

**Introduction**

Black flies are best known as blood-sucking pests of birds and mammals, including humans. Less appreciated is the beneficial role they play in running-water food webs (Adler et al. 2004). The Simuliidae are a relatively small family of flies with about 2,140 extant species recognized worldwide (Adler and Crosskey 2013). The immature stages occupy every conceivable running-water habitat, from tiny headwater trickles to mighty rivers and from hot springs to glacier meltwaters — anywhere there is freely flowing water. Only the polar regions and high mountain areas are uninhabited by members of the family. It is not surprising, therefore, that black flies are also represented in the grasslands of Canada.

Characterizing black flies from the full range of Canadian grasslands habitats presents a number of challenges. Neither the adults nor immature stages have a close association with grasses, except as oviposition sites and attachment substrata for larvae and pupae. Furthermore, the fragmented nature of grasslands habitats across Canada — in combination with the strong dispersal capabilities of adults — means that a majority of Canada’s 165 species have the potential to be encountered in such habitats. This chapter explores whether the nature of grasslands has any marked influence on black fly community assembly; coverage is therefore restricted to the largest contiguous tract of grasslands in Canada — the prairie grasslands of Alberta, Saskatchewan, and Manitoba.

The Canadian prairie grasslands are a continuation of the Great Plains region of the United States, which extend south to Texas in a broad expanse of relatively flat land between the Rocky Mountains and the Mississippi River (Wishart 2004). Published records of black flies suggest that the Great Plains fauna is meagre, although the intensity of research varies greatly throughout the region. Taking Nebraska as an example of a well-known area that falls more or less entirely within the Great Plains, only 18 species have been recorded from that state so far (Pruess and Peterson 1987; Adler and Crosskey 2013). In contrast, Mono County, California — which has just one-twenty-fifth the land area of Nebraska — supports 55–60 species of black flies in a mosaic of different stream habitats ranging from desert to high mountain elevations (Adler in Hershey et al. 1995). Such marked regional differences suggest that stream habitat heterogeneity is positively correlated to species richness. What attributes of the Great Plains limit black fly species richness?
Ecological Setting

Among the most important determinants of black fly species distribution is the availability of suitable breeding sites. Accordingly, it is important to understand the attributes of prairie streams and their potential impact on black fly development. Topographical and climatic factors likely impose the greatest influence on breeding-site availability. The immature stages require running water for their development; both larvae and pupae attach themselves to submerged substrates and therefore require specific substrate and flow conditions. The generally flat terrain and aridity of the prairies influences both the quality and quantity of breeding sites. The Canadian prairies are situated within three major drainage basins, two originating in the Rocky Mountains (the Saskatchewan and Missouri rivers) and one originating on the Great Plains of North Dakota and Minnesota (the Red River). While rivers originating in the mountains are relatively cool, clear, and rapidly flowing near their sources, they rapidly transform as they empty onto the prairies (Rosenberg et al. 2005). As the gradient declines, the river channel assumes a more meandering course, with few areas of rapid current. The ability of the current to transport bed materials (gravel, sand, silt) also changes. Organic and inorganic particles that were once entrained in the current begin to settle, and the once rocky riverbed becomes covered by sediments. This limits the amount of substrate available for colonization by larvae and pupae, as they typically cannot attach themselves to heavily silted surfaces (Crosskey 1990). With much of the stream bottom rendered unsuitable for attachment, larvae and pupae are confined to siltation-resistant substrata such as trailing grasses (Pruess 1989) or submerged branches, greatly limiting the ability of black flies to colonize prairie streams. Although the slower current causes much of the larger-sized particles to settle, the finest materials continue to be carried in the current. Consequently, prairie streams are typically turbid (cloudy).

Another limiting factor is the relative scarcity of tributaries feeding the three major rivers, a product of the gently undulating terrain and low annual precipitation, which averages only 454 mm across the Canadian prairie grasslands (McGinn 2010). Furthermore, many tributaries are intermittent, drying shortly after snowmelt in spring. Depending on nutrient inputs (e.g., from surrounding agriculture), dissolved oxygen can also decline in slow-moving sections, especially during winter (Rosenberg et al. 2005), further limiting survival of aquatic organisms.

