Chapter 3
Arthropods Associated with Livestock Grazing Systems

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Abstract. The life cycles and biology of the arthropods that affect livestock in Canadian grasslands are reviewed. The blood-feeding dipterous parasite complex consists of members of the families Culicidae, Ceratopogoinidae, Simuliidae, Tabanidae, and Muscidae. Field ectoparasites that affect grazing livestock include several species of ixodid ticks. The blood-feeding dipterous parasite complex and the field ectoparasites consist mainly of native species that were able to readily colonize introduced domestic livestock. A few important species of Muscidae were introduced with livestock, and these species tend to be more specialized. Populations of field ectoparasites and the blood-feeding dipterous complex have responded positively to various environmental perturbations, including irrigation, dam construction, and animal feeding practices. Cultivation may have reduced habitat for some field ectoparasites. Endo- and ectoparasitic arthropods are more specialized and were most likely introduced with their domestic hosts. Populations of these arthropods are affected by host factors such as body temperature, grooming, and immunity.

Résumé. Le présent chapitre examine le cycle biologique des arthropodes nuisibles au bétail dans les prairies canadiennes. Le complexe des diptères hématophages se compose de membres de diverses familles : culicidés, cératopogonidés, simulidés, tabanidés et muscidés. Les ectoparasites qui s'attaquent au bétail dans les pâturages comprennent diverses espèces de tiques (ixodidés). Ces diptères hématophages et ces ectoparasites appartiennent principalement à des espèces indigènes qui se sont adaptées facilement aux animaux d'élevage. Quelques espèces importantes de muscidés ont été introduites avec le bétail et ont tendance à être plus spécialisées. Les populations d'ectoparasites et de diptères hématophages ont réagi positivement aux diverses perturbations de l'environnement, y compris l'irrigation, la construction de barrages et les pratiques d'alimentation des animaux. L'agriculture pourrait toutefois avoir réduit l'habitat de certains ectoparasites. Les arthropodes endo et ectoparasites sont plus spécialisés et ont donc vraisemblablement été introduits en même temps que leurs hôtes domestiques. Divers facteurs liés aux hôtes — par exemple, la température corporelle, les soins du pelage et l'immunité — influent sur ces populations d'arthropodes.

Introduction

Livestock are a common feature of grassland habitats and support a diverse assemblage of native and introduced arthropod species. These arthropods show a wide diversity of life-history specializations and adaptations that allow them to exploit livestock as a resource. The current chapter provides a general overview of the livestock species common in the prairie provinces of Canada and their associated arthropod species. Many additional arthropod species are parasites of non-domesticated vertebrate species, but these will not be discussed here.

Livestock are maintained in a variety of production systems, ranging from intensive indoor confined systems to expansive grazing systems (Axtell 1986). Livestock species and

Lysyk, T. J. 2011. Arthropods Associated with Livestock Grazing Systems.
In *Arthropods of Canadian Grasslands (Volume 2): Inhabitants of a Changing Landscape.*
Edited by *K. D. Floate. Biological Survey of Canada. pp. 45-69.*

ISBN 978-0-9689321-5-5
doi:10.3752/9780968932155.ch3

their associated arthropod-parasite complexes are associated with particular production systems. Poultry and swine are typically housed in indoor confined systems; dairy and some beef cattle are housed in outdoor confined systems; and cattle, horses, sheep, and farmed wildlife are maintained in grazing systems that are broadly categorized as pasture and rangeland. Grazing systems have a number of characteristics that distinguish them from confined systems (Lysyk and Moon 1994). Vegetation growing within the system is the primary source of animal feed. Environmental conditions and forage growth are determined by weather, which typically limits use of a grazing system to spring, summer, and autumn. Supplemental feed produced externally to the system may be provided during periods when vegetation growth is severely reduced, such as winter or periods of drought; however, this is not typically the goal in grazing systems, as it is in confined systems. Grazing systems are large and animal density is low. Stocking rates range from approximately 0.4 to 9.7 ha/animal unit (AU) on pastures and from approximately 2.8 to 20.2 ha/AU on native range (Alberta Agriculture 1989). Animal units are the numbers of animals of a species that consume a defined amount of forage in one day; a cow–calf pair is considered 1 AU, a steer is approximately 0.7 AU, a ewe is 0.2 AU, and a mature horse is 1.5 AU. The animals are mobile and may cover large distances during a day when grazing. Pastures are distinguished from rangelands in that pastures are "tamed" and may be seeded, irrigated, and fertilized to produce forage more uniformly throughout the growing season.

Arthropods associated with grazing livestock exist in a variety of relationships with the host animal. These associations can be considered parasitic because the arthropod spends a portion of its life cycle in an obligate, intimate association with the host, survives at the expense of the host, and usually does not kill the host. The arthropods exploit the host to acquire protein for growth and reproduction. In doing so, the arthropods may face a variety of challenges, including finding a host, extracting nutrition from the host for growth or reproduction or both, avoiding the host's defensive behaviours, finding a safe habitat to digest the blood meal, finding a place to oviposit, and surviving periods of inclement conditions (Ribeiro 1996). Arthropods have developed a number of life-history strategies to cope with or even eliminate these challenges, and can accordingly be classified into ecological groups depending on how they exploit livestock in grazing systems. Although several ecological classification systems have been proposed for arthropod parasites, I use a modified system based on work by Nelson *et al.* (1975), Balashov (1984, 2006), and Haufe (1987) to focus specifically on the parasitic arthropod fauna directly associated with grazing livestock in Canadian grasslands. Cattle are the major host species considered, with some discussion of sheep and horses. These species of domestic livestock were introduced with European settlement.

The ecological grouping of arthropod parasites includes hematophagous flies of the order Diptera that feed periodically on the host. These have been termed the blood-feeding dipterous parasite complex (Haufe 1987), free-living bloodsuckers (Balashov 1984), and micropredators (Balashov 2006). Next, I will consider what Nelson *et al.* (1975) called field ectoparasites, which spend most of their life cycle free-living in the environment, but have an obligate period when they must feed on the host for a limited time. Members of this group have also been called slow-feeding temporary ectoparasites (Balashov 1984) or temporary ectoparasites with prolonged feeding (Balashov 2006). Nest ectoparasites have been included in most arthropod parasite classification systems (Nelson *et al.* 1975; Balashov 1984, 2006) but will not be considered here. These parasites live in the immediate environment of the host and complete their life cycle within the host's nest. Nest ectoparasites do not seem important in relation to grazing animals because the hosts range over large areas and tend not to construct nests. I include some discussion of endoparasites, which spend much of their life cycle deep within the host's tissues, but retain a free-living component. Finally, consideration is given to host ectoparasites (Nelson *et al*. 1975), also called permanent ectoparasites (Balashov 1984, 2006), which live permanently on the host.

