Chapter 2
Sand Hill Arthropods in Canadian Grasslands

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Abstract. Sand hill environments in the Canadian grasslands can be classified as sandstone outcrops, upland dunes, sand features associated with water, non-human disturbances, anthropogenic disturbances, beach dunes, or sandbars. Insects and other arthropods use these environments for burrow construction, access to sand-associated host plants, open ground predation and scavenging, thermoregulation, and locomotion in a quiet substrate. The arthropod faunas of sand hills in the Canadian grasslands are diverse, include organisms that are specific to sand hills, and include a number of rare or endemic taxa. Dune stabilization is cause for conservation concern, whereas the threat of global warming may reverse the stabilizing trend and create larger areas of open drifting sand.

Résumé. Les milieux dunaires des prairies canadiennes peuvent être divisés en plusieurs catégories : affleurements de grès, dunes des hautes terres, terrains sableux liés à la présence de l'eau ou aux perturbations liées ou non à l'homme, plages ou barres de sable. Les insectes et les autres arthropodes utilisent ces milieux pour creuser leurs terriers, accéder aux plantes hôtes adaptées à ces conditions, profiter du terrain découvert pour trouver leurs proies vivantes ou mortes, assurer leur thermorégulation et se déplacer sans bruit. La faune des arthropodes des dunes des prairies canadiennes est diversifiée et comprend des organismes spécialement adaptés à ce milieu, y compris un certain nombre de taxons rares ou endémiques. La stabilisation et la préservation des dunes suscitent des préoccupations, et le changement climatique risque de renverser la tendance à la stabilisation et de créer ainsi de vastes superficies de sables mouvants.

Introduction to Sand Hill Environments

Among the various subregions of the prairie grasslands in Canada, "sand hills" are associated with one of the most distinctive faunas of insects and other arthropods. Some, such as tiger beetles (Coleoptera: Carabidae, Cicindelinae) and sand wasps (Hymenoptera: Crabronidae, Bembicinae), are classic open sand organisms. However, the diversity of arthropods associated with sandy substrates also includes a variety of organisms with less obvious sand adaptations and sand-adapted members of groups generally not associated with sandy habitats. The terms ammophilous and psammophilous are used ambiguously for both sand-adapted and sand-associated terrestrial arthropods (e.g., Hefetz *et al.* 1984; Sole *et al.* 2005), as well as for marine organisms in benthic sands under water or in the intertidal zone. For clarity, the terms "sand-adapted" and "sand-associated" will be used in the current chapter.

Sand hill environments, as defined here, have been formed by the actions of wind and/or water on reworked sandstone bedrock. Indeed, much of the bedrock underlying the grassland region of Canada consists of poorly consolidated sandstone, most of it dating from the Cretaceous and Paleogene periods (Acorn 2007*a*). Erosion of this sort of bedrock results in ample volumes of loose sand, which may be reshaped to form dunes, sandbars, blowouts, and other types of sandy sites. Further disturbance of these topographic features,

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both anthropogenic and "natural," contributes to a broad spectrum of sandy sites on the prairies. These sites are briefly characterized in the following sections to provide an informal classification of sand hill arthropod habitats.

Sandstone Outcrops

It is important to distinguish between reworked sandy landscape features and simple sandstone outcrops. The latter consist of exposed bedrock, typically along watercourses, roads, or railway lines, as well as in badlands. Because the bedrock remains more or less consolidated, sandstone outcrops resist tunnelling by arthropods and support many fewer specialized species of plants than do sandy landscapes. Furthermore, outcrops usually have steep slopes, such that surface temperatures on south-facing exposures may exceed 50 °C on sunny summer days (JHA, pers. obs.).

Upland Dunes

Classic dune fields are formed in areas where loose sand has been blown into dunes by the prevailing winds. Dunes take on a predictable profile, with a shallow slope where sand is brought into motion by the wind and a steep slope where it spills over the top of the advancing dune. In the Canadian grasslands, a parabolic shape is the most common (Wolfe *et al.* 2001). "Blowouts" may also form when the wind removes sand from a roughly oval area and deposits it as a dune downwind. Many biologists use the term "sand dune" to refer to dunes on which some of the sand is unvegetated and blown by the wind, and "stable dune" to refer to dunes that are entirely vegetated. Both of these terms are combined and referenced in the current chapter as "sand hills."

In the grassland regions of the prairie provinces, major dune fields include the Middle Sand Hills (largely within the Suffield Military Base in Alberta, but including the Empress

Fig. 1. Sand dune near Pakowki Lake, Alberta, with blooming sunflowers and chokecherry shrubs.

Fig. 2. Small blowout in the Middle Sand Hills of Alberta, large enough to provide habitat for a wide variety of sand-associated arthropods.

Dunes to the northeast; see Fig. 2), the Pakowki Lake Dunes (in southeastern Alberta; see Fig. 1), the Great Sand Hills (in southwestern Saskatchewan; see Shorthouse 2010), and Spruce Woods Provincial Park, Manitoba. The latter dune field is referred to here as "the Manitoba Dunes," but also has been named the Spirit Sand Hills, Aweme Dunes, Bald Hills, Carberry Dunes, and Glenboro Dunes. Various maps show the major dune areas in Canada (e.g., Acorn 1992; Wolfe *et al.* 2001) and the dune areas mentioned in the following text are shown in Fig. 3.

These dune fields likely originated with the production of great volumes of loose sand by the actions of the continental ice sheets of the Wisconsin glaciation and massive hydrological forces at the time of ice melt (see Shorthouse 2010) with a subsequent period of activity (with open, blowing sand). Dunes become active mainly as a result of cumulative moisture stress (Wolfe *et al.* 2001) and are mainly stabilized by plant growth during periods of renewed moisture. Once set in motion by drought, dunes can remain active for centuries. The Great Sand Hills have been active since about 1800 after many decades of low precipitation and a severe drought in the late 1700s (Wolfe *et al.* 2001). In contrast, the Duchess Sand Dunes (also known as the Gem Sand Dunes) have been stable for the past 230 years, possibly because they receive more precipitation (Wolfe *et al.* 2002).

