Dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung on native grasslands of southern Alberta, Canada

K.D. Floate,[1] N. Kadiri

Abstract—Surveys of dung beetles establish the dominance of exotic taxa associated with cattle dung on native grasslands in southern Alberta, Canada. Of the 12 species recovered, eight were of European origin and comprised 92.2% of the total catch of 187 963 beetles. Most common were *Chilothorax distinctus* (Müller), *Onthophagus nuchicornis* (Linnaeus), and *Colobopterus erraticus* (Linnaeus) (Coleoptera: Scarabaeidae). The abundance of *C. distinctus* has been known in the region since the 1920s, whereas that of *O. nuchicornis* only was first reported in the 1990s. The abundance of *C. erraticus* has not previously been observed in the region and identifies the species as the newest addition to the endemic fauna. The diversity of native species on pastures in southern Canada and adjacent states is depauperate, such that the establishment of European taxa has appreciably increased levels of bioturbation in pasture ecosystems. The success of these exotic species on northern pastures may reflect a level of cold-tolerance greater than that of most native species.

Résumé—Les études menées sur les coléoptères coprophages montrent la dominance des taxons exotiques associées aux déjections du bétail dans les prairies natives du sud de l'Alberta, Canada. Sur les douze espèces récoltées, huit étaient d'origine européenne constituant 92,2% du total des 187 963 coléoptères capturés. Les plus fréquentes étaient *Chilothorax distinctus* (Müller), *Onthophagus nuchicornis* (Linnaeus) et *Colobopterus erraticus* (Linnaeus) (Coleoptera: Scarabaeidae). L'abondance de *C. distinctus* est connue dans la région depuis les années 1920, alors que *O. nuchicornis* n'a été signalée pour la première fois que dans les années 1990. *Colobopterus erraticus* n'avait pas été observée auparavant dans la région, et l'espèce est considérée comme étant le plus récent ajout à la faune endémique. La diversité des espèces natives dans les pâturages du sud du Canada et des États voisins est appauvrie, compensée par l'établissement de ces taxons d'origine européenne qui ont nettement augmenté les niveaux de bioturbation dans les écosystèmes pâturés. Le succès de ces espèces exotiques dans les pâturages du nord peut refléter un niveau de tolérance au froid supérieur à celui de la plupart des espèces natives.

Introduction

Dung beetles are among the most abundant insects in fresh cattle dung (Mohr 1943; Fincher 1981; Nichols *et al*. 2008; Floate 2011). They include members of Geotrupidae (some species of Geotrupinae) and Scarabaeidae (some species of Aphodiinae and Scarabaeinae) (Coleoptera). Through their tunnelling, burial, and feeding activities, these beetles contribute to the cycling of nutrients by accelerating the return of cattle dung to pasture soils. This promotes soil fertility and helps maintain the pasture free of dung pats that would otherwise physically block the growth of new forage. By disrupting the pat, they also reduce its suitability as a breeding site for pest flies and parasites (*e.g.*, nematodes) of cattle (*Bos taurus* Linnaeus (Mammalia: Bovidae)). The extent of these benefits (Fincher 1981; Nichols *et al*. 2008) varies with the

Received 19 February 2013. Accepted 26 April 2013. First published online 10 September 2013.

K.D. Floate,[1] Lethbridge Research Centre, Agriculture and Agri-Food Canada, Lethbridge, Alberta, Canada T1J 4B1
N. Kadiri, Laboratoire de Zoogéographie, UMR 5175 CEFE, Université Paul-Valéry Montpellier 3, Route de Mende, 34199 Montpellier cedex 5, France

[1]Corresponding author (e-mail: Kevin.Floate@agr.gc.ca).
Subject editor: Andrew Smith
doi:10.4039/tce.2013.50

reproductive behaviour of the species. "Dwellers", mainly Aphodiinae, are species whose larvae develop within the pat. "Tunnellers" and "rollers" are species whose larvae develop in dung that the adults have removed from the pat and have buried beneath (tunnellers) or at some distance (rollers) from the pat. Whereas the larval feeding activity of dwellers slowly disrupts the pat over the course of several weeks, the activity of adult tunnellers and rollers can scatter and bury a pat within days. Thus, members of these latter two guilds are of particular interest.