Blood-Feeding Dipterous Parasite Complex

Members of the blood-feeding dipterous complex are flies (Diptera) and include mosquitoes (Culicidae), no-see-ums (Ceratopogonidae), black flies (Simuliidae), horse and deer flies (Tabanidae), and some species of Muscidae. Typically, egg, larval, and pupal stages develop in aquatic and semi-aquatic (dung, moist soil) environments. Adults are free-living, but must visit a host to obtain protein and move to oviposition sites to lay eggs. Thus, they are highly mobile and have highly evolved visual and olfactory systems that aid in host location (see Allan *et al*. 1987 for a review). Members of this complex have highly specialized mouthparts that are adapted for piercing, cutting, or abrading skin or other host surfaces and extracting protein. Feeding duration is relatively short, usually a matter of minutes, and as a result, the time spent on the host is short, although this may vary. Most of the native species in this complex are generalists and developed their feeding habits on native hosts prior to the introduction of livestock. The generalist strategy is advantageous when hosts of a given species are not readily located (Lyimo and Ferguson 2009). Non-native species in this complex that were introduced with European settlement tend to be more host specific because they have a longer evolutionary association with livestock.

Culicidae

A number of mosquito species are associated with livestock in the prairie regions of western Canada (Shemanchuk 1959; Wood *et al*. 1979; Scholefield *et al*. 1981). In southern Alberta, these species commonly include *Culiseta inornata* (Williston), *Culex tarsalis* Coquillet, *Aedes dorsalis* (Meigen), and *Ae. vexans* (Meigen) (Lysyk 2010). In central Alberta, *Ae. dorsalis* and *Cx. tarsalis* are less common (Graham 1969), and *Ae. vexans*, *Cs. inornata*, and the *Ae. communis and Ae. fitchii* groups are attracted to cattle (Shemanchuk 1978; Hudson 1983). Ralley *et al*. (1993) list 15 species of mosquito that attack cattle in Manitoba, with *Ae. punctor* (Kirby) and *Ae. vexans* being the most abundant.

These species are native and are opportunistic; they feed on cattle when cattle are nearby but will also feed on a variety of other hosts (Shemanchuk *et al*.1963). *Culex tarsalis* readily feeds on birds (Shemanchuk 1969) and *Cs. inornata* feeds on other large mammals such as horses (Anderson and Gallaway 1987). The adults generally have crepuscular or nocturnal feeding habits, feeding on hosts that rest at night, presumably to aid in avoiding detection by the host (Day and Edman 1984). Host defensive behaviours can reduce blood-feeding success and the size of blood meals (Klowden and Lea 1979), which in turn reduces egg production. Blood meals average from 5 to 12 μL but vary with the size of the mosquito and the duration of feeding (Roitberg and Gordon 2005). The rewards from successful blood feeding are great, as females may mature 150–300 eggs per batch (Buth *et al*. 1990) (Fig. 1).

Both *Cs. inornata* and *Cx. tarsalis* overwinter as adults. They emerge in the spring and lay eggs in rafts on the surface of temporary and permanent standing water, where the larvae complete development. Standing water created by irrigation seepages are particularly conducive for immature development of these species. Populations typically peak in early

Fig. 1. *Culex tarsalis* feeding on a mammalian host. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

to mid-August, and then decline as adults enter diapause. In irrigated areas, seasonal activity is relatively consistent each year because larval development is tied to the flow of irrigation water rather than to rainfall (Lysyk 2010); however, this may not be the case in areas without irrigation (Buth *et al*. 1990). Overwintering typically occurs in the burrows of small mammals (Shemanchuk 1965). *Aedes* spp. overwinter as eggs that have been laid in depressions in the soil. Developmental sites include a variety of temporary pools such as ditches and low-lying areas of pastures subject to periodic flooding. Populations of these species often increase following periods of heavy rainfall, but do not show consistent seasonal trends annually (Shemanchuk 1969; Lysyk 2010). *Aedes vexans* may occur later in the season because egg hatching requires flooding with warmer water (Brust and Costello 1969; Enfield and Pritchard 1977).

A number of viruses have been isolated from mosquitoes in western Canada, including overwintering adults of both *Cs. inornata* and *Cx. tarsalis* (Spalatin *et al*. 1963; Shemanchuk and Morgante 1968). *Culex tarsalis* is the principal vector of the introduced West Nile virus in western Canada. The introduction and spread of West Nile virus in North America indicates that it is possible for arthropod-borne pathogens to enter into new associations with vector species that do not occur within a pathogen's native geographical distribution. This has increased concerns about the possible introduction of other exotic mosquito-borne viruses into North America (Turell *et al*. 2008) that might have devastating effects on cattle production. Heavy populations of mosquitoes can cause livestock to bunch and perform other avoidance behaviours (Shemanchuk 1959) and can cause significant economic losses (Steelman *et al*. 1973). Populations of all species are greater in irrigated areas compared with dryland areas (Shemanchuk 1959)

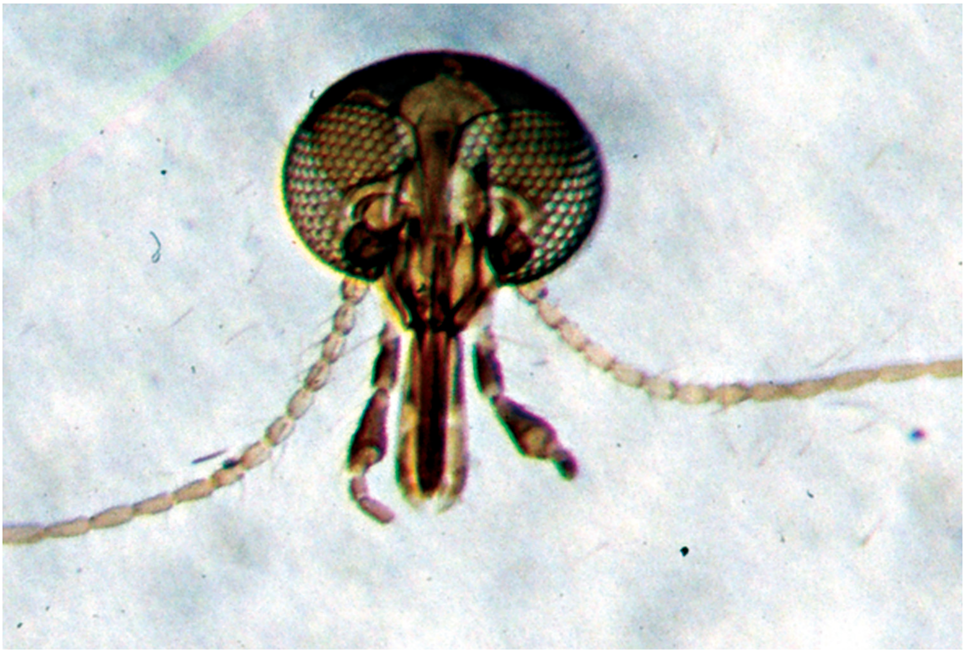

Fig. 2. Head and biting mouthparts of blood-feeding *Culicoides*. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