Over much of the grassland region, the main dune-stabilizing plants during early stages of stabilization include lemon scurf pea (*Psoralea lanceolata* Pursh), sand grass (*Calamovilfa longifolia* (Hook)), Indian rice grass (*Oryzopsis hymenoides* (Roem. and Schult)), skeletonweed (*Lygodesmia juncea* (Pursh)), and veiny dock (*Rumex venosus* Pursh). As these and other plant species stabilize the sand and begin to create a soil profile with an organic horizon at the surface, the vegetation of sand hills becomes increasingly

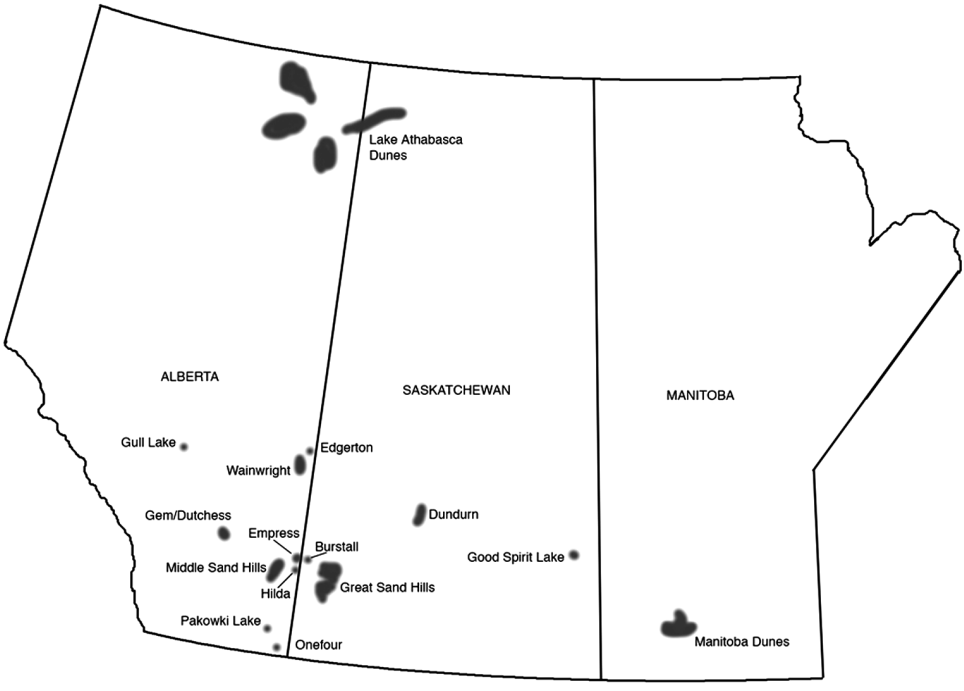

Fig. 3. Map of sand dune fields mentioned in text (adapted from Acorn 1992; Wolfe *et al.* 2001).

like that of the surrounding prairie, and the arthropod fauna likewise becomes increasingly less distinctive. During long-term periods of activity, however, open sand dune fields are unique habitats that support the evolution of endemic species or subspecies (Acorn 1992).

Sand Features Associated with Water

Many upland dunes may have originated as water-sorted deposits of sand from beaches, deltas, or sandbars. These processes are also important today, but produce relatively few of the grassland sand features on the Canadian prairies. Beach dunes are maintained in part by the action of waves, but also by windblown ice pushing sand ashore in spring and by the prevailing winds. The dunes on the east side of Good Spirit Lake, Saskatchewan, are an exceptional example. Another is the now fully vegetated dunes along the south margin of Gull Lake, Alberta, which were formed when declining water levels and the use of a tractor and cultivator to keep the beach free of "weeds" made a great volume of sand available to the wind (Acorn 2001). Sandbars along river courses support many species of sand-associated arthropods, but these habitats are usually seasonal and allow colonization only during late summer when water levels are low.

Non-human Disturbance

Disturbance is defined here as that which exposes open sand on the ground surface. It maintains, for highly sand-adapted arthropods, an open-sand habitat that would otherwise become stabilized and heavily vegetated. Abiotic factors appear to be of little importance. Extreme weather, such as the touchdown of a tornado, can potentially have this result (although the occurrence of such events in creating sand exposure is unknown in Canada).

Fire can initiate sand exposure, but visits to stabilized sand dunes in Alberta after recent grass fires (in the Empress Dunes, Hilda Dunes, and Middle Sand Hills) indicate that fire does not expose open sand to wind erosion and that vegetation grows back both quickly and vigorously (JHA, pers. obs.).

Biotic factors appear to be more important. Fossorial mammals often bring open sand to the surface during burrow construction. Mounds of sand formed by pocket gophers (*Thomomys talpoides* Richardson and *Geomys bursarius* Shaw) are especially obvious and are commonly visited by open sand insects, such as tiger beetles and sand wasps. The thirteen-lined ground squirrel (*Spermophilus tridecemlineatus* Mitchill) also inhabits stabilized dunes and is a strong burrower. Ord's kangaroo rat (*Dipodomys ordii* Woodhouse), found in more open sand areas, also creates extensive burrow systems. Other mammals, such as large ungulates, may occasionally create areas of open sand, but the often-encountered suspicion that trampling and wallowing by bison (*Bison bison* L.) was important in maintaining open sand environments is without clear support.

An unexplored but potentially important factor in dune sand is the action of insects themselves. If a large dune has 100,000 relatively large burrowing insects living on it (not an unreasonable estimate), and each brings one cubic centimetre of sand to the surface every few days (also not unreasonable), then over this period the equivalent of numerous rodent mounds will become exposed, or further exposed, to wind. In this manner, burrowing insects may well perpetuate their own open sand habitats over much longer periods than would otherwise occur (although this certainly remains to be documented).

Anthropogenic Disturbance

Sand-adapted arthropods benefit from anthropogenic disturbances. Road and railway cuts are the most abundant of these, and it may well be that open sand along such linear disturbance has served to allow dispersal of sand-adapted organisms between dune fields. Intergrades between two subspecies of the tiger beetle *Cicindela limbata* Say are found only along sandy road cuts in the vicinity of La Ronge, Saskatchewan (Acorn 1992).

