Chapter 4
Arthropods in Cattle Dung on Canada's Grasslands

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Abstract. Fresh cattle dung is a nutrient-rich habitat that is quickly colonized by a speciose and abundant assemblage of organisms. The ease with which this habitat is manipulated by using artificially formed pats (size, shape, site, and time of deposition), the speed of community succession, and the complex interactions among its diverse inhabitants combine to make the dung pat a model ecosystem for scientific study.

This chapter is intended to provide an overview of the arthropod species found in cattle dung on pastures of the Canadian prairies. It introduces the features of cattle dung that affect the activity of these arthropods and the key arthropod groups. It summarizes patterns of arthropod succession and discusses some of the more intriguing aspects of the cow pat community. Success will have been achieved if at least a few readers develop a desire to delve into dung.

Résumé. Le fumier frais de bétail est un habitat riche en éléments nutritifs qui est rapidement colonisé par des organismes nombreux et diversifiés. La facilité avec laquelle elle se prête à diverses manipulations (taille, forme, site et moment du dépôt), la vitesse de succession des communautés d'organismes qu'elle abrite et les interactions complexes qui s'observent entre les divers types d'organismes qu'elle contient font de la bouse un écosystème modèle pour l'étude scientifique.

Le présent chapitre vise à fournir un aperçu des espèces d'arthropodes que l'on trouve dans les bouses du bétail, dans les pâturages des prairies canadiennes. Il décrit les caractéristiques des bouses qui influent sur les activités des arthropodes, et présente les principaux groupes auxquels appartiennent ces arthropodes. Il résume les schémas de succession des espèces, et traite de certains des aspects particuliers des communautés d'arthropodes des bouses. L'objectif consiste à convaincre au moins quelques lecteurs de se pencher de près sur ce sujet.

What's in Dung…

At the time of deposition, cattle dung is about 80% water (Lysyk *et al.* 1985; Lee and Wall 2006) and supports a matrix of undigested plant material that is rich in nutrients, micro-organisms, and their by-products. By dry weight (DW), dung contains about 0.8% K, 0.4% Na, 2.4% Ca, 0.7% P, and 0.8% Mg (Marsh and Campling 1970). Levels of nitrogen in dung DW range from 2.5 to 4.0% (Marsh and Campling 1970; Lysyk *et al.* 1985), which is comparable to that reported for many species of plants (Fig. 2.2 in Bernays and Chapman 1994). Unlike the nitrogen in plants, however, much of the nitrogen in dung is in the form of bacteria, which may comprise 10–20% of dung DW (Lohnis and Fred 1923, as cited in Marsh and Campling 1970). Other organisms present in dung at the time of its deposition may include protozoa, parasitic nematodes, trematodes (flukes), and cestodes (tapeworms) passed from the cow.

The coprophilous ("dung loving") organisms that subsequently colonize fresh dung include fungi, nematodes, earthworms, and arthropods (e.g., insects, mites). This latter

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group contains the most prominent members of the dung pat community and is the focus of the current chapter. Blume (1985) lists more than 450 species of arthropods associated with cattle dung in North America, but includes many species that do not breed in dung (see next paragraph). Studies in British Columbia (Macqueen and Beirne 1974) and Alberta (Floate 1998) report a combined total of 112 taxa from cattle dung on pastures. However, this number does not include many species known to be common in dung, rarer species, or species that colonize dung in later stages of decomposition. These two studies reported three species of pteromalid wasps (Pteromalidae), but at least 20 species in Canada are known to parasitize flies that breed in dung (Floate and Gibson 2004). Macqueen and Beirne (1974) reported only 4 of the 36 species of coprophilous hister beetles (Histeridae) known from Canada (Bousquet and Laplante 2006). Examination of the published literature suggests that at least 300 species are members of the dung arthropod community in Canada, representing close to 50 taxonomic families (Table 1). By comparison, Skidmore (1991) reports about 275 species of insects in dung of cattle in Britain.

Many other species of arthropods occur in cattle dung, but are not typically considered to be members of the dung arthropod community. Such species most often are found in dung in the latter stages of degradation and are best considered casual visitors from adjacent habitats searching for prey or hosts, or species associated with rich organic soils or rotting vegetation. Such incidental species include centipedes (Chilopoda), woodlice (Isopoda), millipedes (Diplopoda), harvestmen (Opiliones), spiders (Araneae), earwigs (Dermaptera), springtails (Collembola), ants (Formicidae), click beetles (Elateridae), ground beetles (Carabidae), and bugs (Hemiptera).

Membership in the cow dung community for other species is ambiguous. As adults, the beetles *Aphodius distinctus* (Müller), *A. granarius* (L.), and *A. prodromus* (Brahm) (Scarabaeidae) are commonly attracted to fresh cattle dung (Floate and Gill 1998; Floate 2007), with up to 1,097 adult *A. distinctus* reported from one pat aged two hours (Mohr 1943). In such numbers, the adults can disrupt the pat to affect the survival and interactions of other species inhabiting the dung. The larvae, however, are detritivores and develop in soil that is rich in organic matter—not in fresh dung. In southern Alberta, composted manure from cattle feedlots is incorporated into cropland in the spring. At such time, large numbers of the adults of these species are attracted to the manure and form large swarms over the fields in which they subsequently oviposit. By early summer, these fields may contain densities of up to 90 larvae (“white grubs”) per square metre (KDF, unpublished). Samples of these larvae have been reared by the author to adults in jars of soil and subsequently identified as *A. distinctus*, *A. granarius,* and *A. prodromus* (also see Seamans 1934; Gittings and Giller 1997; and section titled “Seasonal Activity”).

Numerous studies have reported on insects associated with dung, but typically these reports are limited to one or few species, or to one guild (see section titled “Guild Structure”) of the dung community. The most widely studied taxa are pest flies (certain species of Muscidae) and dung beetles (Scarabaeidae). The former represent a small fraction of the total number of coprophilous species, but are important economic pests. Dung beetles are of interest primarily for their role in dung degradation, but they have additional roles in ecosystem function (see review by Nichols *et al.* 2008). For more comprehensive coverage of arthropod assemblages in dung, readers are directed to Hammer (1941), Mohr (1943), Laurence (1954), Skidmore (1991), and Hanski and Cambefort (1991).

… And Why Should We Care?

The biotic and abiotic factors that affect the rate of dung degradation have important practical applications. An estimated 140 million dung pats (308,000 tonnes of fresh manure) are deposited daily by cattle across Canada. This reflects an average deposition of 10 pats (approximately 22 kg of fresh dung) per animal per day (references in Fincher 1981) for a national herd of 14 million animals (Statistics Canada 2010). The cost of this accumulated manure is considerable.

Assuming no overlap of dung pats, a cow will cover an area of about 0.8 m^2 in dung each day. High levels of nitrogen and other nutrients immediately adjacent to the pat and released during dung decomposition cause the growth of unpalatable ("rank") vegetation. Avoidance of this vegetation by cattle may remove from grazing an additional area equivalent to five more dung pats (references in Fincher 1981). Hence, for a grazing season of 150 days, 100 head of cattle could remove 7.2 ha of pasture from beef production.

The cost of forage removed from grazing because of pat deposition in Canada has not been calculated, but data are available for the United States. In the foothills of northern California, undegraded dung on pastures totalling 2,024 ha and supporting 455 head of cattle was estimated to cost a cumulative $4,858 over three years, calculated in $US for the year 1984 (Anderson *et al.* 1984). This cost represents lost forage, which translated into a loss of 2,730, 628, and 112 kg of beef in the first, second, and third growing season after dung deposition, respectively. This cost would occur for each group of 455 cattle grazed per year. The foothills of northern California have a dung fauna and hot, dry summers similar to those on the Canadian prairie (Anderson *et al.* 1984).

The loss of nitrogen and minerals from pasture soils is another cost of undegraded dung. If not rapidly returned to the soil, the nitrogen in dung is lost into the atmosphere in the form of ammonia (Yokoyama *et al.* 1991). Additional nutrients in undegraded dung may be unavailable for plant growth for months or years.