Ceratopogonidae

Biting flies in the genus *Culicoides* (Diptera: Ceratopogonidae) occur throughout much of western Canada, although there are regional differences in species composition (McMullen 1978; Lysyk 2006). In southern Alberta, the grassland fauna tends to be dominated by *Culicoides gigas* Root and Hoffman, *C. sonorensis* (Wirth and Jones), and *C. davisi* Wirth and Rowley (Downes 1958; Lysyk 2006), especially in areas containing alkaline sloughs and irrigation lakes with shallow-sloped shorelines. *Culicoides denningi* Foote and Pratt is also common near rivers and irrigation canals (Fredeen 1969). In central Alberta, *C. yukonensis* and *C. obsoletus* occur near cattle (Shemanchuk 1978).

Kettle (1977) summarized the bionomics of blood-sucking Ceratopogonidae. The adults are typically weak fliers and do not move far from the larval developmental sites. Adults are crepuscular and use carbon dioxide and various odours to locate hosts. Adults feed by slashing capillaries near the surface of the skin and drinking blood. Adults typically exhibit gonotrophic concordance, producing a clutch of eggs for each blood meal. A few species, such as *C. gigas*, are autogenous and develop the first batch of eggs without a blood meal. Eggs are laid near the larval developmental site, which are usually areas of high moisture. These areas vary among species, ranging from animal dung to aquatic sediments. Larval development is temperature dependent, with pupation occurring in drier habitats.

Culicoides spp. are important vectors of viruses (Mellor *et al*. 2000) and cause irritation during feeding (Fig. 2). They transmit the viruses that cause bluetongue, epizootic haemorrhagic disease, and vesicular stomatitis, which affect a variety of ruminant species, including cattle and sheep. *Culicoides sonorensis* is a competent vector of these pathogens, along with other species that have been implicated as vectors of epizootic haemorrhagic disease and vesicular stomatitis in North America. Canada is largely free of these diseases. However, vesicular stomatitis was diagnosed in 1949 in Canada (Hanson 1952) and recently has occurred in Montana. Epizootic haemorrhagic disease killed nearly 500 deer in 1962 during an outbreak in southern Alberta (Chalmers *et al*. 1964) and has since occurred in the Okanagan Valley of British Columbia (Shapiro *et al*. 1991) and Montana. Bluetongue was diagnosed in a number of cattle in the Okanagan Valley during 1975–1976 and at least four times since. It is not known to have been transmitted in Canada outside the Okanagan, but caused clinical disease in southern Montana in 2007 (Miller *et al*. 2010). Transmission in northern climates is limited by the effects of temperature on life history and population growth of the vector, viral development, and overall reduced vectorial capacity (Mullens *et al*. 2004; Lysyk 2007; Lysyk and Danyk 2007).

The bites are accompanied by anticoagulants (Pérez de León *et al*. 1998) and can cause intense pain and itching. Bites may cause serious dermatitis and allergic reactions in sensitized animals, which will rub against objects until they bleed, resulting in local hair loss, bleeding, and secondary infections. Biting midges cause a condition known as "sweet itch" in horses. Anderson *et al*. (1988) reported the prevalence of this condition was 26% in British Columbia, occurring from April to October, with onset mainly during April and May. Horses are debilitated for lengthy periods and affected animals cannot be ridden, worked, or shown.

Simuliidae

Currie (1986) listed 51 species or species complexes of black fly in Alberta, and Fredeen (1985*a*) indicated that there were 31 species in Saskatchewan. Mason and Shemanchuk (1990) listed 11 species that attack cattle, of which 6 also attack horses. Of these, the most problematic species include *Simulium arcticum* Malloch and *S. luggeri* Nicholson and Mickel, whereas *S. vittatum* Zetterstedt and S. *venustum* Say can be significant livestock pests (Shemanchuk 1978; Fredeen 1981). Some of these are species complexes and represent several distinct cytospecies (Adler and Mason 1997).

Mason and Shemanchuk (1990) describe the black fly life cycle. Larvae of all species occur in flowing water. Black flies typically overwinter as eggs in riverbeds, although a few species overwinter as larvae. Eggs hatch in the spring, and larvae attach themselves to the river substrate with silk pads. Larvae feed on particulate matter filtered from the stream, pass through a variable number of instars, and pupate attached to the substrate. Adults emerge, are carried to the surface in an air bubble, and fly to a resting site. After mating, females feed on blood for egg maturation and oviposit on submerged plants and rocks or scatter eggs as they fly over the surface of rivers. The number of generations per year depends on the species and environmental conditions. Some species are univoltine, whereas others are multivoltine.

Two species of black flies are serious pests of livestock in western Canada. *Simulium arcticum* has been an ongoing problem in Alberta along the Athabasca River and was a problem along the Saskatchewan River prior to the mid-1970s. *Simulium arcticum* only occasionally attacks man, but readily attacks cattle and horses (Fig. 3). It has a tendency to feed on the undersides of cattle, causing scrotal and sheath infection and interruption of bull breeding activities. This species also has a salivary toxin that has severe effects on cattle and can result in cattle death (Fredeen 1977*a*). Rempel and Anderson (1947) indicated that 95, 70, and 438 cattle were killed by this species during outbreaks in Saskatchewan in 1944, 1945, and 1946, respectively. The affected area changed annually, but generally was within 160 km of the North Saskatchewan River. A larviciding program initiated in

Fig. 3. Black flies attacking a steer. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

1948 reduced cattle deaths. Adult *S. arcticum* emerge in two to three cohorts per year along the Athabasca River in central Alberta (Anderson and Shemanchuk 1987), with outbreaks occurring between June and September. The most severe attacks occur during June.

Simulium luggeri has had severe outbreaks in Saskatchewan originating from the North Saskatchewan River since about 1976. This species became a problem following the construction of dams, which changed the characteristics of the river, making it a more suitable habitat for this species (Fredeen 1977*b*) and replacing *S. arcticum* as the major problem. The species has also caused problems in community pastures in central Alberta lying along the North Saskatchewan River, specifically in the Two Hills area (Shemanchuk 1988). *Simulium luggeri* readily bites humans as well as cattle. It tends to feed near the heads of cattle, but also on the underside. *Simulium luggeri* is multivoltine, with up to five generations per year, from May through August. Losses to cattle producers can be spectacular during outbreaks. Fredeen (1985*b*) evaluated the economics of an outbreak of *S. luggeri* in Saskatchewan in 1978 and estimated losses of over $2.9 million in a 5700 km^2 area, including weight loss, calf death, interruption of breeding activity, unrealized weight gains, damage to fences and structures from stampeding, and underutilization of pasture.