Sand borrow pits and stockpiles are also home to sand-adapted arthropods, as are tractor scrapes, tire tracks, and sandy paths on which the vegetation has been trampled. Some of these features can become blowouts if they are sufficiently large and if there is a strong prevailing wind. Fire guards are another form of anthropogenic open sand, as are the shell craters and related disturbances that result from military activities. With military bases on sandy ground at Suffield and Wainwright in Alberta, and at Shilo in Manitoba, these sorts of disturbance are apparently not uncommon. However, not all anthropogenic sand environments are attractive to sand-adapted arthropods. Off-road vehicle trails and golf bunkers are too frequently disturbed to offer habitat for most sand-associated organisms.

Reasons for Sand Association among Arthropods

As will become apparent in the taxonomic overview that follows, certain arthropods are associated with sandy substrates for a number of obvious reasons.

Fossorial organisms often burrow in sand, and many show a very tight association with sandy substrates. Most excavate burrows for shelter (e.g., tiger beetle adults at night), for rearing young (e.g., sand wasps), or as refuges for sit-and-wait predation (e.g., burrowing wolf spiders (Lycosidae)). Some appear to tunnel through the sand in search of food. Yet others are associated with mammal burrows in sandy substrates.

Plant-specific herbivores are associated with sand-associated plants (e.g., *Psoralea lanceolata*, *Rumex venosus*) or with more widespread plants growing on open sand. It is not clear whether such plants are physiologically stressed and therefore prone to attack by herbivores, or if other aspects of the open sand environment make these plants more readily available as a food resource (Larsson 1989).

Open ground predators, such as tiger beetles, orient to prey visually and attack rapidly. For these reasons, open ground is favoured because it presents fewer physical barriers. Sit-and-wait predators also prefer open habitats without much vegetation. These predators include tiger beetle larvae and antlions (Neuroptera: Myrmeleontidae).

Detritivores may also find that open sand substrates allow easy foraging for food, brought to the sand surface by wind drift.

Maxithermal organisms use open sands in part because these microhabitats can be much warmer than nearby vegetated microhabitats. The presence of sparse vegetation allows thermoregulation when these organisms shuttle between shaded and sunny patches (Dreisig 1985).

Sand may also provide a relatively quiet substrate for arthropods that are active nocturnally and at the surface. Such may be the case for kangaroo rats (*Dipodomys* spp.), which are preyed on heavily by owls, but this has not been documented in the field (R. Dzenikiw, pers. comm.). Large arthropods are also likely to make more noise when moving through ground-level vegetation than they do on open unvegetated sand.

Descriptive Taxonomic Overview

Unless indicated otherwise, the overview that follows is based primarily on the author's collections (largely from the Empress Dunes, which are along the Alberta–Saskatchewan border, approximately 11 km south of Empress, Alberta), photographs, and observations, as well as the collections of the University of Alberta E.H. Strickland Entomology Museum. Because few thorough biodiversity surveys have been conducted in grassland sand hills, what follows originates in part from the opinions and unpublished observations of other entomologists. A primary theme that runs through this account is the paucity of ecological data available for most taxonomic groups of sand hill arthropods in our region.

Acari

Behan-Pelletier and Kanashiro (2010) state that "The mite fauna of grassland soils in Canada is remarkably poorly known," and mention only one sand-associated mite in the Canadian grasslands, the terpnacarid genus *Alycosmesis,* found on dune sands near Onefour, Alberta. However, ixodid ticks (particularly *Dermacentor* spp.) are obvious and abundant creatures on sand hills, especially in the Great Sand Hills and in the Manitoba Sand Dunes in spring and early summer.

Araneae

Of the remaining non-insect arthropods, only a few types of spiders seem to show a strong association with open sandy areas. The sit-and-wait wolf spiders *Geolycosa wrightii* (Emerton) and *G. missouriensis* Banks (Lycosidae) are probably our most strongly sand-associated species, as they live in deep, silk-lined vertical burrows in the sand. Less tightly sand-associated wolf spiders include *Schizocosa minnesotensis* (Gertsch), *S. mccooki* (Montgomery), and *Pardosa concinna* (Thorell) (Dondale and Redner 1990). The Gnaphosidae also includes some facultative sand dwellers, such as *Micaria riggsi* Gertsch,

M. emertoni Gertsch, and *Zelotes exiguoides* Platnick and Shadab (Platnick and Dondale 1992). Some jumping spiders (Salticidae) also take advantage of open microhabitats as visual predators. Personal observations, and those of David R. Maddison (pers. comm.), suggest that these spiders include various species of *Habronattus* (*H. amicus* (Peckham and Peckham), *H. americanus* (Keyserling), and *H. decorus* (Blackwall) at a minimum) and grassland species of *Terralonus*. On plants in sparsely vegetated sand areas, one can find *Pelegrina* species and *Evarcha hoyi* (Peckham and Peckham).

Archaeognatha

Jumping bristletails are included here on the basis of three pinned specimens (and field notes mentioning others) from the Empress Dunes and one photograph from the Middle Sand Hills (Drowning Ford Grazing Reserve) of Alberta. All are members of the Meinertellidae, but species-level identification is not possible. No published information exists on the Canadian grassland species, and identification of the Canadian fauna is problematic (Wygodinsky and Schmidt 1980). Of the two extant families of archaeognathans, the Meinertellidae is more strongly associated with arid environments, with at least one species, *Machilinus* (*Nearctolinus*) *aurantiacus* (Schött), known from as far north as Kamloops, British Columbia (Sturm and de Roca 1992).

Odonata

Various dragonflies (Suborder Anisoptera) are often found perched on open ground, including non-vegetated sand, from which they fly up in pursuit of prey and potential mates (Dunkle 2000). Typical open-ground species include *Ophiogomphus severus* Hagen and *Stylurus intricatus* (Hagen) (Gomphidae), as well as species in the genus *Sympetrum* (Libellulidae). Most other anisopterans prefer to perch in vegetation, as do species of damselflies (Suborder Zygoptera). However, on sand hill sites near water, various damselflies (e.g., *Enallagma* spp., *Coenagrion* spp., *Lestes* spp.) will forage in the relatively open vegetation on and around open sand patches.