Cattle dung also supports the development of pests that affect cattle. Horn fly (*Haematobia irritans* (L.)), stable fly (*Stomoxys calcitrans* L.), and face fly (*Musca autumnalis* (DeGeer)) are dung-breeding pests that affect cattle in North America. Horn fly has been estimated to cause potential losses in the United States approaching $1 billion per year (Kunz *et al.* 1991). These species are discussed in more detail by Lysyk (see Chapter 3). Eggs and immature stages of gastrointestinal parasites are passed from infected animals into dung, where they develop to stages that infect other animals.

In the United States, with a national herd of about 110 million animals, accelerated degradation of dung could potentially result in annual savings of $2 billion (Fincher 1981). This estimate reflects the increased availability of forage otherwise lost to pasture contamination, the increased return of nitrogen to pasture soils, and the reduced incidence of pest flies (Moon *et al.* 1980) and gastrointestinal parasites (Fincher 1973).

The cost of undegraded dung has been most widely recognized in Australia. The introduction of cattle to that country generated an abundance of manure, which supports large populations of buffalo fly, *Haematobia irritans exigua* De Meijere, and bush fly, *Musca vetustissima* Walker (Diptera: Muscidae). Native species of dung beetles evolved to breed in the dung of marsupials and are unable to effectively degrade cattle dung. Thus, the federal government funded a program that introduced 55 exotic species of dung beetles to Australia from 1968 to 1983 (Tyndale-Biscoe 1990; Doube and Macqueen 1991). To accelerate dung degradation, exotic species have also been introduced or redistributed in the United States (see references in Hoebeke and Beucke 1997).

Table 1. Arthropod taxa known, or likely, to be associated with cattle dung in Canada. Species numbers are derived from reports in the indicated references.

ORDER Family (Common Name*)	Guild	Minimum No. of Species	Reference
DIPTERA (flies)			
Anthomyiidae (anthomyiid flies)	Dung-feeders	5	1, 2, 8, 18
Calliphoridae (blow flies)	Dung-feeders	9	1, 2, 8
Cecidomyiidae (gall midges, gall gnats)	Dung-feeders	1	8
Ceratopogonidae (biting midges, punkies, no-see-ums)	Dung-feeders	4	1, 2, 8
Chironomidae (midges)	Dung-feeders	2	1
Chloropidae (grass flies)	Dung-feeders	4	8
Empididae (dance flies)	Predators	3	1, 8
Ephydridae (shore flies)	Dung-feeders	4	8
Lauxaniidae	Dung-feeders	1	8
Milichiidae	Dung-feeders	3	8
Muscidae (muscid flies)	Dung-feeders, mixed diet, predators	25	1, 2, 8, 18
Mycetophilidae (fungus gnats)	Dung-feeders		
Otitidae (picture-winged flies)	Probably dung-feeders	1	2
Psychodidae (moth flies)	Dung-feeders	2	8
Sarcophagidae (flesh flies)	Dung-feeders	13	2, 8, 12
Scathophagidae (dung flies)	Dung-feeders	2	1
Scatopsidae (minute black scavenger flies)	Dung-feeders	1	1
Sciaridae (dark-winged fungus gnats)	Dung-feeders	4	1, 8
Sepsidae (black scavenger flies)	Dung-feeders	8	2, 8
Sphaeroceridae (small dung flies)	Dung-feeders	17	1, 2, 7, 8
Stratiomyidae (soldier flies)	Dung-feeders	6	2, 8
Tachinidae	Parasitoids	2	8
Therevidae (stiletto flies)	Predators	1	8
HYMENOPTERA (wasps, bees, ants)			
Braconidae	Parasitoids	4	1, 2, 13, 17, 18
Diapriidae	Parasitoids	2	1, 2
Encyrtidae	Parasitoids	1	1
Eucoilidae	Parasitoids	2	1, 2, 18
Figitidae	Parasitoids	3	2
Ichneumonidae	Parasitoids	1	13, 15, 18
Mymaridae (fairyflies)	Parasitoids	1	1
Proctotrupidae	Parasitoids		
Pteromalidae	Parasitoids	15	2, 13, 14, 15, 16, 18
Scelionidae	Parasitoids	1	1

Table 1. (continued)

ORDER Family (Common Name*)	Guild	Minimum No. of Species	Reference
COLEOPTERA (beetles)			
Clambidae (fringe winged beetles)	Fungus-feeders	1	1
Cryptophagidae (silken fungus beetles)	Fungus-feeders		
Geotrupidae	Dung-feeders (tunnellers)	2	6, 10
Histeridae (hister beetles)	Predators	36	2, 4
Hydrophilidae (water scavenger beetles)	Dung-feeders, predators	12	1, 2, 9
Lathridiidae (minute brown scavenger beetles)	Fungus-feeders	1	1
Pselaphidae (short-winged mold beetles)	Fungus-feeders, predators		
Ptiliidae (feather-winged beetles)	Fungus-feeders	1	1
Scarabaeidae	Dung-feeders		
Aphodiinae	- dwellers	25	1, 2, 5, 6, 7, 10, 11
Scarabaeinae	- tunnellers, rollers	9	1, 2, 6, 7, 10, 11
Staphylinidae (rove beetles)	Mainly predators, some fungus-feeders, some parasitoids	26	1, 2, 3, 10, 18
ACARINA (mites)			
Eviphididae	Predators	1	3
Halolaelapidae	Predators	2	3
Macrochelidae	Predators	1	2
Parasitidae	Predators	3	3
Pyemotidae	Parasitic	1	2
Uropodidae	Predators, saprophagous	1	3
Minimum estimate of total species		267	

* From Borror *et al.* (1989).

[1] Floate (1998); [2] Macqueen and Beirne (1974); [3] KDF, unpublished; [4] Bousquet and Laplante (2006); [5] Gordon (1983); [6] Floate and Gill (1998); [7] Floate (2007); [8] Stone *et al.* (1965 – cited in Blume 1985); [9] Smetana (1978); [10] Bousquet (1991); [11] Howden and Cartwright (1963); [12] O'Hara *et al.* (2000); [13] Gibson and Floate (2004); [14] Peck (1974); [15] Depner (1968); [16] Gibson and Floate (2001); [17] Krombein *et al.* (1979); [18] Wylie (1973).

Guild Structure

Insects that colonize dung have been classified by Skidmore (1991) into one of seven main guilds (Fig. 1, Table 1). Three guilds contain species of flies (Diptera) that are distinguished by differences in larval diet. Larvae of "dung" flies feed only on micro-organisms. Most coprophagous Diptera are members of this guild. Early-instar larvae of "mixed-diet" flies feed on micro-organisms and then switch, usually in the third and final larval instar, to feed on insects. Larvae of "predatory" flies feed only on insects. A fourth guild contains species of wasps (Hymenoptera) that are mainly parasitic on flies in each of the preceding three guilds. The final three guilds contain species of beetles (Coleoptera). Fungivorous beetles colonize pats at later stages of decomposition to feed on fungal hyphae and spores. Predatory beetles feed on other insects, particularly the eggs and larvae of flies. Dung-feeding beetles feed solely or primarily on dung. By far the most prominent members of this latter guild are species of Scarabaeidae. Adult scarabs are filter-feeders (Holter *et al.* 2002) and obtain nutrition mainly by ingesting the micro-organisms present in the fluid component of fresh dung (Aschenborn *et al.* 1989). In contrast, scarab larvae feed mostly on undigested plant fibre from which nutrients are extracted through the action of symbiotic cellulose-digesting bacteria housed in the larval hindgut (Terra 1990).