While topography and climate on the prairies produce generally unfavourable conditions for black flies, other attributes actually promote larval development. With little or no overhanging riparian vegetation, prairie streams have greater exposure to sunlight than do forested streams, with concomitant increases in water temperature and primary productivity (e.g., Vannote et al. 1980); however, high turbidity can limit light penetration and primary productivity if sediment levels are too high. Temperature is the most important factor influencing the development of black fly larvae (Merritt et al. 1982; Ross and Merritt 1988), and the increased production of diatoms and filamentous algae has the potential to promote larval growth. Primary production is further enhanced by the input of nutrients from the naturally fertile prairie soils (Rosenberg et al. 2005). In addition to these natural phenomena, the development of irrigation systems has markedly extended the breeding sites of black flies, both seasonally and geographically, in areas that were previously too arid to produce streams except briefly during spring runoff or flash floods (Fredeen and Shemanchuck 1960).

In summary, prairie streams are influenced by a unique set of factors that influence both the quality and quantity of watercourses available for colonization by black flies.
While some of these attributes are favourable for development (i.e., relatively warm water, abundance of nutrients), others (i.e., slow water current, lack of suitable substrata for larval and pupal attachment) are not. On balance, the negative aspects evidently outweigh the positive, as simulid species richness on the Great Plains is low relative to that of most other ecozones in North America.

**Annotated Checklist of Black Flies from the Canadian Prairie Grasslands**

Listed here are 18 species of black flies that are considered residents of the grasslands of the Canadian Prairies Ecozone of Alberta, Saskatchewan, and Manitoba (as defined by Shorthouse (2010) and Shorthouse and Larson (2010); see also Table 1). The list was compiled with reference to the distribution maps of North American black flies in Adler et al. (2004). Species were considered residents if distributional records fell decisively within the grasslands of the Canadian Prairies Ecozone. Species whose ranges fell predominantly in adjacent areas (i.e., the Aspen Parkland of the Prairies Ecozone, the Boreal Plains Ecozone, and the Montane Cordillera Ecozone), but only peripherally onto the prairie grasslands, were excluded.

**Family Simuliidae Newman 1834**  
**Subfamily Simuliinae Newman 1834**  
**Tribe Simuliini Newman, 1834**

**Genus Cnephia Enderlein, 1921**

1. *Cnephia dacotensis* (Dyar and Shannon, 1927)  
*Distribution*: Alberta to Quebec south to Kansas.  
*Grasslands Records*: There are numerous records of this species throughout the southern grasslands of Manitoba (Crosskey 1994), Saskatchewan (Fredeen 1985a), and Alberta (Currie 1986).  
*Biological Information*: Populations of *C. dacotensis* have ranges that extend west only as far as the foothills of the Rocky Mountains, which evidently serve as a barrier to dispersal into the grasslands of south-central British Columbia. The immature stages occur abundantly in streams enriched by pastures and feedlots, especially at the outlets of impounded water (Adler et al. 2004). Females are obligatorily autogenous (i.e., do not blood-feed), their mouthparts not being armed with serrations and teeth and thus being incapable of piercing skin.

**Genus Ectemnia Enderlein, 1930**

2. *Ectemnia invenusta* (Walker, 1848)  
*Distribution*: Alberta to Quebec, south to Georgia.  
*Grasslands Records*: The distribution of *E. invenusta* on the Canadian prairies is uncertain, as females—the most frequently encountered life stage—are structurally similar to those of the closely related species *E. taeniatifrons*. The only known record of *E. invenusta* so far is a single pharate pupa collected from the South Saskatchewan River in southwestern Alberta (Currie 1986). It is possible that certain records of *E. taeniatifrons* from Manitoba are actually *E. invenusta* (Wood in Crosskey 1994).  
*Biological Information*: The immature stages of *E. invenusta* typically live in deep, rapidly...
Table 1. Black flies (Diptera: Simuliidae) of the prairie grasslands of Canada, with distributional data and feeding habits. Abbreviations for distribution: AB = Alberta, SK = Saskatchewan, MB = Manitoba. Abbreviations for feeding habits: A = autogenous, O = ornithophilic, M = mammalophilic.

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<tr>
<th>Taxon</th>
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<td><strong>SIMULIUM</strong> Latreille, 1802</td>
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<td><em>Simulium rostratum</em> (Lundström, 1911)</td>
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flowing streams and rivers. Larvae hatch in the fall and develop throughout the winter. The adults are among the earliest black flies to emerge in spring (Wolfe and Peterson 1959; Davies et al. 1962). Females are known to bite ruffed grouse, wild and domestic ducks, and Canada geese (Bennett 1960; Tarshis and Herman 1965; Tarshis 1972).