Surveys of dung beetles on pastures in Canada and the northern United States of America reveal an assemblage dominated by aphodiine taxa of exotic origin unintentionally introduced to the continent during European settlement. Eleven species were recovered on rangeland near Kamloops, British Columbia, Canada, of which six originated from Europe (Macqueen and Beirne 1974). These include *Aphodius fimetarius* (Linnaeus), *Calamosternus granarius* (Linnaeus), *Chilothorax distinctus* (Müller), *Otophorus haemorrhoidalis* (Linnaeus), *Teuchestes fossor* (Linnaeus) (Aphodiinae), and *Onthophagus nuchicornis* (Linnaeus) (Scarabaeinae). A three-year survey on pastures near Lethbridge, Alberta, Canada recovered 156 500 beetles (17 species) of which 95% comprised species of European origin, primarily *O. nuchicornis* (38.6% of total), *Melinopterus prodromus* (Brahm) (34.9%), *C. distinctus* (14.0%), and *A. fimetarius* (6.2%) (Floate and Gill 1998). Similar surveys report the dominance of one or more of these exotic species on pastures in northern California, United States of America (Merritt and Anderson 1977), Michigan, United States of America (Rounds and Floate 2012), Minnesota, United States of America (Cervenka and Moon 1991), New York, United States of America (Valiela 1969), South Dakota, United States of America (McDaniel *et al*. 1971; Kessler and Balsbaugh 1972), and southern Québec, Canada (Matheson 1987).

This dominance by European species is somewhat surprising and may reflect two phenomena. An estimated 40–60 million bison, *Bison bison* (Linnaeus) (Mammalia: Bovidae) roamed the plains of North America prior to European settlement (Soper 1941). Based on estimates for cattle (Marsh and Campling 1970), each bison would have deposited about 25 kg of fresh dung per day to provide ample habitat for a rich assemblage of native species (Mohr 1943). If this was indeed the case, the near extirpation of bison by the late 1800s may have caused the extinction of native scarabs that left ecological voids filled by European species. However, Tiberg and Floate (2011) experimentally tested this hypothesis and concluded that the dung of bison and cattle are ecologically equivalent. Thus, native species that historically bred in bison dung should be present today in cattle dung. A second possibility is that the introduction and subsequent spread of European species has competitively excluded native species in cattle dung. Lobo (2000) compared the relative abundance of exotic and native species along a longitudinal gradient in North America and concluded that the less speciose native fauna of northern climes were prone to such invasions.

A third possibility is that changes in land use have adversely affected native species. The decline of native rollers in coastal environments on the Iberian peninsula in Spain has been attributed to urbanisation (Lobo 2001). Changes in traditional methods of animal husbandry may explain the decline and possible extinction of Aphodiini and *Onthophagus* species in Finland (Bistrom *et al*. 1991). If disturbance contributes to the rarity of native species on pastures in Canada and the northern United States of America, then undisturbed grasslands are predicted to harbour a greater richness of native species than altered grasslands. This may explain the dominance of exotic species in previous surveys on pastures (often irrigated) planted to tame grasses and forbs (Sanders and Dobson 1966; Valiela 1969; Macqueen and Beirne 1974; Matheson 1987; Cervenka and Moon 1991; Floate and Gill 1998; Rounds and Floate 2012).

Critical tests of this third possibility require comprehensive surveys of dung beetles on native grasslands, but few if any studies meet this criterion. In addition to being done on altered grasslands, many previous surveys have not begun until June or later (Sanders and Dobson 1966; McDaniel *et al*. 1971; Kessler and Balsbaugh 1972; Macqueen and Beirne 1974; Matheson 1987). This practice excludes species that are active at other times of the year and can misrepresent the overall diversity and relative

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press

abundance of local assemblages. In southern Alberta, for example, dung beetles are active from mid-March to mid-November with some species rare or absent during summer months (Floate and Gill 1998).