Although this guild classification is useful to describe general features of dung insect communities, Skidmore (1991) himself acknowledges that it oversimplifies the complexity of interactions and excludes non-insect arthropods. The yellow dung fly, *Scatophaga stercoraria* (L.) (Scathophagidae), is classified as a dung fly by virtue of its coprophagous larvae, but the adults are voracious predators. Species of *Aleochara* (Staphylinidae) are classified as predatory beetles, but their larvae are parasitoids of fly puparia. Species of

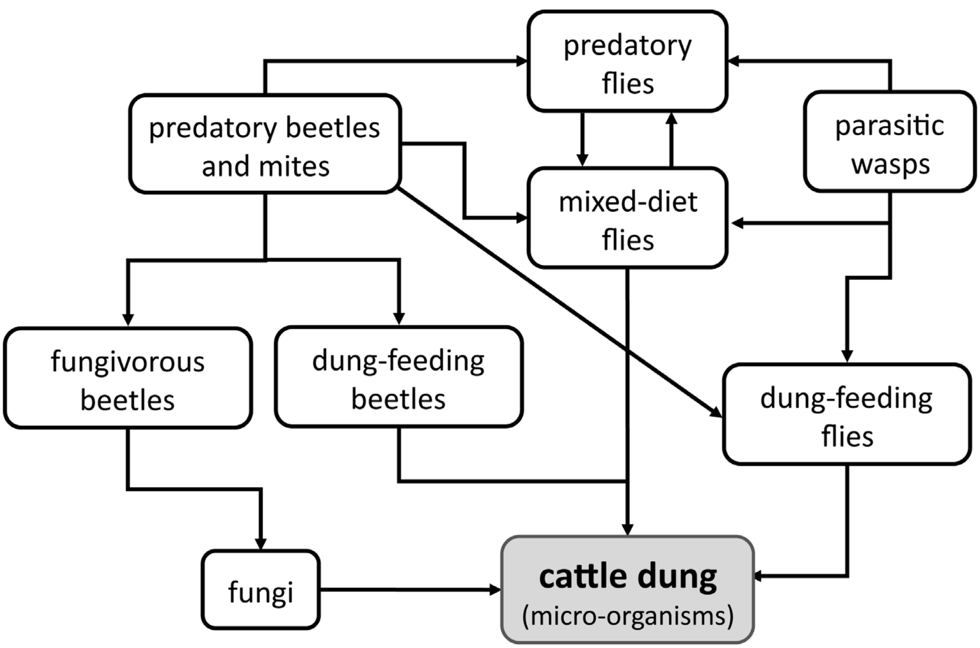

Fig. 1. Type and interactions among arthropod groups common in cattle dung.

Sphaeridium (Hydrophilidae) are classified as dung-feeding beetles, but their larvae may be facultative carnivores. Many different species of mites (Acarina) can be common in cattle dung (Table 1 and see section titled "Phoresy"). Most of these species are in the family Macrochelidae and feed on immature stages of insects or other mites, or on nematodes. Other species of mites (e.g., Pyemotidae) are parasites of insects.

The guild classification also overlooks key differences among species of dung-feeding Geotrupidae and Scarabaeidae (Aphodiinae, Scarabaeinae), which form three functional groups termed "dwellers," "tunnellers," and "rollers" (Cambefort and Hanski 1991, Fig. 2). Dwellers (mainly Aphodiinae) do not form nesting chambers or burrows, and they complete egg-to-adult development within the pat or at the interface between the pat and soil surface. Pat degradation occurs mainly through the feeding activity of larvae, which slowly change much of the pat mass into dry, granular material. This material is scattered by wind, penetrated by vegetation growing below, or worked into the soil by biotic and abiotic factors. Removal of the dung pat from the soil surface by dwellers normally takes weeks to months. At certain times of the summer, however, large numbers of adults may be attracted to pats that may be scattered in a period of days (see text on *A. distinctus* in section titled "Seasonal Activity"). Dwellers tend to be relatively small and nondescript beetles; are the dominant group in temperate climates, including Canada (Table 1); and typically include species of *Aphodius* (Fig. 3). Many of these species have recently been placed in different genera (Gordon and Skelley 2007). However, they are referenced here as members of the genus *Aphodius*, in conformity with most of the existing literature.

Adult tunnellers and rollers remove portions of dung from the fresh pat and pack it into the blind end of more or less vertical tunnels that may extend 10 cm or more into the soil. For tunnellers (Geotrupidae, Scarabaeinae), adults construct tunnels that extend from beneath

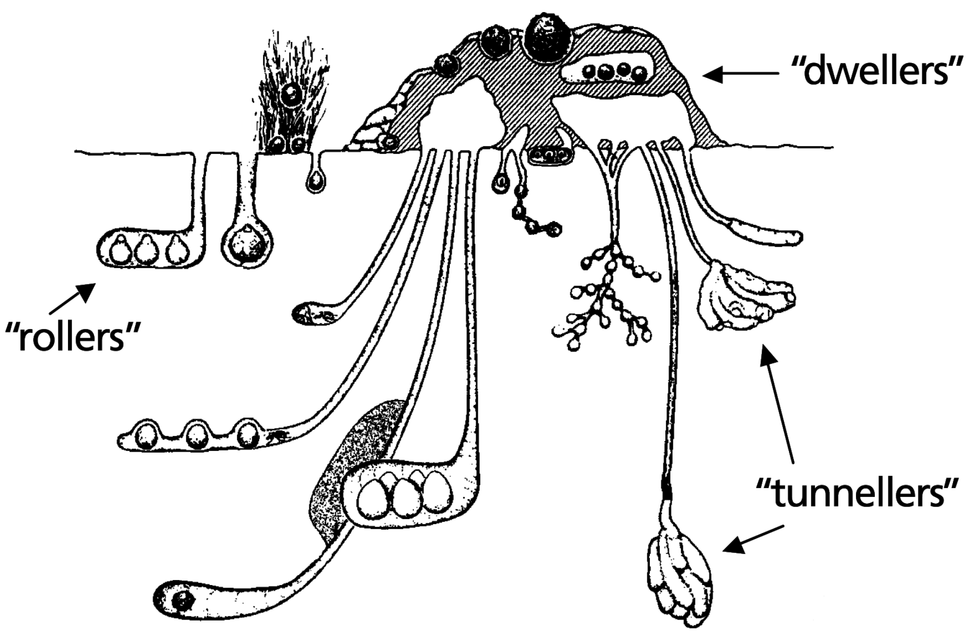

Fig. 2. Species of dung beetles (Scarabaeidae) are grouped as "dwellers," "tunnellers," or "rollers" on the basis of differences in their nesting behaviour (modified from Doube 1990).

the pat (Fig. 2). For rollers (Scarabaeinae), adults form balls of dung from fresh manure, which they then roll some distance from the pat prior to burial and formation of the "brood ball" (Fig. 2). Adults of both groups form an egg chamber within the packed mass of dung into which one egg is laid, and then seal this chamber with an excrement cap. The egg and the associated mass of dung form the brood ball. No further care is given to the offspring, and each brood ball constitutes the total quantity of food available to a single larva. The adult activities of tunnellers and rollers can remove most of a fresh dung pat from the soil surface in less than a week, increasing the aeration, water filtration, and nitrogen levels of the soil beneath and beside the pat. Tunnellers and rollers typically are larger than dwellers, have more ornate morphological traits, and tend to dominate in subtropical and tropical climates. In Canada, species of tunnellers and rollers include species of *Onthophagus* and *Canthon*, respectively (Fig. 3).

Pattern of Succession

The colonization of dung occurs in a series of sequential stages heavily influenced by the age of the pat (Hammer 1941; Mohr 1943; Laurence 1954). The earliest colonists are mainly adult flies, which begin to arrive within minutes of dung deposition to oviposit. Horn flies, which normally rest on the backs and sides of cattle, may colonize dung literally within seconds of deposition (McLintock and Depner 1954). Colonization by adult flies usually declines within a few hours after deposition. This decline coincides with the formation of a crust on the pat surface that slows the release of volatile chemicals used by the flies and other insects to locate the pat. Eggs laid during this first stage generally will produce a new generation of adult flies in 10–20 days. This rapid development time is facilitated by the feeding of larvae on nutrient-rich micro-organisms or on other insects.