3. *Ectemnia taeniatifrons* (Enderlein, 1925)
*Distribution:* Alberta and Manitoba, south to Kansas.
*Grasslands Records:* This species is widely but sparsely distributed throughout the three Prairie Provinces.
*Biological Information:* Ecological details are similar to those described above for *E. invenusta*. Hosts include ring-necked pheasants, ruffed grouse, chickens, and domestic turkeys (Anderson and DeFoliart 1961). Females are attracted to humans and, in Saskatchewan, are reported to occasionally bite people (Fredeen 1985a). Although Fredeen (1985a) reports that adults are pests of mammals, the females possess bifid tarsal claws, a character associated with bird feeding. Consequently, birds are more likely to be the primary hosts of *E. taeniatifrons*.

**Genus Simulium** Latreille, 1802

**Subgenus Boreosimulium** Rubtsov and Yankovsky, 1982

4. *Simulium johannseni* Hart in Forbes, 1912
*Distribution:* Alberta and Manitoba, south to Texas and Georgia.
*Grasslands Records:* *Simulium johannseni* is distributed widely, if not abundantly, across the prairie grasslands of Canada.
*Biological Information:* Immature stages occur typically in large-size streams and rivers throughout their range, with larvae hatching shortly after ice breakup in spring (Fredeen 1981; Westwood and Brust 1981; Currie 1986). The female tarsal claw is bifid and adapted for ornithophily, and gallinaceous birds such as ring-necked pheasants, domestic turkeys, and chickens are among the known hosts (Anderson and DeFoliart 1961). However, females are also attracted to mammals and are known to occasionally bite horses, cattle, and humans (Westwood and Brust 1981). Even in the absence of blood feeding, females can be a significant pest of humans and other mammals due to their swarming and probing activities (Adler et al. 2004).

**Subgenus Byssodon** Enderlein, 1925

5. *Simulium meridionale* Riley 1887
*Distribution:* Alberta and Manitoba, south to California and Alabama.
*Grasslands Records:* The immature stages of *S. meridionale* inhabit all the major drainage basins of the Canadian prairies.
*Biological Information:* This multivoltine species breeds in meandering rivers with sandy or alluvial substrata (Fredeen 1981; Adler et al. 2004). Although the tarsal claws of females are adapted for ornithophily, blood meals are taken from both avian and mammalian hosts. Ring-necked pheasants, mourning doves, starlings, purple martins, tree swallows, bluebirds, chickens, and domesticated turkeys are among the confirmed avian hosts (Anderson and DeFoliart 1981; Gaard 2002; Adler et al. 2004; Currie and Hunter...
Outbreaks of *S. meridionale* are of major concern to poultry operations, with deaths attributed to exsanguination reported in Saskatchewan (Fredeen 1981). Females are also pests of mammals. They are attracted to moose and can be a nuisance to horses, cattle, and humans (Pledger *et al.* 1980; Westwood and Brust 1981; Peterson and Kondratieff 1995). In addition to their status as bloodsucking pests, females of *S. meridionale* are vectors of *Leucocytozoon smithi* and equine encephalitis virus to poultry (Anderson and DeFoliart 1961; Anderson *et al.* 1961; Fredeen 1981; Pinkovsky *et al.* 1981).

**Subgenus Eusimulium Roubaud, 1906**

6. *Simulium pilosum* (Knowlton and Rowe, 1934)

*Distribution:* Transcontinental.

*Grasslands Records:* Most historical records of “*Simulium aureum* Fries” from the Canadian prairies are probably *S. pilosum*. This species is unquestionably more common across the prairies than suggested by the distributational map in Adler *et al.* (2004). The apparent absence of *S. pilosum* from Saskatchewan and Manitoba probably reflects the lack of cytological screening in those provinces (see the next section, Biological Information).