The current study tests the hypothesis that native grasslands have a greater richness of native dung beetles associated with cattle dung than has been reported for altered grasslands. For this purpose, surveys were performed on native grasslands in southern Alberta, Canada for periods of two to three years from spring through autumn. Results refute the hypothesis and document ongoing changes in the composition of the endemic fauna.

Materials and methods

Pitfall traps baited with cattle dung were operated at three sites (Onefour, Stavely, Purple Springs) that represent a range of native grassland and soil types. Purple Springs is located roughly mid-way between Onefour and Stavely, which are separated by a distance of about 275 km.

The Onefour site was on native pastures at the Agriculture and Agri-Food Canada (AAFC) Onefour Range Substation (49°N, 110°W). Located at an elevation of ~920 m, the Onefour substation comprises 17 000 ha of short grass prairie in the province's dry mixedgrass natural subregion. The subregion is characterised as undulating plains vegetated by drought-tolerant grasses, shrubs, and herbs, albeit 45% of the subregion has been converted to farming. The physiography is mainly glacial till with significant amounts of eolian, fluvial, and lacustrine materials; brown chernozemic and solonetzic soils are the main soil types (Natural Regions Committee 2006). AAFC weather records (1981–2010) for the substation identify annual precipitation of 354 mm with mean daily temperatures for January and July of −8.7 and 19.7 °C, respectively. There is an average of 115–125 frost-free days per year (Chetner and Agroclimatic Atlas Working Group 2003). Traps were operated at this site from 2 June to 17 October 2008 (20 weeks) and from 17 April to 9 October 2009 (24 weeks).

The Purple Springs site was on native pastures at the Purple Springs Grazing Reserve (49°N, 111°W). Located at an elevation of ~800 m, the grazing reserve comprises 1530 ha of short grass prairie and also is in the province's dry mixedgrass natural subregion (Natural Regions Committee 2006). However, soil at the site is noticeably lighter than that at Onefour with unvegetated patches of sand. The city of Taber is ~18 km from the study site. Weather records (1971–2000) for Taber identify annual precipitation of 368 mm, an average of 125+ frost-free days per year, and mean daily temperatures for January and July of −8.6 °C and 18.8 °C, respectively (Chetner and Agroclimatic Atlas Working Group 2003; Environment Canada 2013). Traps were operated at this site from 19 May to 17 October 2008 (22 weeks), from 20 April to 9 October 2009 (25 weeks), and from 20 April to 15 October 2010 (26 weeks).

The Stavely site was on native pastures at the AAFC Stavely Range Substation (50°N, 114°W). Located at an elevation of ~1300 m, the Stavely substation comprises 400 ha of rough fescue grassland in the province's foothills fescue natural subregion. The topography of the subregion is characterised as hummocky and rolling to undulating, with mainly glacial till and significant amounts of lacustrine materials; the main soils are black chernozem (Natural Regions Committee 2006). AAFC weather records for the substation (1981–2010) identify average annual precipitation of 445 mm, and mean daily temperatures for January and July of −4.4 °C and 15.6 °C, respectively. There is an average of 105–115 frost-free days per year (Chetner and Agroclimatic Atlas Working Group 2003). Traps were operated at this site from 19 May to 17 October 2008 (22 weeks) and from 25 May to 2 October 2009 (19 weeks).

To accommodate differences in their relative size, 25, 15, and 10 traps were operated at Onefour, Purple Springs, and Stavely, respectively. Traps were clustered in groups of five. Traps within groups were separated by ~10 m, whereas groups were separated by at least 500 m. Traps were baited each week, operated for three to four days and then emptied. Beetles were stored in 70% ethanol until sorted, counted, and identified. On rare occasions, trap catches were lost due to flooding or inaccessibility.