The arrival of adult dung beetles signals a second stage of colonization. It normally peaks between the first and fifth day after dung deposition, with numbers of colonists declining rapidly thereafter (e.g., Holter 1975). Development of dung beetle larvae, in

Fig. 3. Three species of dung beetles that differ in their nesting behaviour. Left: *Aphodius fimetarius* (L.) (6–8 mm) is one of the more colourful dweller species in Canada. Middle: *Onthophagus nuchicornis* (L.) (6–8 mm) is a species of tunneller that locally can be abundant. Right: *Canthon pilularius* (L.) (12–17 mm) is a species of roller and is perhaps the largest species of dung beetle in Canada. Whereas it is a native species, the other two are of European origin. Photo credit: H. Goulet, Agriculture and Agri-Food Canada, Ottawa, Ontario.

contrast to fly larvae, may take several weeks to months. This slower development time reflects the low nutrient value of the plant fibres upon which the beetles feed. Larvae of the European species *Aphodius rufipes* L. (Scarabaeidae) assimilate only 7–10% of the plant fibre consumed and may ingest 175–530% of their dry body weight each day to obtain the nutrients needed to complete development (Holter 1974). Little further colonization of dung by coprophilous arthropods occurs two to three weeks after deposition.

The first and second stages of colonization coincide with the arrival of parasitic wasps and predacious beetles. Depending upon the species of wasp, they may lay their eggs in the eggs, larvae, or pupae of the host insect species. Some parasitoid species are gregarious, laying several eggs in a host. Other species may be solitary, laying only one egg per host. Some species may also be hyperparasites, parasitizing immature stages of wasps that, in turn, are parasitic on other insects. Adult flies and beetles that colonize the dung frequently arrive carrying phoretic mites (see section titled "Phoresy"). Numbers of these organisms begin to increase about 10 days after arrival at the dung and continue to increase for several weeks. The tunnelling and feeding activity of first- and second-stage colonists and their offspring accelerates the degradation of the pat to allow it to be more easily penetrated by vegetation and incorporated into the soil.

The final stage of colonization occurs with the breakdown of the interface between the dung and the surface of the soil. This process allows soil-dwelling organisms (e.g., earthworms, springtails, oribatid mites) to enter the pat and complete the breakdown of the dung to its component parts. Fungal spores, likely ingested by cattle and excreted fecally, germinate at various times during the decomposition process to further accelerate degradation and provide food for fungivorous species.

Factors Affecting Succession

The speed of succession and subsequent rate of dung pat degradation reflects a complex interaction of abiotic and biotic factors (Fig. 4). Climate, soil, and economics dictate the type of pasture maintained by the rancher. Pasture type determines forage productivity, productivity affects stocking rate, and stocking rate affects both the frequency of dung deposition and the likelihood that pats will be disrupted by trampling. In grassland regions of Alberta, stocking rates on irrigated pastures planted to tame forages may be 17.5 times the rates on native pastures in excellent condition (Alberta Agriculture 1992).

The moisture content of pasture forages generally declines during the grazing season to affect the moisture content of the pat (Lysyk *et al.* 1985) and its subsequent size and shape upon deposition. This change has both direct and indirect effects on dung degradation, the latter by influencing the number and species of insects colonizing the pat. Thus, cattle grazing on lush forage early in the season typically deposit thin, watery pats that readily degrade, whereas cattle grazing on dry forage later in the season deposit more substantial pats that resist degradation.

Other factors that affect succession include climate (temperature, humidity, precipitation), time (day vs. night), and the location of pat deposition (shaded woodland vs. open grassland) (Merritt and Anderson 1977; Fincher *et al.* 1986). For example, many species of coprophilous arthropods are active only during daylight hours, by which time dung deposited the previous night may have already formed a thin crust and be less attractive (Merritt and Anderson 1977). Biogeographical region is very important. Cattle dung on pastures in warmer climates can be completely buried, or scattered, or both in a matter of hours because of the dominance of tunnellers and rollers in local dung beetle assemblages.

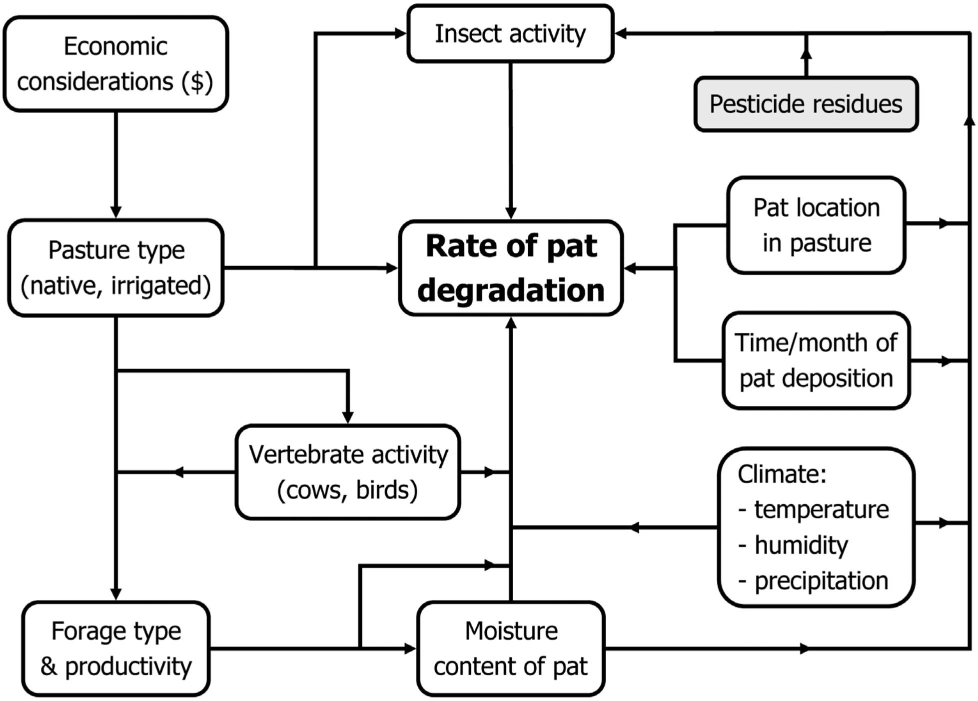

Fig. 4. Simplified flow chart illustrating the interaction of abiotic and biotic factors that influence the degradation rate of cattle dung pats on grassland pastures. From Floate (2006), as adapted from Merritt and Anderson (1977); reproduced with the authors' permission of the publisher.

In contrast, degradation may require months or years on temperate pastures (Merritt and Anderson 1977), where dung beetle assemblages are dominated by species of dwellers. Patterns of seasonal activity and fecal chemical residues are two further factors that affect succession. Each of these is described in more detail in the following two sections.

Seasonal Activity

The month of deposition is a further major factor that affects the pattern and rate of succession. In general, insect activity tends to be highest when conditions are warm and/or wet and lowest when conditions are cold and/or dry. In Canada, peak colonization of fresh dung occurs from late May to late June, with a secondary peak of activity in early autumn. However, individual species of insects exhibit different patterns of seasonal activity.

Flies are present from spring to fall to colonize fresh dung, although their abundance and species composition vary during this time (Hammer 1941). The seasonal activities of pest flies have been best studied and show a common pattern. Each species attains peak adult density in late summer or autumn because of the increase of populations over several generations in the preceding three to four months. The overwintering stage is the most conspicuous difference among these species. Horn flies overwinter as diapausing pupae, face flies overwinter as adults, and stable flies overwinter as slow-developing larvae.