*Biological Information:* *Simulium pilosum* is one of five North American species referable to the *Simulium aureum* species complex. As only some of these species can be distinguished morphologically in one or two life stages, most of the historical literature refers to them collectively as “*S. aureum*” (a strictly Palearctic species), or the “*S. aureum* complex.” In general, species in the complex can be distinguished reliably only through examination of the giant polytene chromosomes of larvae (Leonhardt 1985). Specific host records for *S. pilosum* are unknown because females of the *S. aureum* complex are undistinguishable morphologically. However, members of the complex are predominantly ornithophilic, with a diversity of hosts in the Galliformes, Anseriformes, Columbiformes, Ciconiiformes, Strigiformes, and Passeriformes. Females are vectors of several species of *Leucocytozoon* and are probable vectors of *Trypanosoma confusum* (Adler *et al.* 2004).

5. *Simulium bivittatum* Malloch, 1914

*Distribution:* Southern Alberta and Saskatchewan south to Mexico.

*Grasslands Records:* In Canada, this species occurs almost exclusively in the grasslands of Alberta and Saskatchewan.

*Biological Information:* The immature stages of *S. bivittatum* live in irrigation canals and rivers in the prairie grasslands of Alberta and Saskatchewan. Females attack a wide variety of large mammals, including horses, cattle, sheep, pigs, and humans (Fredeen and Shemanchuck 1960; Fredeen 1981). Occasional severe outbreaks of this multivoltine species have forced residents of Saskatoon, Saskatchewan, and Medicine Hat, Alberta, indoors (Fredeen 1981).

8. *Simulium griseum* Coquillett, 1898

*Distribution:* Southern Alberta and Saskatchewan south to California and New Mexico.

*Grasslands Records:* As with *S. bivittatum*, the Canadian distribution of this species is almost exclusively within the grasslands ecoregions of the Prairies Ecozone of Alberta and Saskatchewan.
Biological Information: The immature stages of this species are often found together with those of S. bivittatum in rivers and irrigation canals, although in relatively larger numbers in the latter habitat (Fredeen and Shemanchuk 1960). Overwintering is in the egg stage, with larvae of this multivoltine species occurring throughout the ice-free period (Currie 1986; Pruess and Peterson 1987). Feeding preferences are similar to those of S. bivittatum, with females attacking large mammalian hosts such as horses, cattle, sheep, pigs, and humans (Fredeen 1981); however, they are also known to attack smaller-sized mammals (black-tailed jackrabbits) in California (Ryckman 1961). Prior to the construction of a hydroelectric dam on the South Saskatchewan River in 1968, outbreaks of S. griseum were substantial enough to drive people indoors in Saskatchewan (Fredeen 1977a).

Subgenus Psilozia Enderlein, 1936
vittatum species complex

9. Simulium tribulatum Lugger, 1897
Distribution: Transcontinental.
Grasslands Records: This species, along with its cryptic sister species Simulium vittatum, are among the most abundant and commonly encountered black flies on the Canadian prairies. Biological Information: The immature stages of members of the S. vittatum species complex occupy an enormous variety of running-water habitats, ranging from tiny trickles to large (>300 m wide) rivers. Optimal habitats include nutrient-rich streams coursing through pasture lands, especially at the outlets of lakes and other sources of impounded water (Adler et al. 2004). In addition to their ability to thrive in different kinds of watercourses, the larvae are tolerant of extreme ranges in temperature (0 °C–33 °C), oxygen tension, current velocity, pH, and salinity (Adler et al. 2004). They also exhibit the greatest tolerance of any North American species to organic and industrial pollutants. Members of the S. vittatum complex can overwinter in either the egg or larval stages and have up to four generations per year on the prairies (Abdelnur 1968; Fredeen 1981). Adults fly from April or May through October (Currie 1986). Hosts include a wide variety of ungulates, including cattle, horses, sheep, elk, moose, and deer (Knowlton and Rowe 1934; Fredeen 1973; Merritt et al. 1978; Pledger et al. 1980). Other less frequently attacked hosts include pigs and domestic geese, ducks, chickens, and turkeys (cf. Adler et al. 2004 for review). Females of the S. vittatum complex are vectors of vesicular stomatitis virus to mice (Mead et al. 1999, 2000), domestic swine (Mead et al. 2004; Smith et al. 2009), and domestic cattle (Mead et al. 2009).

10. Simulium vittatum Zetterstedt, 1838
Distribution: Transcontinental.
Grasslands Records: Simulium vittatum and its cryptic sister species S. tribulatum are among the most abundant and frequently encountered black flies on the Canadian prairies. Biological Information: See entry for S. tribulatum.