Each trap comprised two plastic pails (1 L capacity), one nested inside the other, buried with the lip of the trap level with the soil surface.

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press

The outer pail prevented the hole from collapsing. The inner pail held a preservative (propylene glycol formulated in a commercial product sold as nontoxic antifreeze) and was easily removed to recover insects. A wire screen (~25 mm grid) over the mouth of each trap supported a dung bait and excluded rodents and birds. Baits comprised fresh cattle dung (~75 g) wrapped in two layers of cheesecloth, made in advance and frozen until needed. Within sites, traps were placed in the same location each year and positioned to avoid disturbance by cattle, which were present at all sites during trap periods.

Weekly collections allowed for observations of seasonal activity, including on some species for which these data have not before been reported for Canada. Presentation of these data is planned for a future manuscript and are only briefly discussed here. Voucher specimens for recovered species were placed in the main insect collection at the Lethbridge Research Centre (Lethbridge, Alberta, Canada).

Results and discussion

General patterns

Results do not support the hypothesis that the abundance of exotic species in previous surveys is an artefact of sampling disturbed grasslands. Of the 12 species recovered in the current study on native grasslands, eight were of European origin and comprised 92.2% of the total catch of 187 963 beetles (Table 1). Most abundant were *O. nuchicornis*, *C. distinctus*, and *Colobopterus erraticus* (Linnaeus). Of the four native species, *Planolinellus vittatus* (Say) was the most abundant followed by *Canthon pilularius* (Linnaeus), *Pseudagolius coloradensis* (Horn), and *C. praticola* LeConte.

When separated by different combinations of year and site, European species comprised 74–98% of collections (Table 1). *Chilothorax distinctus* comprised 32% of the total catch, but breed in organic rich soil (Jerath and Ritcher 1959; Sears 1978; Floate 2011). Thus, their status as members of the dung beetle assemblage is debatable. Even with the exclusion of *C. distinctus*, however, the remaining European species still comprised 70–96% of collections (Table 1).

Within sites, differences between years can be partially attributed to variation in trap period. At Onefour, the trap period in 2008 began in early June versus mid-April for 2009. This likely explains the 14-fold greater recovery in 2009 of *P. vittatus*, whose peak adult activity occurs in April and May (Floate and Gill 1998). Conversely, peak adult activity of *C. distinctus* occurs in mid-October to late October (Seamans 1934; Floate and Gill 1998). Thus, the 4.7-fold greater recovery of this species in 2008 may reflect a trap period ending two weeks later than that in 2009. At Stavely, trap periods in 2008 and 2009 were more comparable in length with between-year differences in the recovery of beetles for each species being less pronounced. Sources of variation in other cases are unclear. At Purple Springs, 60-fold more *C. granarius* were recovered in 2009 than in 2010 even though traps were operated for the same period.

Between sites, the abundance of individual species is best attributed to idiosyncratic responses to abiotic and biotic factors. *Chilothorax distinctus* and *C. granarius* breed in soil (Christensen and Dobson 1976; Sears 1978; Floate 2011). Because they are not reliant on cattle dung, their rarity at Stavely relative to Onefour and Purple Springs likely reflects the lighter soils at the latter sites. The abundance of these species in pitfall catches also may reflect the size of populations in adjacent farmland. Soil type also may explain the presence of *C. pilularius* and *C. praticola* at these two sites. Because of lighter soils, warmer temperatures, and lower precipitation, vegetation is sparser at Onefour and Purple Springs than at Stavely. Such habitat is well-suited to the reproductive behaviour of *C. pilularius*, which includes the rolling and burial of cattle dung (Matthews 1963). In contrast, *C. praticola* is a smaller species that is closely associated with the dung of prairie dogs (*Cynomys* Rafinesque species) (Mammalia: Sciuridae) (Gordon and Cartwright 1974). It may indirectly benefit from the lighter soils at Onefour and Purple Springs, which favour populations of fossorial rodents (*e.g.*, Richardson's ground squirrel, *Urocitellus richardsonii* (Sabine) (Mammalia: Sciuridae)) that provide the pellet-type dung favoured by *C. praticola*.