Adult dung beetles (Scarabaeidae) exhibit one of two general patterns of seasonal activity in Canada (Floate and Gill 1998). The first pattern has two peaks of activity: one in spring and the other in autumn (Fig. 5A–D). The spring peak reflects overwintered adults

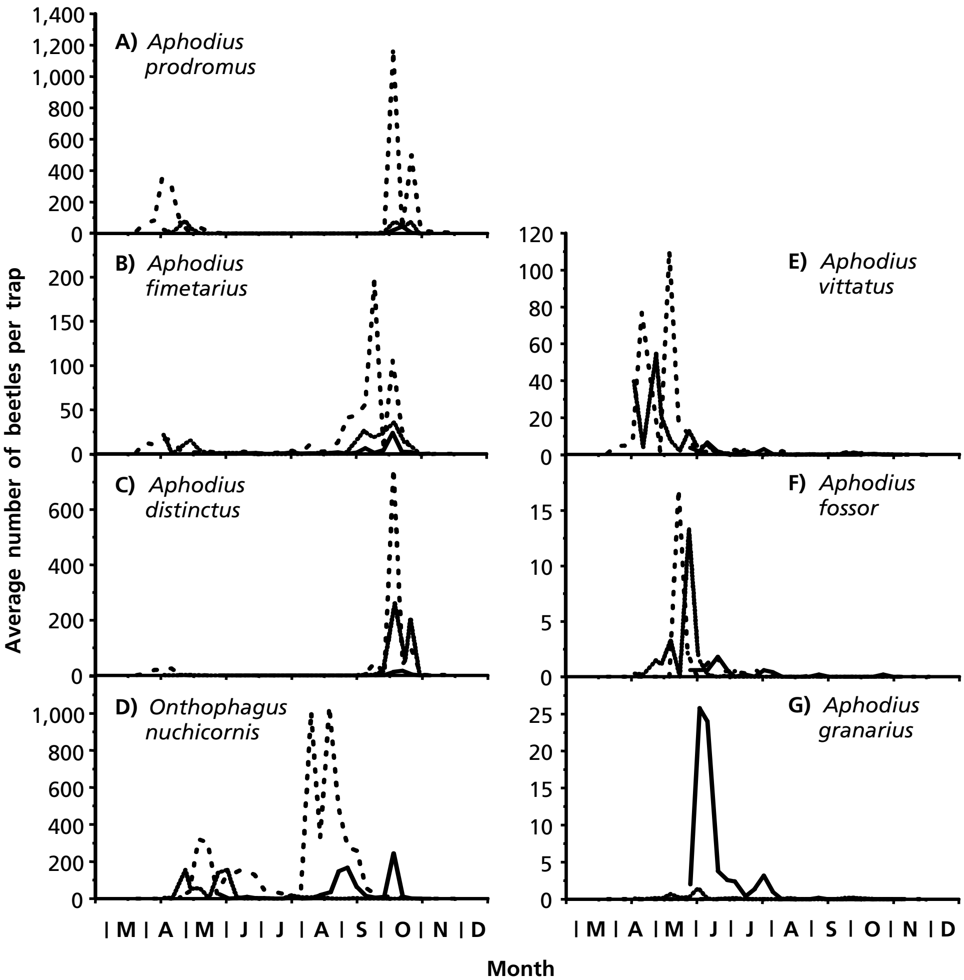

Fig. 5. Seasonal activity of adult dung beetles (Coleoptera: Scarabaeidae) recovered from pitfall traps ($n = 10$) at the Animal Disease Research Institute near Lethbridge, Alberta. Species identified in panels A–D exhibit a bimodal pattern, whereas species identified in panels E–G exhibit a unimodal pattern. Modified from Floate and Gill (1998).

that emerge to colonize fresh dung and lay eggs. The autumn peak reflects the emergence of adults that have developed from eggs laid in the spring. Species that exhibit this bimodal pattern include *Aphodius prodromus*, *A. fimetarius* (L.), *A. distinctus,* and *Onthophagus nuchicornis* (L.). The second pattern is unimodal. Species overwinter in immature stages, complete their development, and then emerge as adults in late spring to early summer to mate and lay eggs (Fig. 5E–G). This group includes *A. vittatus* Say, *A. coloradensis* Horn, *A. granarius* (L.), *A. fossor* (L.), and *A. haemorrhoidalis* (L.) (Floate and Gill 1998). This separation in seasonal activity limits the number of species that co-occur in a given dung pat. Of 16 species of *Aphodius* recorded in the North Pennines in England, no more than four species may be common at any one time (White 1960).

Seasonal activity and overwintering stage also vary with latitude. In colder climates, new adults of *A. prodromus* may not emerge in the current year, but instead overwinter in pupal cavities (White 1960). In Illinois, *A. fimetarius* lays eggs in autumn that hatch the following spring, such that eggs and adults may overwinter in the same dung pat (Mohr 1943). In North Carolina, peak adult activity for *A. granarius* occurs in March through April, with the autumn peak of *A. distinctus* in late November through December (Bertone *et al.* 2005). In contrast, peak activity of *A. granarius* in Canada occurs in late May through early June, with that of *A. distinctus* occurring in late September through early October (Seamans 1934; Floate and Gill 1998).

The seasonal activity of *A. distinctus* was the subject of study from 1921 to 1930 in Lethbridge, Alberta (Seamans 1934). Peak flights of this species are usually pronounced, of relatively short duration (see Fig. 5C), and impressive, as described below (and KDF, pers. obs.):

> The flight of beetles usually occurs on a still, bright, warm day. Without any preliminaries the beetles appear in countless thousands. The air to a height of ten or 15 feet *(3-5 meters)* [italics added] seems filled with flying beetles. Clouds of them hover over manure piles or over horse droppings on the roads or fields. The manure itself is literally filled with beetles and in less than an hour fresh horse droppings are reduced to a coarse dust spread over a two or three foot circle on the surface of the ground. (Seamans 1934)

Seamans (1934) suggested that flights of *A. distinctus* do not appear to be triggered by preceding temperatures, but rather by temperatures immediately thereafter. He observed that the first flight in spring was usually followed by the last period of cold and snow prior to the start of the growing season. The autumn flight immediately preceded the first snow or severe frost to forecast the end of the growing season. If autumn temperatures remained mild, occasionally there was a second flight followed by severe weather.

Fecal Chemical Residues

The past two decades have seen increased awareness about the possibility that use of certain veterinary products may also affect dung degradation (reviewed in Floate *et al.* 2005). Such products are regularly applied to livestock to control internal parasites (e.g., nematodes, cattle grub) and external parasites (e.g., lice, ticks, mites). Cattle treated with some of these products fecally excrete insecticidal residues. If the residues reduce normal levels of insect activity, they also have the potential to reduce expected levels of dung pat degradation. This potential non-target effect of product use is of particular concern because of the costs associated with undegraded cattle dung (see section titled "… And Why Should We Care?").

The insecticidal activity of fecal residues received little attention until the use of the parasiticide ivermectin, in a slow-release bolus formulation, was shown to reduce insect activity in the dung of treated cattle and to greatly slow dung degradation, relative to the dung of untreated cattle (Wall and Strong 1987). More recent studies have examined the effects of residues for endectocide products (e.g., doramectin, eprinomectin, ivermectin, moxidectin) applied to cattle in an injectable formulation, or applied topically. In Canada, recommended topical doses of ivermectin (Floate 1998) or doramectin (Floate *et al.* 2008), respectively, have been shown to reduce numbers of insects developing in dung deposited by cattle treated up to 12 and 16 weeks previously. Use of pyrethroid products has also been shown to reduce insect activity in cattle dung (Wardhaugh *et al.* 1998; Vale *et al.* 2004). Flies in the suborder Cyclorrhapha and their parasitoid wasps appear to be most susceptible to residues, although reductions are commonly observed for species of beetles (Scarabaeidae, Sphaeroceridae, Staphylinidae) (e.g., Floate 1998; Floate *et al.* 2002, 2008).

The effects of product use on dung degradation are less clear. All else being equal, reduced insect activity in dung because of fecal residues is expected to reduce the rate of pat degradation. However, measuring the effect of residues on degradation is confounded by factors that affect natural levels of insect activity. These factors include the season (e.g., spring vs. summer), time (e.g., morning vs. night), and location of dung pat deposition (Fig. 4). The role of insect activity may also be overshadowed by other factors that affect pat degradation, which include trampling by cattle, weather, or the disruption of pats by foraging birds (Anderson and Merritt 1977). A further confounding factor is that residues may alter expected patterns of insect colonization (e.g., Floate 2007). In one non-intuitive finding, use of ivermectin on cattle and sheep increased the number of dung beetles attracted to fresh manure to accelerate dung degradation, despite the insecticidal action of residues (Wardhaugh and Mahon 1991).

Phoresy

The ephemeral and patchy nature of fresh dung favours arthropods that can quickly locate fresh deposits over long distances. Most species achieve this by directed flight in response to volatile cues emitted from the dung. Phoresy provides an alternate mechanism that allows small wingless arthropods such as mites (Acari) to achieve the same goal. As defined by Farish and Axtell (1971), "Phoresy is a phenomenon in which one animal actively seeks out and attaches to the outer surface of another animal for a limited time during which the attached animal (termed the phoretic) ceases both feeding and ontogenesis, such attachment presumably resulting in dispersal from areas unsuited for further development, either of the individual or its progeny." Houck and O'Connor (1991) modified this definition in their review of phoresy in mites, but retained its essential elements.