Subgenus Apathia Enderlein, 1935
metallicum species group

11. Simulium hunteri Malloch, 1914
Distribution: Southern Alaska and Yukon west to South Dakota, south to Mexico.
Grasslands Records: This species occurs marginally on grasslands ecoregions in the Prairies Ecozone, with records only from the foothills of the Rocky Mountains (Alberta)
and Cypress Hills (Saskatchewan). The Cypress Hills population is isolated from the nearest foothills population by almost 300 km.

**Biological Information:** The immature stages of this widely distributed Cordilleran species live in predominantly cool small-sized streams. Overwintering is probably in the egg stage, with larvae first appearing in June. Adults fly until well into September (Currie 1986). Adult females are known to bite cattle (Malloch 1914), humans (Peterson 1956; Currie 1997), and blue grouse (Williams *et al.* 1980).

12. *Simulium piperi* Dyar and Shannon, 1927

**Distribution:** A common and widely distributed species in western North America, from southern British Columbia and Saskatchewan south to Mexico.

**Grasslands Records:** This species occurs mainly in the Montane Cordillera Ecozone of Canada, with grasslands records near the foothills of the southern Rocky Mountains and Cypress Hills. The Cypress Hills population—which represents the only record of this species from Saskatchewan—is isolated from the nearest foothills population by a distance of nearly 300 km.

**Biological Information:** This multivoltine species occurs in small-sized streams throughout its range. Outlets of beaver ponds and other small bodies of impounded water are especially favourable habitats (Currie 1986). Ungulates such as horses, cattle, and sheep are among the primary hosts of females (Hearle 1932; Jones 1961).

**Subgenus Simulium Latreille, 1802**


**Distribution:** Southern Northwest Territories south to Oklahoma, east to New Hampshire and South Carolina.

**Grasslands Records:** *Simulium luggeri*, the most northern and western member of the *S. jenningsi* species group, is distributed widely in the three Canadian Prairie Provinces.

**Biological Information:** Cytological studies reveal that *Simulium luggeri* is likely a complex of at least two species: one eastern and one western (Moulton and Adler 1995; Adler and Mason 1997). Both entities are included under the name *S. luggeri* pending further study (Adler *et al.* 2004; Adler and Crosskey 2013). The immature stages occur in relatively warm large-sized rivers throughout their range. Larvae and pupae are present from May until November on the Canadian prairies, with three to five generations per year depending on location (Depner 1971; Fredeen 1981; Westwood and Brust 1981; Currie 1986). Females attack a wide variety of mammalian hosts, including ungulates (cattle, horses, elk, pigs, and sheep), humans, and dogs (Anderson and Defoliart 1961; Fredeen 1985b; Mason and Kusters 1990). Massive outbreaks of *S. luggeri* in east-central Saskatchewan during the 1970s and 1980s had a severe economic impact on cattle farmers in the vicinity of breeding sites (Fredeen 1977a, 1984, 1985b); however, population levels were subsequently controlled by using the biological control agent *Bacillus thuringiensis var. israelensis* (*Bti*) (Khachatourians 1990).

**malyschevi species group**


**Distribution:** Southernmost Northwest Territories, Alberta, and Saskatchewan.
Grasslands Records: *Simulium vampirum* is found in irrigation canals in southern Alberta and is the only member of the *Simulium arcticum* species complex that breeds in the prairie grasslands of Canada (Procunier and Shemanchuk 1983).

**Biological Information:** The *Simulium arcticum* complex includes at least nine reproductively isolated sibling species (i.e., “cytospecies”) and a number of additional chromosomally distinct forms that may or may not represent valid species (i.e., “cytotypes”) (Adler et al. 2004). *Simulium vampirum*—one of the nine reproductively isolated cytospecies—is without question the most notorious member of the complex. Massive outbreaks of this species were responsible for mortality in livestock and wildlife in northern Alberta and Saskatchewan up until the 1980s, after which control measures such as treatment with methoxychlor and other larvicides successfully reduced population sizes (Adler et al. 2004). The immature stages of *S. vampirum* typically occur in the rapids of large silty rivers, such as the North Saskatchewan, Athabasca, and Slave rivers of northern Alberta and Northwest Territories; the species is included here because it is also found in irrigation canals in southern Alberta (Procunier and Shemanchuk 1983). Larvae can be found from April to September, representing a single generation with up to three cohorts (Procunier 1984; Procunier et al. 1984; Anderson and Shemanchuck 1987). Females are major pests of cattle and other large ungulates in the northern part of their range; however, the problem is not as severe in the south—perhaps a consequence of southern populations managing just one cohort before flow is terminated in irrigation canals (Procunier 1984). Ungulates, including cattle, horses, pigs, sheep, bison, moose, caribou, elk, and white-tailed deer, are among the primary targets of blood-seeking females. Humans and other animals (including chickens) may be attacked during severe outbreaks (Rempel and Arnason 1947; Fredeen 1969, 1977b; Shemanchuk 1988; Adler et al. 2004).