Tabanidae

Teskey (1990) provided an excellent account of the biology of horse and deer flies in Canada. Females actively seek blood meals using odour and visual cues associated with the host, much the same as black flies. Tabanids are generally diurnal and fly when temperatures exceed 12 °C (McElligot and Galloway 1991*b*). They are strong fliers with a tremendous potential for flight and can disperse up to 7 km in a day (Sheppard and Wilson 1976). Tabanids prefer to remain in specific habitats and are generally most abundant in open areas near the edge of woods (Sheppard and Wilson 1977). Adults can live for several weeks (Thornhill and Hays 1972), producing several batches of eggs. Only the female tabanid blood feeds, but both sexes feed on nectar for flight energy. Females will take 20–600 mg of blood per meal, depending on size, but the host may lose more blood because of flow from the wound (Hollander and Wright 1980).

Eggs are laid in masses of 200–1,000 on objects near water, usually emergent vegetation. Eggs hatch in about one week and the larvae drop into the adjacent water or wet soil near shore. Larvae burrow into the substrate and usually remain there until they pupate in drier areas the following spring. Some species that are active early in the spring may complete larval development by late summer and fall, but typically, one generation per year is the rule. The flight periods for individual species may extend from 6 to 14 weeks, but the majority of activity occurs over shorter periods, about 4–6 weeks. Different species begin activity in succession so that animals may be attacked between mid-June and mid-August (McElligot and Galloway 1991*a*; Ralley *et al.* 1993).

Tabanids have painful bites, causing intense discomfort and worry to humans and livestock. Many species appear to prefer cattle, bovids, and large animals (Fig. 4). Tabanids seem to have preferred landing sites on cattle, especially the legs (Hollander and Wright 1980). Attacked cattle exhibit individual behaviours such as foot stomping, tail switching, and head tossing, as well as herd behaviours such as formation of grazing lines and bunching (Ralley *et al.* 1993). Horse flies have caused 12% reduction in cattle weight gains and 16.8% reduction in feed efficiency (Perich *et al.* 1986). The painful bites cause the host to react and dislodge the fly, which returns to feed, often on another host (Foil

Fig. 4. Tabanids attacking a steer. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

1983). Horse flies are well-suited as mechanical vectors because of their requirement for blood, large blood meals, and movement from host to host. Among the potential pathogens that they mechanically transmit are those that cause anaplasmosis, anthrax, tularemia, and equine infectious anaemia.

Muscidae

Three species in the family Muscidae can be significant pests of pastured cattle in North America. These species include the horn fly, *Haematobia irritans* (L.); stable fly, *Stomoxys calcitrans* (L.); and face fly, *Musca autumnalis* DeGeer. These three species were introduced to North America and live in close association with cattle. Horn fly was introduced to North America in the 1880s and first reported in Canada in 1889 (McLintock and Depner 1954). Stable fly was common in the United States during colonial times (Brues 1913) and was reported in Canada as early as 1898. Face fly was introduced into North America in the early 1950s and by 1967 had been reported throughout much of western Canada (Depner 1969). Both horn fly and stable fly are members of the subfamily Stomoxinae and have elongate, sclerotized mouthparts adapted for cutting skin and blood feeding. The face fly is a member of the subfamily Muscinae and has sponging mouthparts that contain rasping teeth that will abrade but not cut skin. This species feeds on nasal and ocular secretions of cattle, but will take blood opportunistically if available.

The basic life cycles of these three species are similar. Females mate within 24 hours after emergence, feed, and produce eggs that are laid in batches. Eggs hatch rapidly and larvae pass through three instars. The pupa is formed within a casing formed by sclerotization of the last larval skin and lasts about as long as the egg and larval stages combined. Key differences among the three species include the degree of association with the host, the requirement for blood feeding, the oviposition substrate and larval habitat, and the presence of a stage of diapause.

The stable fly (Fig. 5) can reach large numbers in confined cattle operations such as feedlots and dairies, but will disperse to pastures and recreational areas during the summer. Dispersal can occur over long distances (Hogsette *et al.* 1989). Fly production occurs in accumulated organic matter, including urine-soaked hay that may have been left in a pasture for supplemental feeding (Broce *et al.* 2005). Cattle, horses, and people are typically bitten on the legs. Both sexes of the stable fly feed on blood, and the bites are extremely painful and cause severe irritation. Livestock react to the bite by moving and dislodging the fly, causing it to leave and return to resume feeding. The flies make numerous visits to the host, with repeated bites to obtain a full blood meal. After feeding, the adult flies rest in protected areas on nearby vertical surfaces such as vegetation, fences, feed bunkers, or the sides of buildings.

Female stable flies produce 60–120 eggs per clutch, with some flies surviving to lay two or more clutches (Foil and Hogsette 1994). The duration of the entire life cycle from egg to egg-laying adult is generally about three to five weeks, with several generations each year. Stable flies in southern Alberta have three generations per year and are active from May to October, with peak activity in August and September (Lysyk 1993). No true diapause has been identified in stable flies. They may overwinter in refuges as slowly developing larvae in sheltered areas indoors (Beresford and Sutcliffe 2009) or in silage mounds, moving to colonize new habitats early in the spring. In some areas, stable flies appear late in the summer, perhaps because of long-distance dispersal.

The face fly is somewhat more adapted than the stable fly to pasture habitats. The face fly prefers pastures that have trees and moist areas such as ponds and streams, and