The degree of specialization exhibited by phoretic mites varies among species (Farish and Axtell 1971). Adult mites may use appendages to grasp onto insects during transport (e.g., Macrochelidae) (Fig. 6B). Conversely, immature stages termed "deutonymphs" may be the phoretic stage and attach to hosts by using appendages (e.g., Parasitidae) (Fig. 6C), substances that literally glue the mite to the host (e.g., Uropodidae), or sucker-like discs (e.g., Acaridae). Deutonymphs of Acaridae can be extremely resistant to desiccation and starvation, surviving in one case for a minimum of 47 days on adult false stable flies, *Muscina stabulans* (Fallen), with the flies dying before the mites (Greenberg 1961).

To facilitate successful transmission from an aging to a fresh dung pat, most phoretics actively seek out potential hosts. Deutonymphs of the mite *Myianoetus muscarum* (L.) (Anoetidae) are attracted to volatile chemicals emitted by the pupa of dung-breeding flies (Greenberg and Carpenter 1960). Thus, although initially scattered throughout the media, large numbers of deutonymphs aggregate on the pupae and then move onto the adult fly during its emergence from the puparium. Upon arrival at the new habitat, chemical or mechanical cues, often associated with egg laying by the host, will trigger the detachment of mites from the host. Once detached, the mites move into the media to breed and feed on immature insects, mites, and nematodes.

It is not uncommon to find several mites of one or more species on insects arriving at fresh dung. Twelve species of mites in 11 genera (10 families) were recovered from adult stable flies on a cattle farm in Britain (McGarry and Baker 1997). An estimated 450 species of mites (representing 48 genera in 18 families) are associated with dung beetles, among which species in the family Macrochelidae are most common (Krantz 1983). The number of mites carried by a host can be highly variable. In the British study, 150 mites were

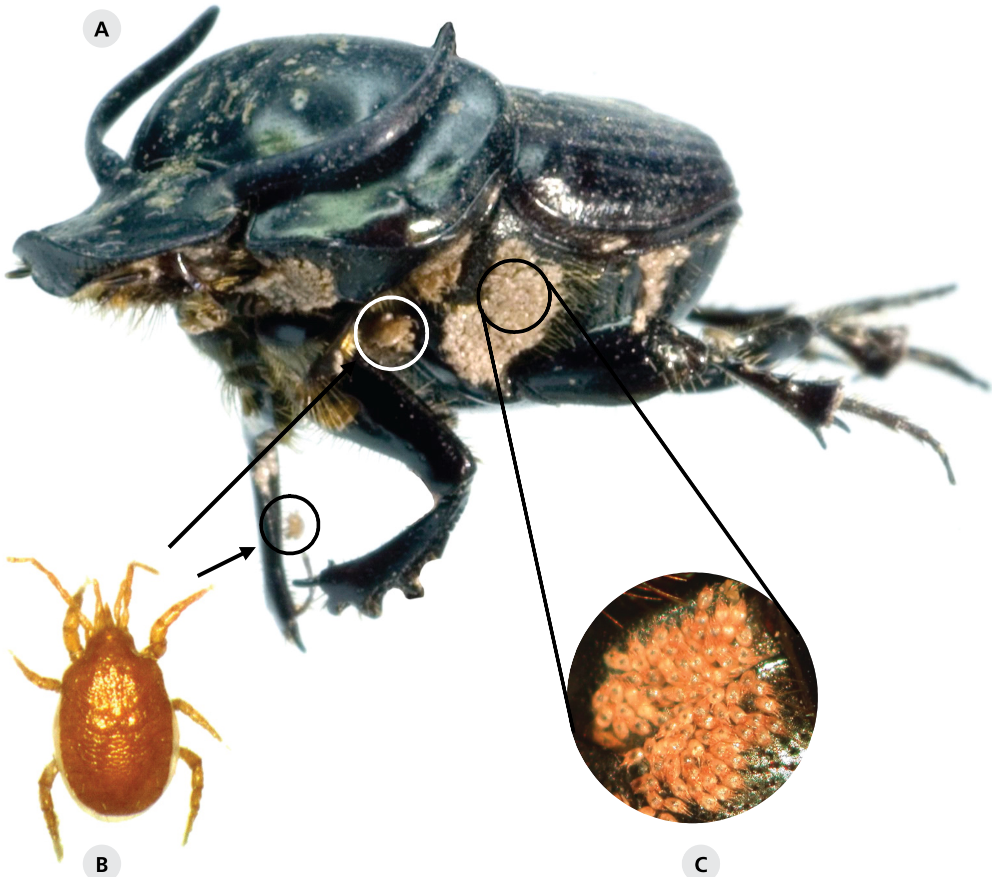

Fig. 6. One insect can provide transport for hundreds of phoretic mites. A, A dung beetle, *Onthophagus taurus* (Schreber). B, An adult mite in the family Macrochelidae. C, A cluster of immature mites ("deutonymphs"). Photo credits: B. Lee (Figs. A and C); R. Spooner (Fig. B).

recovered from a single fly (McGarry and Baker 1997). Many hundreds of phoretic mites may attach to one dung beetle (Fig. 6).

The diversity of coprophagous mites in Canada is little known (Table 1). Macqueen and Beirne (1974) reported three species of mites (one each in the families Pyemotidae, Parasitidae, and Macrochelidae) from cattle dung in British Columbia. A further two species of Parasitidae, two species of Halolaelapidae, and one species each of Eviphididae and Uropodidae were recovered from cattle dung in southern Alberta (KDF, unpublished; identifications by E. Lindquist).

Dung Attraction

Coprophilous insects tend to be generalists. Although they exhibit preferences, they are attracted to the dung of many different animal species. For example, dung beetles rely mainly on the dung of herbivorous mammals. In North America, one group of species is associated with the dung of ungulates (e.g., deer), a second group with the nests or burrows of rodents, and a third group with open pastures and cattle dung (Gordon 1983). However, Fincher *et al.* (1970) reported the attraction of the same set of beetle species to the dung of human, opossum, rat, swine, cow, horse, rabbit, sheep, dog, fox, and racoon. Finn and Giller (2002) found the dung of sheep to be more attractive to coprophilous beetles than the dung of horse or cow. Dormont *et al.* (2004) reported cattle dung to be more attractive to dung beetles than horse dung. Thus, fresh dung of different animals deposited at the same time and location will likely attract the same set of dung insect species, only differing in relative abundance.

Some species may even change their behaviour to make the best use of available dung. The beetle *Canthon praticola* LeConte (Scarabaeidae) has a particular association with prairie dog dung (Gordon and Cartwright 1974), which takes the form of small pellets that can be easily rolled by the beetles to suitable sites for burial. In the absence of its preferred dung, however, *C. praticola* will form balls of manure from fresh cattle dung (Gordon and Cartwright 1974).

Attraction is a response to the release of volatile compounds from fresh dung. The strength of attraction may reflect the concentration of a given volatile and/or its co-occurrence with other volatiles. For example, more than 160 volatile compounds have been associated with livestock manure (Mackie *et al.* 1998). These compounds can attract insects at very low concentrations, which aids the insect in locating the dung deposit from long distances. *Geotrupes* spp. (Coleoptera: Geotrupidae) responds to skatole at a concentration of 2.3×10^{-1} M (Warnke 1931, as cited in Dethier and Chadwick 1948). However, the insect requires physical contact with the dung to best assess its suitability and will leave the deposit if its suitability is found lacking. This attraction explains why, for example, large numbers of adult *A. distinctus* are attracted to cattle dung even though the beetle breeds in organic-rich soils.