Orthoptera

Although the crickets *Allonemobius griseus* (Walker) and *A. allardi* (Alexander and Thomas) are found on dry, open sand (Vickery and Kevan 1985), and the bush katydid *Scudderia pistillata* Brunner may be found in shrubby interdune areas, most of the sand-associated orthopterans are short-horned acridid grasshoppers. At most sites, *Psoloessa delicatula* (Scudder) is a common species, whereas *Trimerotropis agrestis* McNeill gives the appearance of being the most cryptic on sand. Other sand-associated acridids include *Cratypedes neglectus* (Thomas), *Melanoplus flavidus* Scudder, *M. angustipennis* (Dodge), *Spharagemon bolli* Scudder, *S. equale* (Say), *S. collare* (Scudder), and *Trachyrhachys kiowa* (Thomas). A number of other grasshoppers are found on sandy and gravelly or other dry soils, including *Amphitornus coloradus* (Thomas), *Arphia pseudonietana* (Thomas), *Cordillacris occipitalis* (Thomas), *Hesperotettix* spp., *Melanoplus gladstoni* Scudder, *M. packardii Scudder*, *M. sanguinipes* (Fab.), *Orphulella speciosa* (Scudder), and *O. pelidna* (Burmeister). *Acrolophitus hirtipes* (Say) is also associated with sand, but only in riverine vegetation (Vickery and Kevan 1985).

Hemiptera

Sucking bugs are not a prominent component of the sand hill arthropod fauna. On sparse grasses and lemon scurf pea, aphids are at least common enough to attract coccinellid

beetles (see under that taxon), but the taxa of aphids involved are not known. Perhaps the most visible hemipterans in sandy environments are ant mimics such as the alydid *Alydus pluto* Uhler and the lygaeid *Uhleriola floralis* (Uhler). Collections from the Empress Dunes also include the coreid *Chelinidea vittiger* Uhler (on *Opuntia* cacti), the thyreocorid *Corimelaena nigra* Dallas, and the pentatomid *Coenus delius* Say (JHA, pers. obs.).

Occasionally, aquatic bugs can be seen on the surface of open dunes, presumably because they mistook the reflective sand surface for water while flying overhead. Both water boatmen (Corixidae) and water striders (Gerridae) seem prone to this unfortunate error in habitat recognition.

Lepidoptera

The most sand-adapted of the lepidopterans are species of micro moths that run quickly on the surface of open dunes, and which may be brachypterous, that is, having short or rudimentary wings. These include members of the genera *Gnorimoschema* (Gelechiidae) and *Areniscythris* (Scythridae). *Gnorimoschema* is also found on dunes in the boreal forest, including the Lake Athabasca Dunes in northern Saskatchewan and the Carcross Dunes in the Yukon, and farther south along the west coast of the United States. What little is known about the biology of this genus is summarized by Powell and Povolny (2001). *Areniscythris* contains only one described species, *A. brachypterus* Powell from California, the larvae of which live in silken galleries in the sand, feeding on buried green plant tissue (Powell 1976). A new full-winged species of *Areniscythris* from the Great Sand Hills and Burstall Dunes of Saskatchewan is currently under description by J.-F. Landry. Suspected of feeding on *Psoralea lanceolata*, the immature stages of this moth remain unknown (J.-F. Landry, pers. comm.).

There are only a few sand-associated species of butterflies, which include the following members of the family Lycaenidae. The ruddy copper (*Lycaena rubidus* (Behr)) is almost always found on prairie sand hills because its larvae feed on the foliage of veiny dock (*Rumex venosus*), a species associated with open sand. The melissa blue (*Plebejus melissa* (Edwards)) is less tightly associated with sand, but is common in sandy areas where its larvae feed on various plants in the family Fabaceae. Recent records have also come to light of the coniferous forest-associated elfin butterflies *Callophrys augustinus* (Westwood) and *C. eryphon* (Boisduval) (both apparently feeding on *Arctostaphylos*, despite *C. eryphon* being considered a specialist on *Pinus*) on sandy sites in the southern prairies (G. Anweiler, D. Glaeske, pers. comm.).

Also using *Arctostaphylos* as a food plant, the day-flying moth *Coranarta macrostigma* (Lafontaine and Mikkola) (Noctuidae: Hadeninae) is found on sand hills near Edgerton, Alberta, disjunct from the nearest conspecific populations in the Rocky Mountains and Caribou Mountains, and somewhat paler in adult colouration (G. Anweiler, pers. comm.).

Among the macro moths, some species of Noctuidae, in the genera *Schinia* (Heliothinae) and *Copablepharon* (Noctuinae), have been considered species at risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2008). The endangered species include the gold-edged gem (*S. avemensis* (Dyar); Fig. 4) and the dusky dune moth (*C. longipenne* (Grote)) on dunes in southern Alberta, Saskatchewan, and Manitoba, as well as the white flower moth (*S. bimatris* (Harvey)) on dunes in Manitoba. In all three provinces, the pale yellow dune moth, *C. grandis* (Strecker), is "of special concern." An additional species, *C. viridisparsa* Dod, is also rare and associated with open and disturbed sand (Anweiler 2005).

Over the past decade, collections by members of the Alberta Lepidopterists' Guild have begun to elucidate the distribution of moths on grassland and parkland sand hills. Published

Fig. 4. The provincially endangered Gold-edged Gem (*Schinia avemensis*) on a sunflower in the Pakowki Lake Dunes, Alberta.

results include a summary for the Wainwright Dunes Ecological Reserve (Macaulay 2004) and various species pages on the University of Alberta's E. H. Strickland Entomological Museum's virtual museum website (e.g., Anweiler 2005). Some moths appear to be more or less restricted to vegetated dunes. Other species have broader habitat associations, but are nonetheless most commonly encountered on dunes. Not all species are present on all dunes, suggesting that dune fields differ in history of colonization by moths, suitability to various moth species as habitat, and sampling effort by collectors.