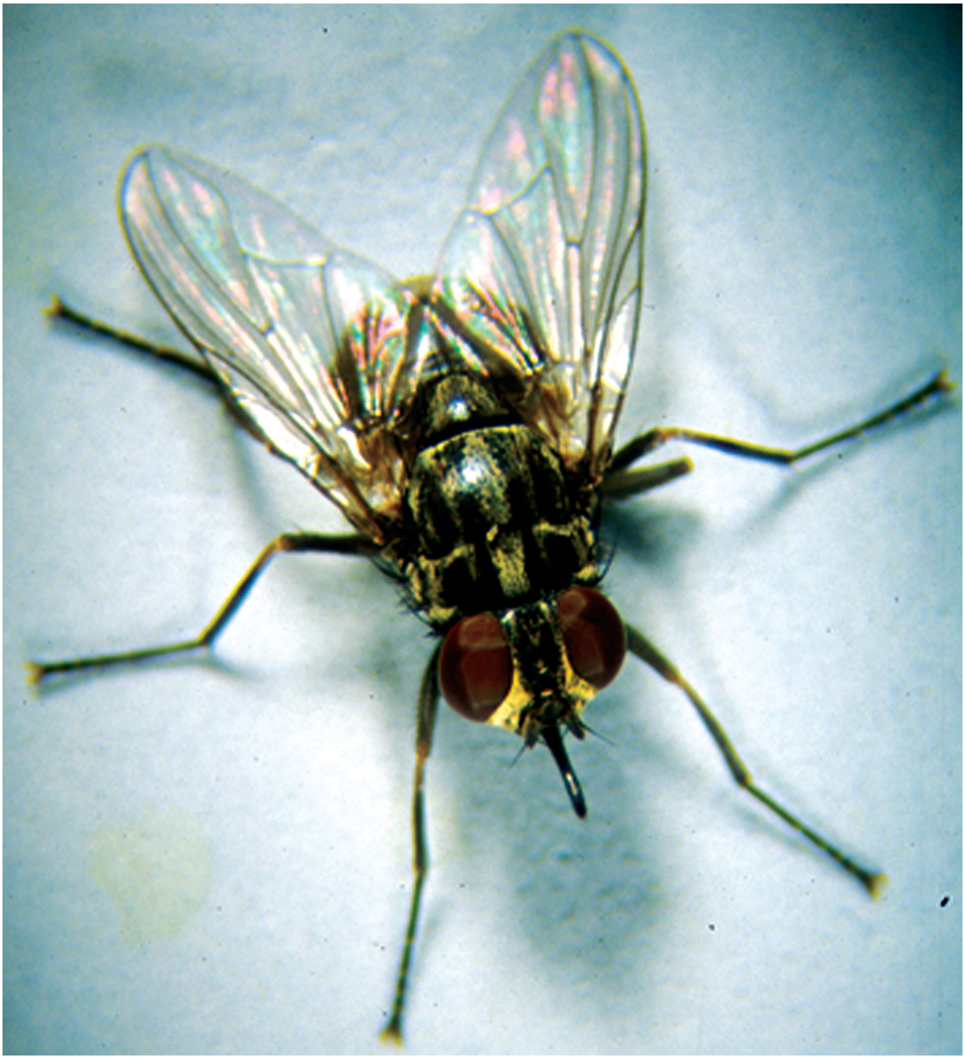

Fig. 5. Stable fly adult. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

is less common in dry, open pasture (Depner 1969). This insect has a true diapause and both sexes overwinter as unmated adults. Diapause is induced during the fall by short photoperiods and cool temperatures during late-larval through early adult stages (Kim and Krafsur 1994). Diapausing adults of both sexes have been collected during the winter from buildings or hollow trees, but survival may be limited because the species is not particularly cold tolerant. Krafsur and Moon (1997) have proposed that successful overwintering might require protection in subnivean or below-ground habitats. Adults leave the hibernacula in the spring and appear in pasture from late May to the middle of June. Mating occurs after spring emergence. Females begin feeding on cattle, using facial secretions and blood as a protein source for egg development. Females oviposit into fresh cattle dung by inserting 16–36 eggs vertically into the pat, varying with female body size (Lysyk and Easton

1986). Eggs are placed so that a tiny respiratory mast protrudes from the dung surface. Larval development strictly occurs in manure from animals on pasture. Hence, this fly is considered a pasture or rangeland pest. The late third instars disperse from the pat to find a suitable place for pupation. Pupae are unusual in that the pupal case has calcium carbonate deposited in it and is white and crystalline. Adults begin to feed shortly after emergence, and females mate within two to four days. Face flies rest near fence posts and trees and visit cattle periodically to feed. These flies cause mechanical damage to the eyes and are the intermediate host for eyeworms in the genus *Thelazia* and a vector for the causative agent of infectious bovine keratoconjunctivitis (Krafsur and Moon 1997).

Horn flies are well adapted to a pasture and rangeland habitat. Adults live in intimate association with the host, primarily cattle, but will also attack horses (McLintock and Depner 1954) (Fig. 6). Adults feed repeatedly on host blood and leave only to oviposit or disperse among hosts. Adult horn flies can survive off the host, but in the absence of blood will not reproduce. The tendency to rest on the host is tied closely to cattle defecation because oviposition occurs in fresh dung pats mainly during the daylight hours (Kuramochi 2000). Gravid females move to the hind legs of cattle and fly to the pat immediately following deposition. Oviposition requires about 10 minutes and usually occurs on the under surface of the pat (Kuramochi 2000). Eggs hatch within a day or so, depending on temperature, allowing rapid penetration and colonization of the dung. Developmental time is temperature dependent, and approximately 50% of the developmental period of immatures is spent in the pupal stage (Lysyk 1992*a*). In the fall, declining temperatures trigger diapause in pupae (Lysyk 1992*b*), which overwinter beneath pats. Overwintering survival is determined by temperatures during the period of diapause induction during the fall (Lysyk and Moon 2001). Pupae are protected from extreme winter temperatures by the insulation provided by

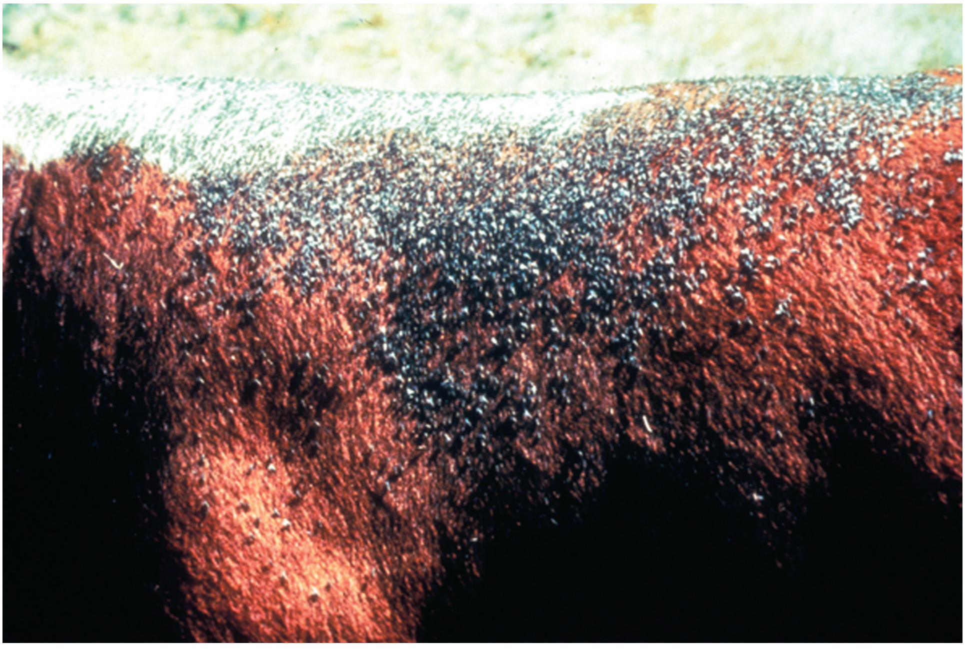

Fig. 6. Horn flies on cattle. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

the pat. Adults emerge the following spring, with peak emergence occurring between late April and mid-May, depending on spring temperatures (Lysyk 1999). Most of the adults that emerge during the spring develop from eggs laid during a three- to six-week period the previous fall. In Canada, adult numbers increase throughout the spring and summer, reaching a peak in early August (Lysyk 2000). Populations decline from August to October as increasing numbers of pupae enter diapause. The occurrence of a true diapausing state associated with dung pats allows the species to persist in rangeland that typically lacks shelter associated with nearby human settlement.