*noelleri* species group

15. *Simulium decorum* Walker, 1848

**Distribution:** Transcontinental.

**Grasslands Records:** This widely distributed species occurs abundantly at suitable sites throughout the grasslands of Alberta, Saskatchewan, and Manitoba.

**Biological Information:** *Simulium decorum* is a habitat specialist whose immature stages live almost exclusively in the food-rich outflows of impounded water. Larvae and pupae can be found in huge numbers in such habitats, thickly festooning submerged twigs and trailing vegetation. Overwintering eggs hatch after ice breakup, with pupae first appearing in late May on the Prairies (Currie 1986). The number of generations annually varies according to location, with up to four recorded in southern Manitoba (Westwood and Brust 1981). Adults have been collected well into October in Alberta (Currie 1986). Females are autogenous for the first gonotrophic (feeding and egg laying) cycle, but most nulliparous and parous females (no egg development having occurred, and egg development having occurred, respectively) are capable of taking a blood meal (Simmons and Edman 1981). Females seek blood meals primarily from large mammalian hosts, including cattle, horses, moose, deer, and bears (Davies and Peterson 1956; Davies et al. 1962; Fredeen 1973; Addison 1980; Pledger et al. 1980). Other hosts include small mammals such as rabbits (Mokry et al. 1981), humans (Davies and Peterson 1956; Currie and Adler 1986), and birds (Bennett 1960). *Simulium decorum* has been implicated in the transmission of legworm (*Onchocera cervipedis*) to moose (Pledger et al. 1980) and in the mechanical transmission of tularemia (rabbit fever) to rabbits (Philip and Jellison 1986).
16. *Simulium tuberosum* (Lundström, 1911)

**Distribution:** Holarctic. Transcontinental at northern latitudes, extending southward into the United States along mountain chains.

**Grasslands Records:** *Simulium tuberosum* occurs commonly in grassland streams throughout Alberta, Saskatchewan, and Manitoba.

**Biological Information:** *Simulium tuberosum* s.s. is one of at least nine sibling species of the *S. tuberosum* complex recognized in North America. Because most ecological studies were undertaken when the complex was treated as a single species, the available literature must be interpreted with caution. The immature stages live in a wide variety of running-water habitats, although large-sized streams and rivers are evidently preferred (McCreadie et al. 1995). In Alberta, smaller-sized streams inhabited by the larvae of *S. tuberosum* are often organically enriched (Adler 1986). The immature stages can be found from spring until fall, suggesting that there is more than one generation per year. Members of the *S. tuberosum* complex feed primarily on small mammals, such as squirrels, rabbits, and foxes. Reports of bloodsucking from larger-sized mammals are probably based on misidentifications (Adler et al. 2004).

17. *Simulium venustum* Say 1823

**Distribution:** Transcontinental.

**Grasslands Records:** *Simulium venustum* occurs only marginally on the grasslands of the Prairies Ecozone.

**Biological Information:** *Simulium venustum* s.s. is one of 10 species of the *S. venustum* complex recognized in the Nearctic region. As a prodigious biter of humans and domestic animals, this species is among the most feared (and loathed) black flies in North America. As with members of the *S. tuberosum* complex, most ecological studies were undertaken when the complex was treated as a single species. Accordingly, much of the previous literature must be interpreted carefully. *Simulium venustum* is one of the most widely distributed and common black flies in North America; however, the most favourable habitats are medium-sized streams in northern and eastern woodlands (Adler et al. 2004). This univoltine species occurs only spottily on the grasslands, their scarcity perhaps related to the dearth of suitable breeding sites. Additionally, females attack hosts more in forested habitats than in open areas (Martin et al. 1994), which further reduces the probability of attacks on the grasslands. In addition to its status as a bloodsucking pest, *S. venustum* is implicated as a vector of the filarial nematode *Dirofilaria ursi* to American black bears in Ontario (Addison 1980).