Among the apparent dune specialists are *Sphinx lucitiosa* Clemens and *Hemaris gracilis* (Grote and Robinson) (Sphingidae), *Grammia phyllira* (Drury) and *G. margo* Schmidt (Noctuidae: Arctiinae), and *Eucosma fandana* Kearfott and *E. fernaldana* (Grote) (Tortricidae). Some uncommon species that are not restricted to sand hills (although they may be found primarily on sand hills in our region) include *Sphinx drupiferarum* Smith (Sphingindae), *Hemileuca nevadensis* Stretch (Saturniidae), *Ethmia albicostella* (Beutenmüller) (Elachistidae), *Stiria rugifrons* Grote (Noctuidae: Stiriinae), *Schizura ipomoeae* Doubleday (Notodontidae), and *Nacophora quernaria* (Smith) (Geometridae).

Neuroptera

Of the neuropterans, only the Myrmeleontidae (antlions) are strongly associated with sandy environments. In Alberta, the genus *Brachynemurus* is found in open sandy environments where the larvae live just beneath the sand surface. The genus *Myrmeleon* is found on finer, silt-sized sediments, along with its characteristic conical larval pits, often at the bases of badlands hills.

Coleoptera

Beetles are probably the best-documented group of sand hill arthropods. The tiger beetles (Carabidae: Cicindelinae), in particular, have received a great deal of attention (e.g., Wallis 1961; Hilchie 1985; Acorn 1991, 1992, 2001). Five species are typical of open and semi-open sand habitats in the Canadian grasslands, and two of these (*Cicindela limbata* Say and *C. lepida* Dejean) are found almost exclusively on open blowing sand. The other three strongly sand-associated species are found on more sparsely vegetated sand: *C. formosa* Say (Fig. 5), *C. scutellaris* Say, and *C. lengi* Horn. Additional species that are occasionally encountered on sand include *C. tranquebarica* Herbst, *C. duodecimguttata* Dejean, and *C. decemnotata* Say. As well, to the north of the grasslands region, *C. longilabris* Say is typical of sandy areas with coniferous trees.

Tiger beetles show interesting patterns of geographical variation, including endemic subspecies whose ranges centre on particular dune fields (Acorn 1992). *Cicindela formosa* is represented in Alberta, in and around the Middle Sand Hills, by *C. f. fletcheri* Criddle, a subspecies that is also found in adjacent Montana and east to North Dakota. The much paler *C. f. gibsoni* Brown is found in the Great Sand Hills, whereas the species is represented by *C. f. manitoba* Leng in the Manitoba Sand Dunes (Fig. 6). This striking geographical pattern has been obscured by the tendency of some American authors to synonymize subspecies that are primarily Canadian with their southern relatives (*C. f. fletcheri* with *C. f. formosa*, *C. f. gibsoni* with an unnamed subspecies from Colorado [*C. f.* "*yampa*" of Gaumer 1977], and *C. f. manitoba* with *C. f. generosa*). Contributing to the confusion, Acorn (1992) previously interpreted *C. f. fletcheri* as an intergrade between *C. f. formosa*

Fig. 5. Mating tiger beetles (*Cicindela formosa*), Middle Sand Hills, Alberta.

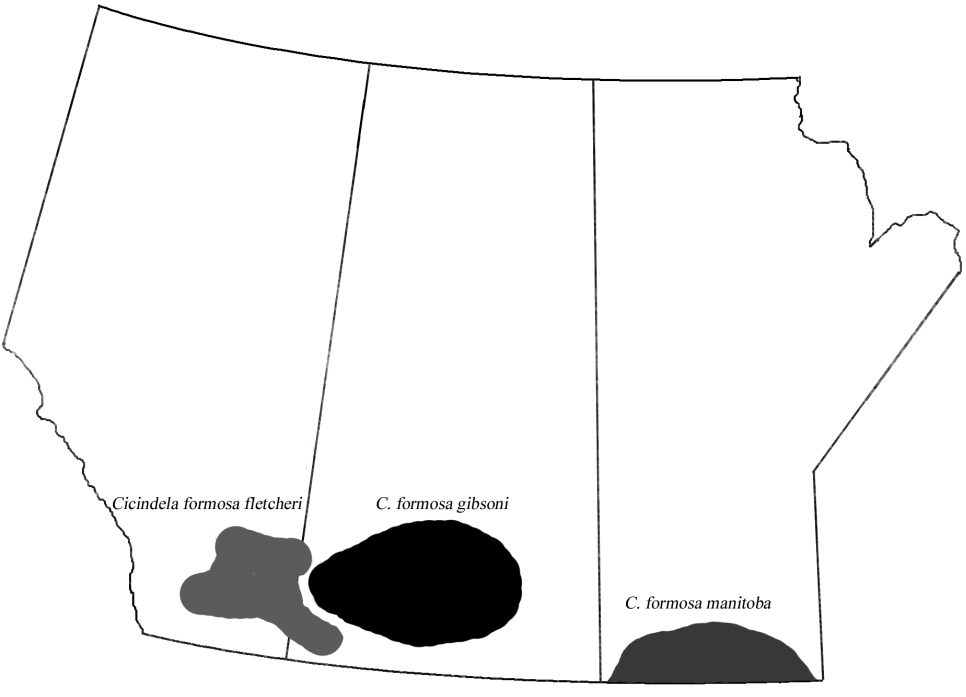

Fig. 6. The approximate geographical ranges of the three subspecies of *Cicindela formosa* in the Canadian prairies (adapted from Wallis 1961; Gaumer 1977; Hilchie 1985; Acorn 2001).

and *C. f. gibsoni* before raising questions about its status (Acorn 2001), being unaware of the description of *C. f. fletcheri*.