Damage to cattle by horn and stable flies results from the painful feeding process that results in reduced cattle productivity. Horn fly is abundant on cattle in pastures and rangelands and is of greater economic significance in these habitats. Horn flies generally attack larger animals such as yearlings and cows and not calves. Feeding on yearlings can result in up to an 18% reduction in weight gain (Haufe 1982), and feeding on cows results in reduced milk production that indirectly reduces weight gain in the calves. Every 100 flies per cow (season average) can reduce calf weaning weights from 3 to 16% (Steelman *et al*. 1991). Horn flies are the intermediate host for *Stephanofilaria stilesi* Chitwood, a nematode parasite of cattle that causes lesions along the midline of the animal belly.

Field Ectoparasites

Field ectoparasites of livestock in Canadian grasslands largely comprise the ixodid ticks, *Dermacentor andersoni* Stiles (the Rocky Mountain wood tick), *D. variabilis* (Say) (American dog tick), and *D. albipictus* (Packard) (the winter or moose tick) (Arachnida: Acari). These species have four stages in the life cycle (adult, egg, larva, nymph). Adults attach to the host and blood feed for extended periods. Females are adapted to take much larger blood meals than are males and will increase their body weight 200–300 times compared with their unfed weight. Engorgement of *D. andersoni* on cattle may take from 10 to 20 days, depending on ambient temperature (Lysyk 2008). This long attachment period exposes the tick to various risks from the host, including mortality from host grooming behaviour and having to overcome the host's hemostatic, inflammatory, and immune responses (Ribiero and Francischetti 2003). Ticks will localize in areas such as the brisket and back to avoid grooming and have developed a large array of salivary chemicals that suppress the host response and permit continuous feeding. Engorged females detach from the host, crawl to a sheltered area, and lay approximately 60–70% of their engorged weight as eggs. Eggs are laid on the ground and, after a developmental period, hatch into the six-legged larva. These larvae will feed on a host, engorge, detach, and then moult to the eight-legged nymph. The nymph also feeds on a host, engorges, detaches, and then moults to the adult stage. The duration of feeding, time required for moulting, host-seeking behaviour, number of host species, and the hosts used vary among the three species.

Dermacentor andersoni and *D. variabilis* have a three-host life cycle, with each feeding stage spent on a different host. Adults are active in the spring, often as soon as the snow is gone, and quest for hosts by climbing vegetation (Fig. 7). Hosts for adults are usually larger mammals such as rabbits, porcupines, dogs, deer, cattle, horses, and humans. Females attach, engorge, drop, and seek sheltered areas to oviposit. Eggs are laid and hatch to the larval stage. Larvae of *D. andersoni* are active and feed on small mammals from mid-June through September and peak in abundance in late July or early September (Sonenshine *et al*. 1976). Engorged larvae drop from the host and moult to nymphs. Nymphs can overwinter and become active the following spring, usually appearing earlier in the year than larvae

Fig. 7. Female (upper tick) and male (lower tick) *Dermacentor andersoni*. Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

(Wilkinson 1984). Engorged nymphs moult to the overwintering adult stage. The life cycle generally takes two years, although it may require three years in some areas (Wilkinson 1967). The seasonal biology of *D. variabilis* is different from that of *D. andersoni*. Adults usually have a longer period of activity, and larvae overwinter and become active early the next spring. Overwintered larvae that feed early in season will produce a unimodal peak of nymphs in mid-summer and ultimately moult to the overwintering adult stage (Garvie *et al*. 1978; Burachynsky and Galloway 1985).

In Canada, *D. andersoni* occurs west, and *D. variabilis* typically east, of a line (i.e., 105° longitude) running north–south through the centre of Saskatchewan (Wilkinson 1967). Gregson (1956) indicated that the two species are separated by a gap of 80 km. However, Dergousoff *et al.* (2009) identified sympatric areas in Saskatchewan that may indicate range expansions. Periodically, *D. variabilis* is identified from collections made in Alberta that are mainly associated with travellers returning from out of province. In the prairies, *D. andersoni* typically is found on south-facing slopes in areas with shrubby vegetation associated with grassland ecozones and is absent from aspen parklands. *Dermacentor variabilis* occurs in ecotonal habitats within deciduous forests and aspen parklands and appears to prefer more mesic environments (Wilkinson 1967).

Dermacentor albipictus parasitizes large ungulates such as moose, elk, deer, and cattle and horses. In Canada, it occurs from the United States border north to the territories (i.e., below 60° latitude) (Wilkinson 1967), with some populations now established in the southern Yukon. It is a one-host tick; that is, all parasitic stages are completed on the same animal. Larvae climb vegetation in the fall and will attach to passing hosts, usually during September through November (Drew and Samuel 1985). Larvae engorge and moult to the nymphal stage in a relatively short period following attachment and are usually no longer present by November (Glines and Samuel 1984; Drew and Samuel 1989). Nymphs are the most abundant during November through February. Most do not feed immediately, delaying engorgement until sometime between January and March. A few may moult to adult males in early December. The on-host diapause exhibited by nymphs is unusual and appears to be absent in the southern parts of the tick's range. It is likely an adaptation to delay female drop until conditions are favourable for survival and oviposition (Addison and McLaughlin 1988). The majority of adults appear between January and March, with engorged females present between late January and early May. Peak drop occurs in March (Drew and Samuel 1989). Females lay eggs during the early summer, which hatch in the fall, several weeks before larvae ascend vegetation (Drew and Samuel 1986).

Reliance on only one host allows *D. albipictus* to complete its life cycle in one year, as opposed to two or three years, as required for *D. andersoni and D. variabilis*. Only the larvae need to search for a host; the remaining stages do not, reducing the risk of failure. Balanced against this may be increased tick mortality from grooming and hair loss. Large ungulates infested with *D. albipictus* groom frequently while tick larvae and adults are feeding and less so during nymphal diapause and feeding (Welch *et al*. 1991). In three-host ticks, grooming loss is incurred by tick larvae (Shaw *et al*. 2003) and nymphs (Norval 1978) when feeding on small mammals and by adults feeding on ungulates (Rich 1973).