18. *Simulium rostratum* (Lundström, 1911)

**Distribution:** Holarctic. Transcontinental in Canada and the northern United States.

**Grasslands Records:** *Simulium rostratum* is among the most commonly encountered black flies on the Canadian prairies.

**Biological Information:** *Simulium rostratum* is one of two species in the *S. verecundum* species complex and the only one to occur on the Canadian prairie grasslands. Members
of this complex are morphologically similar to those of the *S. venustum* complex, and so much of the ecological literature is muddled. The immature stages live in variously sized low-gradient streams throughout their range, but are especially prevalent in enriched flows such as the outlets of ponds and lakes. This multivoltine species overwinters in the egg stages, with larvae present from spring until fall. There are few reliable bloodsucking records for this species, but females evidently have a preference for larger-sized ungulates such as horses, cattle, and deer (Adler et al. 2004).

**Diversity Patterns and Ecology**

The 18 species here considered residents of the Canadian prairies represent less than 11% of the Canadian simulid fauna. Species richness for the region is exactly the same as that recorded for Nebraska, although only 12 species are shared between the two areas. This suggests that the black fly fauna of the Great Plains is far from uniform, perhaps reflecting differences in geographical history and local topography. Nonetheless, the relative paucity of species is consistent with observations from other regional studies on the Great Plains (e.g., Fredeen 1958; Snyder and Huggins 1980; Pruess and Peterson, 1987; Mock and Adler 2002). In comparison, Yukon, which has about the same land area as the Canadian Prairies Ecozone, supports about three times the number of species (55)—despite being considerably farther north (Currie 1997). The higher species richness in Yukon is related, in part, to its unique geographical history. However, the terrain is also considerably more complex than the prairie landscape, and the resulting mosaic of breeding habitats is likely a major factor behind higher species richness in the Yukon.

Diversity in the prairie grasslands is also low at the generic level. The 18 prairie grasslands resident species are distributed among just three of 13 genera recognized in North America (Table 1). This number is low relative to the 11 genera recorded from the Canadian Prairie Provinces as a whole, reflecting the absence of mountain- and woodland-adapted genera. But as in other regions of North America, the prairie fauna is dominated numerically by species of *Simulium s.l.*, which constitute 83% of all black flies known from the region. This figure is high compared with the North American fauna, in which *Simulium s.l.* constitutes about 60% of all species. The only other genera present on the Canadian prairies are *Cnephia* (one species) and *Ectemnia* (two species), both well adapted for life in lowland streams and rivers.

The black flies of the Canadian prairies grasslands consist mainly of species that occur in other ecozones, including a combination of widespread species (e.g., *Simulium pilosum, S. tribulatum, S. vittatum, S. tuberosum, S. decorum, S. venustum*), predominantly Cordilleran species (*S. hunteri, S. piperi*), and predominantly northern woodlands species (*S. vampirum*). While no species of black fly is restricted to the Great Plains, at least two—*S. johannseni* and *S. meridionale*—have the great bulk of their ranges within that grasslands-dominated region. If any black flies could be considered characteristic of North American grasslands, it would be these. Special comment is warranted about *S. bivittatum and S. griseum*, both members of the subgenus *Psilopelmia*. While most North American species of this subgenus are restricted to the American Southwest, *S. bivittatum* and *S. griseum* have their ranges extended much farther north into southern Alberta and Saskatchewan. These species are distributed widely in both grasslands and intermountain valley habitats in the western United States and cannot, therefore, be considered strictly grasslands specialists. Nonetheless, these species evidently thrive in such habitats and are known in Canada exclusively from the prairie grasslands of Alberta and Saskatchewan.
Because widely distributed species are typically tolerant of a wide range of environmental conditions, it is perhaps not surprising that such species dominate the prairie grasslands simuliid fauna. In contrast, relatively few species are specially adapted for life on the prairies. Consequently, because of the generally unfavourable conditions of grasslands for supporting black flies, the Canadian prairies support the lowest species richness of any major ecozone in Canada outside the High Arctic.