Cicindela scutellaris is represented by the unmarked subspecies *C. s. scutellaris* in Alberta and Saskatchewan and by *C. s. criddlei* Casey in Manitoba (Fig. 7). *Cicindela scutellaris scutellaris* mimics a distasteful blister beetle (Acorn 1988) and *C. s. criddlei* has typically been synonymized with the American subspecies *C. s. lecontei* Haldeman. *Cicindela limbata*, a much better disperser, is represented throughout our region by *C. l. nympha* Casey. These patterns, along with endemism around the Lake Athabasca Sand Dunes in northern Alberta and Saskatchewan, are still coming into focus, and they underscore the fact that Canadian sand dunes are indeed ecological islands for some sand-associated insects.

Other species of ground beetles (Carabidae) can also be found in sand hills, most notably the pale-coloured sand burrower *Geopinus incrassatus* (Dejean). In 1984, pitfall traps at the Empress Dunes produced the following dry land or sand-associated species: *Calosoma lepidum* LeConte, *C. luxatum* Say, *Pasimachus elongatus* LeConte, *Dyschirius tenuispinus* Lindroth, *Bembidion obscurellum* (Motschulsky) (especially abundant), *B. nitidum* (Kirby), *B. nudipenne* Lindroth, *B. acutifrons* LeConte, *Pterostichus lucublandus* (Say), *Amara thoracica* Hayward, *A. obesa* (Say), *A. apricaria* (Paykull), *A. quenseli* (Schonherr), *A. convexa* LeConte, *A. pallipes* Kirby, *Piosoma setosum* LeConte, *Euryderus grossus* (Say), *Harpalus erraticus* Say, *H. desertus* LeConte, *H. amputatus* Say, *Selenophorus planipennis* LeConte, *Stenolophus conjunctus* (Say), *Lebia vittata* (Fabricius), *Microlestes curtipennis* (Casey), *Calleida viridis* Dejean, and *Cymindis interior* Lindroth. Records of rare species,

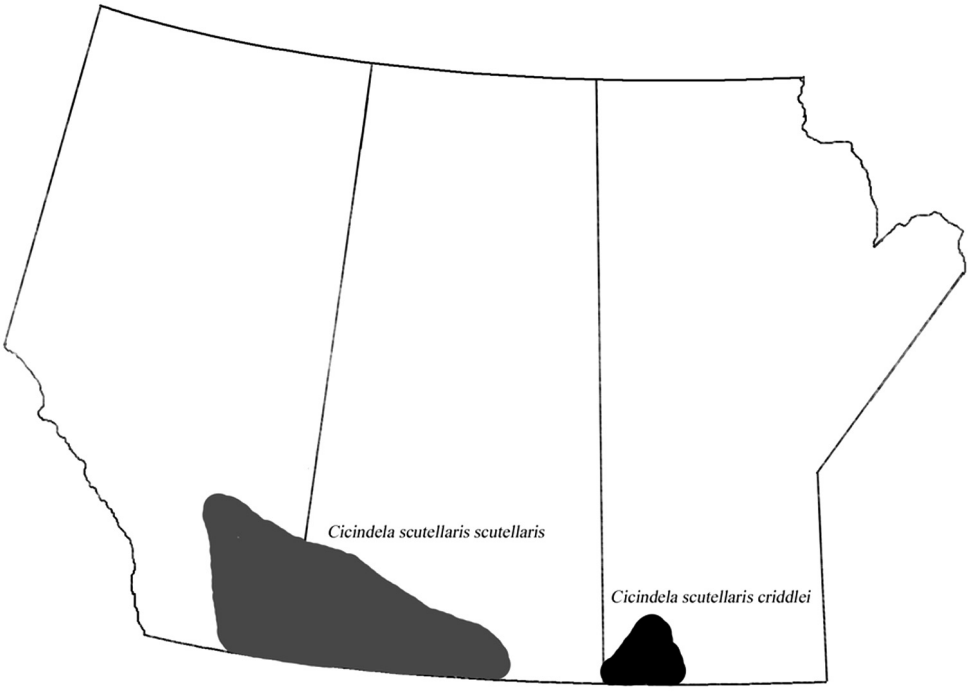

Fig. 7. The approximate geographical ranges of the two subspecies of *Cicindela scutellaris* in the Canadian prairies (adapted from Wallis 1961; Acorn 2001).

such as *Schizogenius ferrugineus* Putzeys at the Empress Dunes (G.J. Hilchie, pers. comm.), demonstrate the possibility for uncommon occurrences in these habitats.

Burying beetles (Silphidae) are often encountered on sand hills, perhaps because sandy substrates facilitate the burial of small vertebrate carcasses. Large numbers of *Nicrophorus guttula* Motschulsky, *N. obscurus* Kirby, and *N. hybridus* Hatch and Angell have been collected on the Empress Dunes (JHA, unpublished). Other members of the superfamily Staphylinoidea are not particularly abundant on dune sands.

Scarab beetles (superfamily Scarabaeiformia) also make use of sandy substrates for burrowing, and this group is both common and diverse in sand hill environments. *Eucanthus greeni* Robinson (Geotrupidae) is an easily recognized sand specialist, as are the smaller adults of *Glaresis canadensis* Brown (Glaresidae) and *Xenochodaeus* spp. (Ochodaeidae). Within the Scarabaeidae proper, the genus *Aegialia* (Aphodiinae) is strongly sand associated, as are species of *Rhyssemus* (Aphodiinae, Psammodiini). Where sand hills are used for rangeland, cattle dung is often underlain by the tunnels of *Onthophagus hecate* Panzer and *O. nuchicornis* (L.), both introduced and both more abundant in sandy areas. Cattle dung is also commonly inhabited by the introduced dung beetles *Aphodius fossor* (L.), *A. distinctus* Muller, and *A. fimetarius* L., none of which are dependent on sand. Various other Aphodiini are doubtless present on sand hills, as generalist dung feeders or as specialists on rodent dung, but only one of the species recorded for the prairie provinces, *Drepanocanthoides walshii* (Horn), is known to be associated with sandy substrates (Gordon and Skelley 2007). Open sand is also a common collecting habitat for the ant-associated scarabs in the genus *Cremastocheilus* (Cetoniinae).