Dermacentor andersoni and *D. variabilis* vector human pathogens such as the agents that cause Rocky Mountain spotted fever, tularemia, and Colorado tick fever, although the incidence of these diseases is low in Canada. Both species can transmit bovine anaplasmosis (Kocan *et al*. 2010). This disease occurs sporadically in Canada, usually associated with cattle importation. However, two outbreaks have occurred in the Assiniboia region of southern Saskatchewan in the absence of cattle importation, and a third outbreak was detected in Manitoba in January 2009 and is ongoing (Howden *et al*. 2010). Anaplasmosis is an important disease because regulations requiring testing of breeding cattle before importation are viewed as a non-tariff trade barrier by Canada's trading partners.

Populations of *D. andersoni* that occur west of the continental divide are referred to as the montane form and are also capable of causing paralysis in livestock, wildlife, and humans. The paralysis is caused by a toxin produced in the salivary glands of the tick. Populations east of the continental divide are referred to as a prairie form and generally do not cause paralysis, having saliva with different antigenic properties (Lysyk *et al*. 2009). However, rare cases of paralysis have been caused by *D. andersoni* collected in portions of Saskatchewan (Scholfield and Saunders 1992). The prairie and montane forms of the ticks have other biological and genetic differences, but exhibit only a minor amount of reproductive incompatibility (Lysyk and Scoles 2008).

The effects of *D. albipictus* on wildlife include hair loss, anemia, weight loss, reduced weight gain, and death (Glines and Samuel 1989). This tick has also caused the death of hundreds of cattle when large numbers attacked cattle left in the bush to graze during the winter (Cameron and Fulton 1926). This situation is periodically repeated in areas where wildlife hosts and cattle coexist.

Endoparasites

The chief arthropod endoparasites of livestock are bot flies (Diptera: Oestridae). Three genera in three subfamilies affect livestock on the western Canadian grasslands. These genera include cattle grubs (*Hypoderma* spp.), sheep bot fly (*Oestris ovis* L.), and horse bots (*Gasterophilus* spp.). The authors in Colwell *et al*. (2006) present an excellent summary of the biology of oestrids. Bot flies that affect livestock on the Canadian grasslands were introduced into North America with settlers and soldiers who brought sheep, cattle, and horses from Europe as work animals and for meat, leather, and wool. Unlike other parasites of livestock, adult bot flies are not parasitic, but the larvae are obligate parasites of mammals. Mature third instar larvae leave the host and pupate on the ground beneath surface litter. Adults emerge 30–60 days later and live for up to two weeks. Adults have no functional mouthparts and are autogenous; that is, females emerge with fully developed ovaries and males with mature gametes. Mating occurs shortly after emergence, followed by either a rest period to develop larvae for larviparous species or an immediate search for suitable hosts for oviparous species.

Hypoderma bovis (L.) and *H. lineatum* (Villers) are two species of cattle grub present on the grasslands. Flies of both species are active on warm, sunny days with low wind speed during the late spring and summer (Fig. 8). Males perch on grasses or small shrubs at characteristic landscape features such as treeless valleys with open, flowing water, where they wait to capture passing females in flight. After mating, the females fly in search of a host on which to oviposit. Flights may exceed 30 km. *Hypoderma bovis* attach eggs singly to the host hair, with a flight episode between each egg. The flight activity may frighten cattle, producing a characteristic "gadding" response in which the animals run with their tails held high. Female *H. lineatum* often approach recumbent hosts on the ground and attach their eggs in rows of up to 30 on a single hair shaft. Eggs hatch in 7–10 days. First instars produce a suite of collagen-digesting enzymes to penetrate the upper skin and to subsequently disperse within connective tissues (Boulard 2006). They spend up to seven months moving through deep tissues prior to arriving at subdermal sites on the hosts' back, where they digest a small hole in the skin and moult to the second instar. The

Fig. 8. Adult cattle grub (warble fly) (*Hypoderma* sp.). Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

host's immune reaction results in a cyst or "warble" around the larvae. The larvae grow rapidly and moult to the third instar within a few weeks. Three to six weeks later, the third instars have reached maturity and leave the host through the enlarged hole in the skin. The endoparasitic period effectively constitutes a successful overwintering period. The very long larval developmental period results in one generation per year for these species.

Hypoderma bovis and *H. lineatum* rarely oviposit on animals other than cattle. When they do, the rare larva that penetrates the skin almost always dies during development. There are reports of larvae being common in horses and occasionally companion animals and people, but there are no reports of the larvae completing development to mature third instar. As a result of the strict requirements for an appropriate host, these invasive species have not become established in indigenous hosts such as cervids or antelope that share their range with grazing cattle. Occasionally, however, these species will develop on the indigenous bovine, American bison.

Dispersing larvae and larvae in subdermal cysts on the back cause little host morbidity or mortality, but do cause significant reductions in productivity through damage to the hide and leather, as well as to the trim of infected meat. Coordinated and highly effective treatments led some provincial governments to enact legislation requiring producers to treat their cattle, in conjunction with provincial monitoring of the populations. New classes of drugs for parasite control, with very high efficacy against *Hypoderma*, were introduced in the 1980s and have resulted in the near extinction of these two invasive species. Relict populations appear to exist in areas where cattle raisers have adopted organic production standards or for other reasons do not use therapeutic antiparasitic drugs.

Sheep nose bots are larviparous. Females will fly past the host's face and direct packets of up to 20 larvae, contained in a small amount of fluid, toward the nose of sheep or goats. Larvae move from the nose surface into the nasal passages and sinuses of the host, where they feed on mucus and develop. Mature larvae crawl out through the nostrils and pupate in the soil. Pupation lasts from 10 to 70 days. There may be one to two generations per year.

Three species of horse bot are known from the Canadian grasslands. They are *Gasterophilus intestinalis* (De Geer), *G. haemorrhoidalis* (L.), and *G. nasalis* (L.). Horse bots are worldwide in distribution and parasitize horses, donkeys, and mules. Eggs are attached to hair, the location depending on the species, and penetrate the soft tissues of the tongue and mouth in response to grooming. Larvae live in the soft tissues for about three weeks, and then move to the stomach where they attach and spend 10–12 months before they detach and pass with the feces where they pupate. Third instar *G. haemorrhoidalis* leave the stomach and complete development attached to the rectum. Adults emerge in two weeks to two months. Attacked hosts may have lesions in the mouth and stomach lining damage, and they may exhibit violent behaviour to avoid female flies.