The Expanding Diversity of Dung Fauna

It is unlikely that any arthropod species became extinct with the disappearance of bison ("buffalo") (*Bison bison* (L.)) from the prairies of North America. An estimated 40–60 million of these animals once ranged from Mexico to northern Canada prior to European settlement, with the species all but exterminated by the late 1880s (Soper 1941). Before about 1640, however, there was an initial mass importation of cattle from Europe to the eastern United States, with a subsequent increase in their numbers and distribution on the continent (Bowling 1942). Thus, cattle and bison would have co-occurred in some areas for a period of time. Because the quality and form of dung from these two bovine species is essentially the same, native arthropods would have been able to successfully shift from bison to cattle dung, the latter of which they persist on to the present day.

Indeed, European settlement has perhaps doubled the diversity of the arthropod dung community in North America. Almost half of the arthropod species recovered from cattle dung in the interior of British Columbia were non-native (Macqueen and Beirne 1974). In southern Alberta, Floate and Gill (1998) recovered 17 species of dung beetles, of which 8 were of exotic origin. The pest species, house fly (*Musca domestica* (L.)), stable fly, horn fly, and face fly, are introduced species. Known or likely exotic species in cattle dung in Canada also include at least 7 species of Histeridae (Bousquet and Laplante 2006), 11 species of Hydrophilidae (Smetana 1978), and 15 species of Staphylinidae (Coleoptera) (Bousquet 1991). With an increasing trend for warmer climates on the prairies (see McGinn 2010), additional coprophilous species can be expected to expand their distributions into the prairies of Canada from the United States.

References

Alberta Agriculture. 1992. The Beef Cow–Calf Manual. *Edited by* P.M. Branch. Alberta Agriculture, Edmonton, Alberta.

Anderson, J.R., and Merritt, R.W. 1977. The impact of foraging meadowlarks, *Sturnella neglecta*, on the degradation of cattle dung pads. Journal of Applied Ecology, **14**: 355–362.

Anderson, J.R., Merritt, R.W., and Loomis, E.C. 1984. The insect-free cattle dropping and its relationship to increased dung fouling of rangeland pastures. Journal of Economic Entomology, **77**: 133–141.

Aschenborn, H.H., Loughnan, M.L., and Edwards, P.B. 1989. A simple assay to determine the nutritional suitability of cattle dung for coprophagous beetles. Entomologia Experimentalis et Applicata, **53**: 73–79.

Bernays, E.A., and Chapman, R.F. 1994. Host-Plant Selection by Phytophagous Insects. Chapman & Hall, New York.

Bertone, M., Green, J., Washburn, S., Poore, M., Sorenson, C., and Watson, D.W. 2005. Seasonal activity and species composition of dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) inhabiting cattle pastures in North Carolina. Annals of the Entomological Society of America, **98**: 309–321.

Blume, R.R. 1985. A check-list, distributional record, and annotated bibliography of the insects associated with bovine droppings on pasture in America north of Mexico. Southwestern Entomologist, **9** (Suppl.): 1–55.

Borror, D.J., Triplehorn, C.A., and Johnson, N.F. 1989. An Introduction to the Study of Insects. Harcourt Brace College Publishing, New York.

Bousquet, Y. (*Editor*) 1991. Checklist of Beetles of Canada and Alaska. Agriculture Canada, Research Branch. Ottawa, Ontario.

Bousquet, Y., and Laplante, S. 2006. Coleoptera Histeridae. NRC Research Press, Ottawa, Ontario.

Bowling, G.A. 1942. The introduction of cattle into colonial North America. Journal of Dairy Science, **25**: 129–154.

Cambefort, Y., and Hanski, I. 1991. Dung beetle population biology. *In* Dung Beetle Ecology. *Edited by* I. Hanski and Y. Cambefort. Princeton University Press, Princeton, New Jersey. pp. 36–50.

Depner, K.R. 1968. Hymenopterous parasites of the horn fly, *Haematobia irritans* (Diptera: Muscidae), in Alberta. The Canadian Entomologist, **100**: 1057–1060.

Dethier, V.G., and Chadwick, L.E. 1948. Chemoreception in insects. Physiological Reviews, **28**: 220–254.

Dormont, L., Epinat, G., and Lumaret, J.-P. 2004. Trophic preferences mediated by olfactory cues in dung beetles colonizing cattle and horse dung. Environmental Entomology, **33**: 370–377.

Doube, B., and Macqueen, A. 1991. Establishment of exotic dung beetles in Queensland: the role of habitat specificity. BioControl, **36**: 353–360.

Doube, B.M. 1990. A functional classification for analysis of the structure of dung beetle assemblages. Ecological Entomology, **15**: 371–383.

Farish, D.J., and Axtell, R.C. 1971. Phoresy redefined and examined in *Macrocheles muscaedomesticae* (Acarina: Macrochelidae). Acarologia, **13**: 16–29.

Fincher, G.T. 1973. Dung beetles as biological control agents for gastrointestinal parasites of livestock. Journal of Parasitology, **59**: 396–399.

Fincher, G.T. 1981. The potential value of dung beetles in pasture ecosystems. Journal of the Georgia Entomological Society, **16**: 316–333.

Fincher, G.T., Blume, R.R., Hunter, J.S., III, and Beerwinkle, K.R. 1986. Seasonal distribution and diel flight activity of dung-feeding scarabs in open and wooded pasture in east-central Texas. Southwestern Entomologist, Suppl. 10: 1–35.

Fincher, G.T., Stewart, T.B., and Davis, R. 1970. Attraction of coprophagous beetles to feces of various animals. The Journal of Parasitology, **56**: 378–383.

Finn, J.A., and Giller, P.S. 2002. Experimental investigations of colonisation by north temperate dung beetles of different types of domestic herbivore dung. Applied Soil Ecology, **20**: 1–13.

Floate, K.D. 1998. Off-target effects of ivermectin on insects and on dung degradation in southern Alberta, Canada. Bulletin of Entomological Research, **88**: 25–35.

Floate, K.D. 2006. Endectocide use in cattle and fecal residues: environmental effects in Canada. Canadian Journal of Veterinary Research, **70**: 1–10.

Floate, K.D. 2007. Endectocide residues affect insect attraction to dung from treated cattle: implications for toxicity tests. Medical and Veterinary Entomology, **21**: 312–322.

Floate, K.D., Bouchard, P., Holroyd, G., Poulin, R., and Wellicome, T.I. 2008. Does doramectin use on cattle indirectly affect the endangered burrowing owl? Rangeland Ecology & Management, **61**: 543–553.

Floate, K.D., Colwell, D.D., and Fox, A.S. 2002. Reductions of non-pest insects in dung of cattle treated with endectocides: a comparison of four products. Bulletin of Entomological Research, **92**: 471–481.

Floate, K.D., and Gibson, G.A.P. 2004. Filth fly parasitoids (Hymenoptera: Pteromalidae) in North America. *In* Encyclopedia of Entomology. *Edited by* J.L. Capinera. Kluwer Academic Publishers, Boston, Massachusetts. pp. 838–840.

Floate, K.D., and Gill, B.D. 1998. Seasonal activity of dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung in southern Alberta and their geographic distribution in Canada. The Canadian Entomologist, **130**: 131–151.

Floate, K.D., Wardhaugh, K.G., Boxall, A.B., and Sherratt, T.N. 2005. Fecal residues of veterinary parasiticides: nontarget effects in the pasture environment. Annual Review of Entomology, **50**: 153–179.

Gibson, G.A.P., and Floate, K.D. 2001. The species of *Trichomalopsis* (Hymenoptera: Pteromalidae) associated with filth flies (Diptera: Muscidae) in North America. The Canadian Entomologist, **133**: 49–85.

Gibson, G.A.P., and Floate, K.D. 2004. Filth fly parasitoids on dairy farms in Ontario and Quebec, Canada. The Canadian Entomologist, **136**: 407–417.

Gittings, T., and Giller, P.S. 1997. Life history traits and resource utilisation in an assemblage of north temperate *Aphodius* dung beetles (Coleoptera: Scarabaeidae). Ecography, **20**: 55–66. doi:10.1111/j.1600-0587.1997.tb00347.x.

Gordon, R.D. 1983. Studies on the genus *Aphodius* of the United States and Canada (Coleoptera: Scarabaeidae). VII. Food and habitat; distribution; key to eastern species. Proceedings of the Entomological Society of Washington, **85**: 633–652.