Table 1. Recovery of dung beetles (Scarabaeidae) on three native grasslands in southern Alberta, Canada.

Species	Onefour (beetles per trap)		Stavely (beetles per trap)		Purple Springs (beetles per trap)			Sites and years combined (% of total)
	2008	2009	2008	2009	2008	2009	2010	
*Onthophagus nuchicornis**	19.0	181.1	78.4	59.8	633.1	1727.7	2184.4	74 571 (39.7)
*Chilothorax distinctus**[,†]	792.4	167.0	2.6	3.6	1592.1	449.2	371.1	60 233 (32.0)
*Colobopterus erraticus**[,†]	86.7	362.5	37.2	95.0	93.6	209.5	176.6	19 748 (10.5)
Planolinellus vittatus[†]	20.0	276.6	46.7	11.8	22.6	9.1	46.6	9173 (4.9)
*Aphodius fimetarius**	51.9	37.7	68.6	81.6	47.1	161.7	130.7	8833 (4.7)
*Calamosternus granarius**[,†]	80.2	134.6	2.0	<0.1	6.3	120.5	2.0	7326 (3.9)
Canthon pilularius	2.0	23.2	0	0	29.1	97.8	109.2	4172 (2.2)
*Melinopterus prodromus**[,†]	1.8	9.9	1.0	0.2	5.4	39.0	41.1	1588 (0.8)
*Otophorus haemorrhoidalis**[,†]	4.5	9.3	1.7	13.2	2.5	13.9	7.3	850 (0.5)
Pseudagolius coloradensis[†]	0.2	19.4	0	<0.1	1.5	0.2	8.9	649 (0.3)
Canthon praticola	0.2	1.7	0	0	9.2	11.4	17.6	620 (0.3)
*Teuchestes fossor**[,†]	<0.1	1	<0.1	3.2	0.9	6.3	2.1	200 (0.1)
European species (% of total)	97.9	73.8	80.4	95.6	97.4	95.8	94.1	92.2
European species (% of total excluding *C. distinctus*)	91.6	69.6	80.2	95.5	92.7	95.1	93.3	88.6
Total	1058.9	1224.0	238.2	268.4	2443.4	2846.3	3097.6	187 963 (100)

Data by year report the recovery of beetles on a "per trap" basis ($n = 25$ traps at Onefour, 10 traps at Stavely, 15 traps at Purple Springs).
Final column reports total number of beetles recovered.
*Of European origin.
†Classified in the genus *Aphodius* previous to Gordon and Skelley (2007).

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press

Ongoing changes to local fauna

The abundance of *O. nuchicornis* at each site is notable because the species fills an ecological niche on native grasslands that hitherto largely may have been vacant across much of Canada (Macqueen and Beirne 1975a). Accidently introduced into northeastern North America prior to 1844 (Melsheimer 1845), this European species was first reported in British Columbia in 1945 (Hatch 1971) and is now common across southern Canada and adjacent states (Hoebeke and Beucke 1997; Floate and Gill 1998). Because it thrives at grassland sites where other species of tunnellers or rollers are absent or rare (*e.g.*, Stavely site), its presence on the native landscape has enhanced historical rates of cattle dung degradation. Each ball of cattle dung buried by *O. nuchicornis* removes about 2.5 g of fresh dung from the cow pat (Macqueen and Beirne 1975a) to improve soil nitrogen and promote plant growth (Macqueen and Beirne 1975b).