Endoparasitism offers a number of advantages, including a safe place to overwinter and a larval diet nutritious enough not only to provide energy for immature growth, but also to allow ovarian development during the late larval and pupal stages. Because the adults do not feed, early ovarian maturation is seen as an adaptation to allow immediate oviposition during a short adult lifespan (Scholl and Weintraub 1988). Being endoparasitic reduces the time in the environment, which limits exposure of the pupa to natural enemies. The adults resemble bumble bees and may escape predation by mimicry (Nilssen *et al*. 2000). However, there are challenges associated with endoparasitism. Adaptations for respiration include obtaining oxygen by diffusion through the cuticle for small larvae buried in tissue, use of oxygen-carrying molecules in stomach-infesting larvae (Keilin and Wang 1946), and spiracular respiration by large larvae in air-filled sinuses or warbles. In the latter case, localization in the warble can lead to predation by birds such as magpies, which may rest on the backs of cattle and pick grubs from their backs (Henny *et al*. 1985). Mortality can be high during skin penetration by first instars, and substantial larval mortality can result from acquired resistance by the host (Baron and Weintraub 1986). Yearling animals are the most susceptible and naïve age class of cattle and typically support most of the immature cattle grub population in an area.

Host Ectoparasites

There are several taxa of ectoparasites that are important to hosts in grazing systems. These taxa include Phthiraptera (lice), various families of mites (Demodicidae, Sarcoptidae, Psoroptidae), and the sheep ked, *Melophagus ovinus* (L.) (Diptera: Hippoboscidae). None have free-living stages, but rather live on the host throughout the entire life cycle and survive off host for only short periods. The host essentially forms the habitat as well as the food source. Most species have broad geographical distributions associated with the host, and those affecting domestic livestock were likely introduced to North America. These arthropods are wingless, often flattened, and may be equipped with various anatomical features such as hooks, spines, and claws that facilitate remaining on the host and not being removed by grooming. These species also have behavioural adaptations to ensure survival on the host, for example, selecting sites that are less likely to be groomed (Watson *et al*. 1997) or in which they are less likely to experience extreme temperatures. Methods used to obtain nutrition vary. Chewing or biting lice (Ischnocera) use mandibulate mouthparts to scrape skin and hair. Sucking lice (Anoplura) and hippoboscids have mouthparts with highly specialized stylets that are used to obtain blood directly from capillaries (Fig. 9). Mites have chelicerate mouthparts and will also feed either on host fluids or on tissues.

The life cycles of lice and mites have incomplete metamorphosis in which the immature stages do not differ greatly in form from the adult and generally have the same feeding habits and locations as the adult. The life cycles of lice include an egg, three nymphal stages, and one adult stage (Grubbs *et al*. 2007). Mite life cycles tend to be more complex. Species of keds belong to the order Diptera in which larvae typically occur in habitats that are distinct from the adult. This is modified in sheep keds: Females produce one egg that is retained within the reproductive tract where it hatches and larval development occurs. The larva is nourished by glandular secretions from the female. The mature larvae are expelled and attach to the host's wool, where they pupate and complete development.

The life histories of these ectoparasites represent some compromises. Small meals are taken, which limits irritation caused by individuals and may reduce mortality from host grooming. Because of the small blood meal size, fecundity is low, with relatively

Fig. 9. Adult sheep ked (*Melophagus ovinus*). Photo provided by Agriculture and Agri-Food Canada, Lethbridge.

few eggs produced daily or throughout the life of the female. Constant contact with a host reduces the need to find a host, extract nutrition, and then find a suitable oviposition site, unless the host dies. However, vertebrate blood is nutritionally deficient such that insects depending on it solely throughout their life cycle (sucking lice, keds) have evolved associations with bacterial symbionts that produce metabolic products that are essential for survival, growth, and reproduction (Douglas 1989). Dispersal to other hosts is limited to times when conspecific hosts directly contact each other, which probably occurs frequently with herding animals.

Populations of most ectoparasites show marked seasonal trends, with numbers typically greatest during the winter and cooler seasons. It may be that skin temperatures during the summer become too great to permit survival; however, other host-related factors play an important role (Sweatman 1956; Nelson and Qually 1958; James *et al.* 1998; Colwell and Himsl-Rayner 2002). The host's immune and inflammatory responses develop over time and reduce the net reproductive rate of the parasites. Populations decline but persist throughout the summer at low levels on sheltered sites on the animals. The arthropods have no mechanism to seek shelter off the host. As populations increase, the arthropods disperse over the host and move onto other hosts when there are opportunities for direct contact. Populations are probably too low during the summer to cause damage while animals are on range. However, host reactions to severe infestations can be debilitating during the cooler seasons.

Conclusions

The arthropod parasites of livestock in Canadian grasslands have responded to several perturbations. Perhaps the main perturbation was the replacement of native ungulate species (i.e., American bison) with the introduction of domestic species such as cattle, horses, and sheep. This perturbation had two effects. The first was that the generalist native fauna, including most of the blood-feeding dipterous parasite complexes and the field ectoparasites, were readily able to exploit the new hosts. In some cases, such as with various species of black flies, winter ticks, and Rocky Mountain wood ticks, the new associations periodically resulted in livestock death. A second effect associated with the introduction of livestock was the concomitant introduction of the more closely associated non-native parasites such as the muscids in the blood-feeding dipterous parasite complex, the endoparasites, and host ectoparasites. Face fly and horn fly primarily affect cattle, with a secondary effect on horses, reflecting their greater degree of host specificity and adaptation to cattle. The endoparasites and host ectoparasites introduced with their hosts have had little effect on native ungulates by nature of their host specificity, and they have confined their effects to their exotic hosts.

Environmental perturbations have primarily affected the blood-feeding dipterous parasite complex and field ectoparasites and less so the endoparasites and host ectoparasites. The latter tend to be more influenced by host immunity. Environmental management practices, such as increasing land under irrigation and dam construction, have provided suitable habitat for native species or caused switching of abundant species. On the other hand, land development in western Canada and increased cultivation have reduced habitat for some of the field ectoparasites. Animal feeding strategies can also influence pest populations. For example, winter feeding has increased habitat for stable flies, and fall grazing in brushy areas that overlap with moose and elk habitat can increase cattle exposure to winter tick. Controlling and reducing damage caused by the field ectoparasites and the blood-feeding dipterous complex in grazing lands remains challenging because of the nature of the landscape and grazing systems, the sensitivity of the systems, and the life-history strategies of the arthropods themselves.

Acknowledgements

The author is grateful to Dr. D. D. Colwell, Lethbridge Research Centre, for supplying information on the Oestridae. Special thanks are extended to Dr. K. D. Floate and two reviewers who provided editorial comments that greatly improved the manuscript.

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