The most visible scarab on sandy sites is probably the ten-lined June beetle (*Polyphylla decemlineata* (Say)), which flies just at and after sunset and develops as a root-feeding larva in the soil. Another large scarab, the goldsmith beetle (*Cotalpa lanigera* (L.)), is regularly found dead on open sand. On 18–19 June 1984 and on 14 June 1985, these beetles were observed at the Empress Dunes emerging from the soil at sundown, flying about in search of mates, mating in the foliage of chokecherry bushes (*Prunus virginiana* L.), and returning to the soil by the time it was dark (JHA, pers. obs.).

One species of click beetle (Elateridae: *Cardiophorus cardisce* (Say)) seems to have a particular affinity for sand. North of the grasslands, this ground-surface scavenger is dark coloured with four light elytral spots, whereas on the prairies these beetles are lighter and presumably better camouflaged and better suited to high sunlight levels. No subspecies names have been proposed for these geographical differences.

One checkered beetle species (Cleridae: *Trichodes nutalli* (Kirby)) is common at the Empress Dunes and presumably on other nearby dune fields as well.

The blister beetle *Lytta nuttalli* Say (Meloidae) is found on lemon scurf pea and other legumes in southern Alberta and Saskatchewan, and sand hills are also good habitat for *Epicauta ferruginea* (Say).

Darkling beetles (Tenebrionidae) are abundant in arid environments in western North America in general, and it is common to find three sorts of large, dark "stink beetles" (although ours do not produce defensive odours) in the genus *Eleodes* wandering on sand hill soils scavenging for food. *Eleodes extricata* (Say) is generally the most common, along with *E. tricostatus* (Say) and *E. hispilabris* (Say). *Asidopsis opaca* (Say) can be found co-occurring with these species. The smaller adults of *Blapstinus substriatus* Champion are also abundant on dune sands. On sandstone exposures and in badlands, one can also find *A. polita* (Say) and *Glyptasida sordida* (LeConte).

The ant-like flower beetles (Anthicidae) are often encountered on sand, especially in pitfall traps. In the Canadian grasslands, the term "flower beetle" appears to be a misnomer. *Notoxus* spp. and *Mecynotarsus candidus* LeConte (with a prothoracic horn) and *Anthicus* (without the horn) are abundant inhabitants of grassland sand hills.

Hister beetles (Histeridae) are common on sandy soils (Fig. 8). Pitfall traps on the Empress Dunes captured 14 species in this family, identified through the courtesy of Yves Bousquet (*Margarinotus harrissii* (Kirby)*, Hister furtivus* LeConte*, H. abbreviatus* Fab.*, Spilodiscus instratus* (LeConte)*, Saprinus oregonensis* LeConte, *Euspilotus cribrum* (Casey), *E. insertus* (LeConte), *Xerosaprinus acilinea* (Marseul), *Hypocaccus acorni* Bousquet and Laplante, *H. fraternus* (Say), *H. iris* (Fall), *H. omissus* (Casey), *H. patruelis* (LeConte), and *H. seminitens* (LeConte)). Most of these beetles, with the exception of the *Euspilotus* spp., appear to be associated with open sand microhabitats.

One member of the Nitidulidae, *Carpophilus pallipennis* (Say), was collected in large numbers on the Empress Dunes in pitfall traps.

Among the lady beetles (Coccinellidae), the rare species *Hyperaspis lugubris* (Randall) appears to be associated with sand hills in the Canadian grasslands (Acorn 2007*b*). As well, the formerly widespread species *Coccinella transversoguttata* Falderman and *C. novemnotata* Herbst are now reliably found in small numbers on open sand habitats since the arrival of the European species *C. septempunctata* L. (Acorn 2007*b*).

Weevils (in the superfamily Curculionoidea) are not particularly abundant in sand hills, but the strawberry root weevil (*Otiorhynchus ovatus* (L.)) is ubiquitous in these environments, and *Perapion wickhami* Kissinger feeds on *Rumex venosa* and is therefore considered a characteristic dune species (G.J. Hilchie, pers. comm.).

Fig. 8. Hister beetle (*Hypocaccus fraternus*), Opal Sand Hills, Alberta.

Diptera

The most characteristic flies of open sandy environments are surely the bee flies (Bombyliidae), which can be observed basking on the ground, or searching for the burrows of other insects in which to place their eggs. The larvae of bee flies include parasites of the immature stages of solitary aculeate Hymenoptera (most species), Lepidoptera, Neuroptera, Coleoptera, or Diptera, as well as predators on acridid grasshopper eggs (Hall 1981; Kits *et al.* 2008). Typical genera on grassland sand hills in Canada include *Systoechus*, *Bombylius*, *Anthrax*, *Exprosopa*, *Poecilanthrax*, and *Hemipenthes*.

Robber flies (Asilidae) are also abundant in some sandy environments. The large adults of *Stenopogon inquinatus* Loew are highly visible predators on other insects, including tiger beetles (*Cicindela* spp.), which they capture in flight. Other typical asilids in these environments include *Lasiopogon quadrivittatus* Jones, *Stichopogon trifasciatus* (Say), *Stenopogon coyote* Bromley, *Proctacanthella cacopiloga* (Hine), and *Dicropaltum mesae* (Tucker). On the Manitoba Dunes, *Laphystia flavipes* Coquillett is also encountered (R.A. Cannings, pers. comm.).

Other sand-dwelling dipterans include the miltogrammine sarcophagid *Senotainia trilineata* Wulp, a nest parasite of aculeate wasps (McCorquodale 1986), and the oestrid bot fly *Cuterebra polita* Coquillett, a parasite of various rodents, including the sand specialist Ord's kangaroo rat (*Dipodomys ordii* Woodhouse) (Gummer *et al.* 1997). Although larvae of the latter species are common on rodents, adults have a very low detectability on the dunes (S. Robertson, pers. comm.), as may be the case with many other sand hill dipterans, a fauna that has not been well studied or surveyed. For example, there may be hill-topping tachinids in these environments that have not yet come to light through careful collecting (J. O'Hara, pers. comm.).