Recovery of large numbers of *C. erraticus* signals the newest addition to the regional dung beetle assemblage. This European species was present in Canada east of western Ontario prior to 1940 (Brown 1940). One specimen was recorded from eastern North Dakota, United States of America prior to 1967 (Helgesen and Post 1967), but *C. erraticus* was not reported west of Manitoba, Canada prior to 1991 (Bousquet 1991). The first records from Alberta and Saskatchewan, Canada were provided by Floate and Gill (1998), who found one specimen in 1995 during a three-year survey at Lethbridge, Alberta. There are no specimens of *C. erraticus* in the main insect collection of the Lethbridge Research Centre (Alberta, Canada) collected prior to the mid-1990s. There are, however, specimens of now co-occurring coprophagous aphodiines in the collection that date back to the early 1900s. Identified as species of *Aphodius* as per the taxonomic convention at that time, these include *A. fimetarius* (1920), *C. granarius* (1926), *C. distinctus* (1923), *Oscarinus rusicola* (Melsheimer) (1920), *Tetraclipeoides denticulatus* (Haldeman) (1932), and *P. vittatus* (1939). Recent collections of *C. erraticus* in the region have numbered in the thousands (Floate 2007; Tiberg and Floate 2011).

The reproductive biology of *C. erraticus* (Rojewski 1983) is unusual for aphodiines and may partially explain its rapid rise to prominence. Most species in this tribe oviposit and develop in or directly beneath the dung pat. In contrast, the behaviour of *C. erraticus* is more similar to that of *O. nuchicornis*. Overwintered adults emerge in spring to feed in fresh cattle dung and mate. Mated females excavate tunnels beneath the pat that they provision with cattle dung and next to which they oviposit. New adults emerge in late summer to feed and then overwinter in tunnels at depths of 20–27 cm. This tunnelling behaviour protects immature stages from predators and from hot dry conditions during summer. Adults overwintering in tunnels would be well protected from cold temperatures. As with *O. nuchicornis*, the establishment of *C. erraticus* has enhanced bioturbation on pastures across southern Canada. A female may bury at depths of 3–12 cm, 500–600 times its weight in cattle dung during an eight-day period (Rojewski 1983).

Why the success of European species in Canada?

European species dominate dung beetle assemblages in cattle dung on grasslands across southern Canada and the northern United States of America. Results of the current study on native grasslands refute the hypothesis that this pattern is an artefact of sampling disturbed grasslands (*e.g.*, Sanders and Dobson 1966; Valiela 1969; Macqueen and Beirne 1974; Matheson 1987; Cervenka and Moon 1991; Floate and Gill 1998; Rounds and Floate 2012). Neither does this result reflect the near extirpation of bison, a hypothesis experimentally tested and rejected by Tiberg and Floate (2011). Nor does it seem likely that competition from introduced species has caused the demise of native taxa. Competition is limited by an abundance of fresh cattle dung that is renewed daily, and by species differing in the season (Floate and Gill 1998) and use (dwellers versus tunnellers and rollers) of the resource. Furthermore, the advent of the most common exotic species in the region (*C. erraticus*, *O. nuchicornis*) has occurred only in recent decades with no reports of native species being locally extirpated.

It seems most likely that the success of exotic species in the region reflects invasion of an ecological niche largely unoccupied by

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press

native species. Native species were eradicated or displaced during the Pleistocene, when glaciers covered much of the northern half of the continent in ice. Species that survived in refugia in the southern United States of America and Mexico subsequently expanded their distributions northward (Howden 1966) to the extent allowed by their tolerance to colder climes. Because most of the surviving species were "warm-adapted", native assemblages in northern localities are depauperate (Lobo 2000). Those species that have established (*e.g.*, *C. pilularius*, *C. praticola*, *Onthophagus hecate* (Panzer)) are at the northern limits of distributions that extend southward into Mexico (Robinson 1948; Howden and Cartwright 1963; Matthews 1963). In contrast, the introduced European species are "cool-adapted" and well-suited to thrive in cattle dung on pastures at northern latitudes. A similar conclusion was reached by Lobo (2000), who suggested that the success of these taxa in the region was facilitated by the lack of competition from native species.