Gordon, R.D., and Cartwright, O.L. 1974. Survey of food preferences of some North American Canthonini (Coleoptera: Scarabaeidae). Entomological News, **85**: 181–185.

Gordon, R.D., and Skelley, P.E. 2007. A Monograph of the Aphodiini Inhabiting the United States and Canada (Coleoptera: Scarabaeidae: Aphodiini). The American Entomological Institute, Gainesville, Florida.

Greenberg, B. 1961. Mite orientation and survival on flies. Nature, **190**: 107–108.

Greenberg, B., and Carpenter, P.D. 1960. Factors in phoretic association of a mite and fly. Science, **132**: 738–739.

Hammer, O. 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. Videnskabelige Meddelelser, Dansk Naturhistorisk Forening, København, **105**: 1–257.

Hanski, I., and Cambefort, Y. (*Editors*) 1991. Dung Beetle Ecology. Princeton University Press, Princeton, New Jersey.

Hoebeke, E.R., and Beucke, K. 1997. Adventive *Onthophagus* (Coleoptera: Scarabaeidae) in North America: geographic ranges, diagnoses, and new distributional records. Entomological News, **108**: 345–362.

Holter, P. 1974. Food utilization of dung-eating *Aphodius* larvae (Scarabaeidae). Oikos, **25**: 71–79.

Holter, P. 1975. Energy budget of a natural population of *Aphodius rufipes* larvae (Scarabaeidae). Oikos, **26**: 177–186.

Holter, P., Scholtz, C.H., and Wardhaugh, K.G. 2002. Dung feeding in adult scarabaeines (tunnellers and endocoprids): even large dung beetles eat small particles. Ecological Entomology, **27**: 169–176.

Houck, M.A., and O'Connor, B.M. 1991. Ecological and evolutionary significance of phoresy in the Astigmata. Annual Review of Entomology, **36**: 611–636.

Howden, H.F., and Cartwright, O.L. 1963. Scarab beetles of the genus *Onthophagus* Latreille north of Mexico (Coleoptera: Scarabaeidae). Proceedings of the United States National Museum, **114**: 1–143.

Krantz, G.W. 1983. Mites as biological control agents of dung-breeding flies, with special reference to the Macrochelidae. *In* Biological Control of Pests by Mites. *Edited by* M.A. Hoy, G.L. Cunningham, and L. Knutson. University of California Special Publication No. 3304. pp. 91–98.

Krombein, K.V., Hurd, P.D., Smith, D.R., and Burks, B.D. (*Editors*) 1979. Catalog of Hymenoptera in America North of Mexico. Smithsonian Institution Press, Washington, D.C.

Kunz, S.E., Murrell, K.D., Lambert, G., James, L.F., and Terrill, C.E. 1991. Estimated losses of livestock to pests. *In* CRC Handbook of Pest Management in Agriculture, 2nd edition. *Edited by* D. Pimental. CRC Press, Boston, Massachusetts. pp. 69–105.

Laurence, B.R. 1954. The larval inhabitants of cow pats. Journal of Animal Ecology, **23**: 234–260.

Lee, C.M., and Wall, R. 2006. Cow-dung colonization and decomposition following insect exclusion. Bulletin of Entomological Research, **96**: 315–322.

Lysyk, T.J., Easton, E.R., and Evenson, P.D. 1985. Seasonal changes in nitrogen and moisture content of cattle manure in cool-season pastures. Journal of Range Management, **38**: 251–254.

Mackie, R.I., Stroot, P.G., and Varel, V.H. 1998. Biochemical identification and biological origin of key odor components in livestock waste. Journal of Animal Science, **76**: 1331–1342.

Macqueen, A., and Beirne, B.P. 1974. Insects and mites associated with fresh cattle dung in the southern interior of British Columbia. Journal of the Entomological Society of British Columbia, **71**: 5–9.

Marsh, R., and Campling, R.C. 1970. Fouling of pastures by dung. Herbage Abstracts, **40**: 123–130.
McGarry, J.W., and Baker, A.S. 1997. Observations on the mite fauna associated with adult *Stomoxys calcitrans* in the U.K. Medical and Veterinary Entomology, **11**: 159–164.
McGinn, S.M. 2010. Weather and climate patterns in Canada's prairie grasslands. *In* Arthropods of Canadian Grasslands, Vol. 1: Ecology and Interactions in Grassland Habitats. *Edited by* J.D. Shorthouse and K.D. Floate. Biological Survey of Canada, Ottawa, Ontario. pp. 105–119.
McLintock, J., and Depner, K.R. 1954. A review of the life-history and habits of the horn fly, *Siphona irritans* (L.) (Diptera: Muscidae). The Canadian Entomologist, **86**: 20–33.
Merritt, R.W., and Anderson, J.R. 1977. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. Hilgardia, **45**: 31–71.
Mohr, C.O. 1943. Cattle droppings as ecological units. Ecological Monographs, **131**: 275–298.
Moon, R.D., Loomis, E.C., and Anderson, J.R. 1980. Influence of two species of dung beetles on the larvae of face fly. Environmental Entomology, **9**: 607–612.
Nichols, E., Spector, S., Louzada, J., Larsen, T., Amequita, S., and Favila, M.E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation, **141**: 1461–1474.
O'Hara, J.E., Floate, K.D., and Cooper, B.E. 2000. The Sarcophagidae (Diptera) of cattle feedlots in Southern Alberta. Journal of the Kansas Entomological Society, **72**: 167–176.
Peck, O. 1974. Chalcidoid (Hymenoptera) parasites of the horn fly, *Haematobia irritans* (Diptera: Muscidae), in Alberta and elsewhere in Canada. The Canadian Entomologist, **106**: 473–477.
Seamans, H.L. 1934. An insect weather prophet. Annual Report of the Quebec Society of Plant Protection, **134**: 111–117.
Skidmore, P. 1991. Insects of the British Cow-Dung Community. Richmond Publishing Co. Ltd., Slough, U.K.
Smetana, A. 1978. Revision of the subfamily Sphaeridiinae of America north of Mexico (Coleoptera: Hydrophilidae). Memoirs of the Entomological Society of Canada, **105**: 292.
Soper, J.D. 1941. History, range, and home life of the northern bison. Ecological Monographs, **11**: 347–412.
Statistics Canada. 2010. Cattle Inventories, by Province (Canada). Available from http://www40.statcan.ca/l01/cst01/prim50a.htm [accessed 12 September 2010].
Terra, W.R. 1990. Evolution of digestive systems of insects. Annual Review of Entomology, **35**: 181–200.
Tyndale-Biscoe, M. 1990. Common Dung Beetles in Pastures of South-western Australia. CSIRO Australia, Division of Entomology, Canberra, Australia.
Vale, G.A., Grant, I.F., Dewhurst, C.F., and Aigreau, D. 2004. Biological and chemical assays of pyrethroids in cattle dung. Bulletin of Entomological Research, **94**: 273–282.
Wall, R., and Strong, L. 1987. Environmental consequences of treating cattle with the antiparasitic drug ivermectin. Nature, **327**: 418–421.
Wardhaugh, K.G., Longstaff, B.C., and Lacey, M.J. 1998. Effects of residues of deltamethrin in cattle faeces on the development and survival of three species of dung-breeding insect. Australian Veterinary Journal, **76**: 273–280.
Wardhaugh, K.G., and Mahon, R.J. 1991. Avermectin residues in sheep and cattle dung and their effects on dung-beetle (Coleoptera: Scarabaeidae) colonization and burial. Bulletin of Entomological Research, **81**: 333–339.
White, E. 1960. The natural history of some species of *Aphodius* (Col., Scarabaeidae) in the northern Pennines. Entomologist's Monthly Magazine, **96**: 25–30.
Wylie, H.G. 1973. Parasites of face fly, *Musca autumnalis* (Diptera: Muscidae) and associated Diptera near Bellville, Ontario. The Canadian Entomologist, **105**: 257–261.
Yokoyama, K., Kai, H., and Tsuchiyama, H. 1991. Paracoprid dung beetles and gaseous loss of nitrogen from cow dung. Soil Biology and Biochemistry, **23**: 643–647.