Since most species require access to avian and/or mammalian hosts for blood meals, one other factor that might influence black fly species richness and distribution is host availability. Ecozones differ in the quality and quantity of potential hosts, although it is unclear how such differences affect simuliid community assembly. Feeding preferences remain an understudied aspect of black fly ecology, with no host information whatsoever for about 60% of North American black flies (Adler et al. 2004). Even for the 40% of species with one or more host records, the information is strongly biased toward domesticated birds and mammals. Nonetheless, it seems possible that prevalence of grasslands-adapted hosts on the Canadian prairies—along with absence of woodland- and mountain-adapted hosts—could exert some influence on black fly community assembly. Unfortunately, intensive studies of prairie black flies did not begin until the mid-20th century, at which point much of the native flora and fauna had already been affected by agriculture. In the absence of historical baseline data, we can only speculate about the composition of prairie black flies prior to the arrival of settlers.

Only one species of black fly on prairie grasslands—*Cnephia dacotensis*—is entirely independent of host availability. Females are obligatorily autogenous and so do not take blood meals. All other prairie black flies are anautogenous (i.e., are capable of blood feeding), although some of these (e.g., *S. decorum*, members of the *S. vittatum* species complex) are facultatively autogenous in the first gonotrophic cycle (Davies and Györkös 1990). Among the anautogenous component, five are classified as predominantly ornithophilic species, whereas 12 are classified as primarily mammalophilic species. The percentage of ornithophilic to mammalophilic species is about 30:70, somewhat lower than for North American fauna as a whole (i.e., 37:63) (Adler et al. 2004).

Black flies are notorious pests of humans, livestock, and wildlife in locations where they are abundant. However, they are evidently not as problematical to wild and domestic animals on the prairie grasslands as they are in northern woodland areas. For example, *Simulium vampirum*, by far the most noxious species in western Canada, is a major pest of cattle in northern Alberta, Saskatchewan, and the southernmost Northwest Territories. Although this species also occurs in the irrigation areas in southwestern Alberta, it has never been considered a pest, perhaps owing to the episodic nature of irrigation and its effect on life history (Procunier 1984). However, it is also possible that irrigation canals simply cannot support the same enormous populations of *S. vampirum* as are found in large northern rivers. Suboptimal breeding conditions might also explain the relatively benign presence of *S. venustum* on the Canadian prairies. Among the most serious bloodsucking pests of humans and other mammals in North America, *S. venustum* breeds in staggeringly large numbers on the Canadian Shield. In contrast, the species occurs only spottily on the prairie grasslands and, even then, occurs in comparatively low numbers. Nonetheless, pest species such as *S. luggeri*, *S. bivittatum*, and *S. griseum* occasionally develop in sufficient numbers to cause discomfort to humans and domesticated animals. While present-day conditions on the grassland prairies are generally unfavourable for supporting large populations of black flies, anecdotal evidence suggests that pest species were once more prominent. For example, during Lewis and Clark’s trek across the Great Plains in
1805, Captain Meriwether Lewis was moved to write that gnats, prickly pear cactuses, and mosquitoes were the “great trio of pests equal to any three curses that ever poor Egypt labored under” (Duncan and Burns 1997).

One important aspect of black fly biology that has been virtually unstudied on the prairies is their role in transmission of disease agents. The North American black fly fauna as a whole is known to transmit at least 10 species of protozoa, four filarial nematodes, an indeterminate number of viruses, and a bacterium (cf. Adler et al. 2004 for review). How many of these disease agents are transmitted by prairie-dwelling populations is unknown, as there have been few attempts to screen either the flies or their prospective hosts on the prairies. Evidence is accumulating that avian-borne diseases in particular are a threat to rare and endangered birds (e.g., Adler et al. 2007; King and Adler 2012). Unfortunately, blood-feeding records are unknown for many prairie-inhabiting bird species such as Sage grouse (*Centrocercus urophasianus* (Bonaparte)), Piping plover (*Charadrius melodus* (Ord)), Burrowing owl (*Athene cunicularia* (Molina)), Ferruginous hawk (*Buteo regalis* (Grey)), and Peregrine falcon (*Falco peregrinus* Tunstall). Along similar lines, there are no blood-feeding records whatsoever for several endangered species of prairie-dwelling mammal, including the black-footed ferret (*Mustela nigripes* Audubon & Bachman)) and swift fox (*Vulpes velox* (Say)). Given that none of the above-mentioned species is immune to attacks by black flies, this is clearly an area that warrants further study.

**Acknowledgements**

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