The invasion of exotic dung beetles into Canada continues. *Onthophagus taurus* (Schreber) is a European species of tunneller that was first reported in North America in Florida in 1971 (Fincher and Woodruff 1975). It recently was reported from northern Michigan, United States of America (Rounds and Floate 2012) and is expected to establish in southern Ontario and Québec if it has not already done so. Its ability to survive in the drier and colder climate of the Prairie Provinces is unknown but merits close examination. If establishment is successful, *O. taurus* will further contribute to the degradation of cattle dung and nutrient cycling on the region's pastures.

Acknowledgements

The authors thank V. Casey, C. Conrad, H. Dorchak, C. Durand, A. Middleton, K. Tiberg, L. Wilde, and particularly P. Coghlin for assistance in field collections and identifications. A. Middleton and I. Walker (Agriculture and Agri-Food Canada) facilitated research at Stavely and Onefour, respectively. J. Willms (Alberta Environment and Sustainable Resource Development) facilitated research at the Purple Springs Grazing Reserve. Partial funding was provided by the Canada/Alberta Livestock Research Trust. This is Lethbridge Research Centre Contribution Number 387-13002.

References

Bistrom, O., Silfverberg, H., and Rutanen, I. 1991. Abundance and distribution of coprophilous Histerini (Histeridae) and *Onthophagus* and *Aphodius* (Scarabaeidae) in Finland (Coleoptera). Entomologica Fennica, **2**: 53–66.

Bousquet, Y. 1991. Checklist of beetles of Canada and Alaska. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada.

Brown, W.J. 1940. Notes on the American distribution of some species of Coleoptera common to the European and North American continents. The Canadian Entomologist, **72**: 65–78.

Cervenka, V.J. and Moon, R.D. 1991. Arthropods associated with fresh cattle dung pats in Minnesota. Journal of the Kansas Entomological Society, **64**: 131–145.

Chetner, S. and Agroclimatic Atlas Working Group 2003. Agroclimatic atlas of Alberta, 1971 to 2000. AF. Agdex 071-1. Alberta Agriculture and Rural Development, Edmonton, Alberta, Canada.

Christensen, C.M. and Dobson, R.C. 1976. Biological and ecological studies on *Aphodius distinctus* (Mueller) (Coleoptera: Scarabaeidae). American Midland Naturalist, **95**: 242–249.

Environment Canada. 2013. Canadian climate normals 1971–2000. [online]. Available from http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html? [accessed 18 February 2013].

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. and Woodruff, R.E. 1975. A European dung beetle, *Onthophagus taurus* Schreber, new to the U.S. (Coleoptera: Scarabaeidae). The Coleopterists Bulletin, **29**: 349–350.

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. 2011. Arthropods in cattle dung on Canada's grasslands. *In* Arthropods of canadian grasslands (volume 2): inhabitants of a changing landscape *Edited by* K.D. Floate. Biological Survey of Canada, Ottawa, Ontario, Canada. Pp. 71–88.

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.

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

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press

Gordon, R.D. and Skelley, P.E. 2007. A monograph of the Aphodiini inhabiting the United States and Canada (Coleoptera: Scarabaeidae: Aphodiini). Memoirs of the American Entomological Institute, **79**: 1–580.

Hatch, M.H. 1971. The Beetles of the Pacific Northwest. Part V: Rhipiceroidea, Sternoxi, Phytophaga, Rhynchophora, and Lamellicornia. University of Washington Press, Seattle, Washington, United States of America.

Helgesen, R.G. and Post, R.L. 1967. Saprophagous Scarabaeidae (Coleoptera) of North Dakota. North Dakota Insects, **7**: 1–60.

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.

Howden, H.F. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Coleoptera). The Canadian Entomologist, **98**: 1177–1190.

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.

Jerath, M.L. and Ritcher, P.O. 1959. Biology of Aphodiinae with special reference to Oregon (Coleoptera: Scarabaeidae). Pan-Pacific Entomologist, **35**: 169–175.