Hymenoptera

Although sawflies and parasitic wasps ("Symphyta" and "Parasitica," respectively—both no longer considered natural groupings) are no doubt present in sand hill environments, there is little on this subject in the literature. Ants, bees, and wasps, however, are among the most visible of all sand dune arthropods. The following account is based largely on the publications of Hilchie (1982) and McCorquodale (1986), as well as time in the field with J. Wojcicki in the Great Sand Hills, taping episodes of my former television series (Acorn 1997*a*, 1997*b*).

Beginning with the superfamily Apoidea (bees and relatives), numerous typical bees (Apidae) inhabit sand hill environments, including honey bees (*Apis mellifera* L.), various bumble bees (Bombini), and digger bees (Anthophorini). Sweat bees (Halictidae) are also common, and their occasional stings are a familiar aspect of fieldwork on sand dunes during warm weather, when some (but not all) of these bees are indeed attracted to one's perspiration. Miner bees (Andrenidae) are also present in sandy environments, along with plasterer bees (Colletidae) and leafcutter bees (Megachilidae).

Some of the most familiar sand dune insects are digger wasps in the family Sphecidae (Fig. 9). Thread-waisted *Ammophila* and *Eremnophila* are often seen dragging paralyzed caterpillars for burial in the sand as food for the wasp's larvae. Formerly included in the Sphecidae, the sand wasps proper are now considered a family in their own right, the Crabronidae. Here again, there are many familiar sand dune representatives, including pemphredonine aphid wasps, *Oxybelus*, *Crabro,* and *Bembix,* which prey on flies, *Tachysphex* on grasshoppers, *Bicyrtes* on stink bugs (Pentatomidae), *Philanthus* on other

Fig. 9. Digger wasp (*Ammophila* sp.) with caterpillar prey, Opal Sand Hills, Alberta.

bees and wasps, *Cerceris* on beetles, *Gorytes* on leafhoppers, and *Microbembix* on a variety of arthropods that they find dead. In addition, members of the genus *Nysson* are nest parasites, laying eggs in the burrows of other digger wasps.

Cuckoo wasps (Chrysidoidea: Chrysididae) are nest parasites of other solitary bees and wasps (some in very tight co-associations) and, because of their brightly iridescent colours, they easily attract the attention of entomologists.

Within the superfamily Vespoidea (wasps, ants, and their relatives) typical wasps (family Vespidae) such as yellowjackets and "hornets" (*Vespula* spp. and *Dolichovespula* spp.) and paper wasps (*Polistes* spp.) are not as abundant as some of their relatives in other families. Spider wasps in the family Pompilidae are especially abundant in sandy places, where they, like many other sand-associated Hymenoptera, take advantage of sandy substrates for digging burrows in which to provision their prey. As their name implies, spider wasps paralyze and provision their young with spiders. Another wasp family commonly encountered on sand is the Tiphiidae, members of which are parasitic on other insects, particularly tiger beetles and scarab beetles. And of course, the velvet ants, in the family Mutillidae, run actively over the open sand in search of other hymenopteran nests to parasitize, protected by their bright colours and painful stings.

With respect to sand hill ants themselves, there is little in the way of published information. However, several species have been collected by the author (kindly identified by James Glasier). *Pogonomyrmex occidentalis* (Cresson), the western harvester ant, is a prairie species that also inhabits sand hills. *Lasius neoniger* Emery is another familiar species because of its circular burrow entrance mounds (approximately 7 cm diameter) with a central conical depression (Fig. 10). Other sand hill ants include *Formica bradleyi* Wheeler, *F. neoclara* Emery, *Myrmica americana* Weber, *M. brevispinosa* Wheeler, and *Tapinoma sessile* (Say). *Formica lasioides* Emery, *F. obscuriventris* Mayr, *F. oreas* Wheeler, *F. podzolica* Francoeur, and *Dolichoderus taschenbergi* (Mayr) also occur on sand hills north of the grasslands (JHA, unpublished).

Conservation, Agriculture, and Changes in Open Sand Areas over Time

The preceding taxonomic overview should suffice to establish the following three facts about sand hill arthropods in the Canadian grasslands: (1) These environments provide habitat for a great diversity of arthropod life, (2) there are arthropod species that are restricted to sandy environments, and (3) some tiger beetles have evolved as endemic subspecies, isolated on dune fields that become ecological islands. Various sand hill moths have been identified as species of conservation concern, and it is predicted that additional taxa will be added to this list as more arthropods come under the scrutiny of conservation biologists. Therefore, sand hills are in need of protection as habitat for rare species.

Fortunately, there are relatively few human threats to dune habitats in Canada. Road construction, particularly for petroleum extraction, is one, especially if it results in new or introduced species of plants colonizing open sand habitats. Colonization by introduced species has not, however, been a problem on Canadian sand hills, although the grass *Ammophila arenaria* has been shown to reduce invertebrate biodiversity on coastal dunes in the United States (Slobodchikoff and Doyen 1977). A more acute problem, for those species that require open blowing sand, is that sand dunes throughout the Canadian grasslands are rapidly stabilizing (Wolfe *et al.* 2001). If present trends continue, the number of actively blowing dunes may decrease dramatically over the next few decades. At the Empress Dunes, roughly 10% of the open sand visible in 1938 air photos was

Fig. 10. Ant colony entrance (*Lasius neoniger*), Middle Sand Hills, Alberta.

present in 1992 (Acorn 1992), and this amount has decreased by at least half since then. During the dry years prior to 2002, small areas of open sand appeared on the Hilda and Gem dune fields. These sites supported populations of the dune tiger beetles *Cicindela scutellaris* and *C. lengi* for a brief period before subsequent rains and plant growth caused their apparent extirpation.

Despite their unique arthropod faunas, open dunes are viewed by many people as eroded wastelands that can expand into adjacent agricultural lands. Although dune fields on the Canadian grasslands are undergoing a period of stabilization, there is growing concern that areas of active dunes will increase with global warming and prairie drought (Wolfe *et al.* 2001). If so, populations of sand-associated species may increase. Conversely, severe and long-term droughts may cause the decline of species more suited to moister conditions that promote plant growth on stabilizing dunes. Only time will tell, and for those interested in sand hill environments, the arthropod fauna will serve as a sensitive barometer of environmental change.

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