Kessler, H. and Balsbaugh, E.U. 1972. Succession of adult Coleoptera in bovine manure in east central South Dakota. Annals of the Entomological Society of America, **65**: 1333–1336.

Lobo, J.M. 2000. Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. The Canadian Entomologist, **132**: 307–321.

Lobo, J.M. 2001. Decline of roller dung beetle (Scarabaeinae) populations in the Iberian peninsula during the 20th century. Biological Conservation, **97**: 43–50.

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.

Macqueen, A. and Beirne, B.P. 1975a. Dung burial activity and fly control potential of *Onthophagus nuchicornis* (Coleoptera: Scarabaeinae) in British Columbia. The Canadian Entomologist, **107**: 1215–1220.

Macqueen, A. and Beirne, B.P. 1975b. Effects of cattle dung and dung beetle activity on growth of beardless wheatgrass in British Columbia. Canadian Journal of Plant Science, **55**: 961–967.

Marsh, R. and Campling, R.C. 1970. Fouling of pastures by dung. Herbage Abstracts, **40**: 123–130.

Matheson, M.M. 1987. Insects associated with cattle dung in southern Quebec [online]. M.Sc. McGill University, Montreal, Québec, Canada. Available from http://digitool.Library.McGill.CA:80/R/-?func=dbin-jump-full&object_id=63895&silo_library=GEN01 [accessed 8 August 2013].

Matthews, E.G. 1963. Observations on the ball-rolling behavior of *Canthon pilularius* (L.) (Coleoptera, Scarabaeidae). Psyche, **70**: 75–93.

McDaniel, B., Boddicker, M.L., and Balsbaugh, E.U. Jr. 1971. Coleoptera inhabiting bovine manure in a pasture on the Big Sioux River flood plain in South Dakota. Proceedings of the South Dakota Academy of Science, **50**: 220–237.

Melsheimer, F.E. 1845. Descriptions of new species of Coleoptera of the United States. Proceedings of the Academy of Natural Science of Philadelphia, **2**: 26–43, 98–118, 134–160, 213–223, 302–318.

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, **13**: 275–298.

Natural Regions Committee. 2006. Natural regions and subregions of Alberta. *Compiled by* D.J. Downing and W.W. Pettapiece. Pub. No. T/852. Government of Alberta, Alberta, Canada.

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.

Robinson, M. 1948. A review of the species of *Canthon* inhabiting the United States (Scarabaeidae: Coleoptera). Transactions of the American Entomological Society, **74**: 83–100.

Rojewski, C. 1983. Observations on the nesting behaviour of *Aphodius erraticus* (L.) (Coleoptera, Scarabaeidae). Polskie Pismo Entomologiczne, **53**: 271–279.

Rounds, R.J. and Floate, K.D. 2012. Diversity and seasonal phenology of coprophagous beetles at Lake City, Michigan, USA, with a new state record for *Onthophagus taurus* (Schreber) (Coleoptera: Scarabaeidae). The Coleopterists Bulletin, **66**: 169–172.

Sanders, D.P. and Dobson, R.C. 1966. The insect complex associated with bovine manure in Indiana. Annals of the Entomological Society of America, **59**: 955–959.

Seamans, H.L. 1934. An insect weather prophet. Annual Report of the Quebec Society for the Protection of Plants, **132/134**: 111–117.

Sears, M.K. 1978. Damage to golf course fairways by *Aphodius granarius* (L.) (Coleoptera: Scarabaeidae). Proceedings of the Entomological Society of Ontario, **109**: 48.

Soper, J.D. 1941. History, range, and home life of the northern bison. Ecological Monographs, **11**: 347–412.

Tiberg, K. and Floate, K.D. 2011. Where went the dung-breeding insects of the American bison? The Canadian Entomologist, **143**: 470–478.

Valiela, I. 1969. The arthropod fauna of bovine dung in central New York and sources on its natural history. Journal of the New York Entomological Society, **77**: 210–220.

https://doi.org/10.4039/tce.2013.50 Published online by Cambridge University Press