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# TEMPORAL AND SPATIAL CHANGES IN THE CANADIAN INSECT FAUNA: PATTERNS AND EXPLANATION THE PRAIRIES

Concerns Ephemeroptera!

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**Abstract**

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The insect fauna of the Canadian prairies is composed of elements recruited from surrounding biomes. Most species appear to have invaded from the southeastern United States following the retreat of the last glaciation. Other distinct centers of origin are the eastern boreal forest, the Rocky Mountains, the Alaskan-Beringian refugium, and the Sonoran or interior basin of the southwestern United States. Because of the youthfulness and instability of the prairies as a biome, true prairie endemic species are rare. While an inventory of prairie insects is far from complete, enough information is available to detect basic patterns of immigration.

The prairies have a long history of settlement and are easily accessible, yet their entomology is poorly known. The prairies are often blank spaces on distribution maps, not so much because of their impoverished fauna, but because entomologists often pass through quickly to reach the more interesting regions on either side of the grasslands. While admitting that the prairies have a less diverse fauna than other areas, it is my purpose to stress that this region has a most interesting assemblage of insects from the point of view of zoogeographical origin and community composition.

Before turning to the insects themselves, it is necessary to make a number of introductory remarks about the region. First, true prairie in the botanical sense is almost non-existent in Canada (Scoggan 1978) and is restricted to a small area near the Manitoba, Saskatchewan, and U.S.A. borders. Yet in the Canadian context of the word, "prairie" usually refers to the major portions of three western provinces, Manitoba, Saskatchewan, and Alberta. These provinces, from the point of view of plant ecologists, are regions of mixed grasslands, parklands, transition zones, and boreal coniferous forests. In this discussion, "prairie" will be used in its broader meaning. In addition to being convenient, this usage can be justified biologically and geologically since prairies have moved with climatic change. It is known from pollen studies that at one time grasslands were pushed by glaciers into the southern U.S.A. and Mexico (Fig. 1). The present day Canadian prairies were ice-covered, and boreal forest and probably tundra were found south of the ice. Later the present Canadian grasslands were covered by a typical boreal coniferous forest. In addition, grasslands once extended much further north than is now the case (Table I). In this paper, prairie will refer roughly to the flatlands east of the Rocky Mountains, west and south of the Precambrian Shield, and south of the Arctic drainage (Fig. 2).

The most important historical fact about the prairie region is that the entire area was glaciated and denuded of its flora and fauna at a relatively recent date (8-12000 B.P.). Thus, we are dealing with a story of immigration with a relatively recent starting date.

A final point of considerable significance is that the prairie itself is relatively young as a biome. Prairie flora and fauna are derivative, rather than endemic. Components of the prairies were present in the middle Miocene, but prairies in the usual sense did not develop until the Pliocene (MacGinitie 1958). Prior to this time, the prairie region was covered by a type of subtropical savanna, the prairie developing in the rain shadow of the uplifting Rocky Mountains. Flora and fauna of the biome were recruited from surrounding biomes. This conclusion has been reached from studies ranging from those on birds to leafhoppers to grasses. Ross (1970) points out that of 82 species of grasshoppers found on the prairies, only three were endemic to the prairie. The ranges of other species extended to the far corners of the continent (Fig. 3).

Munroe (1956) in his extensive review of Canada as an environment for insects, stressed that at that time too little was known about the insect fauna of the prairies to discuss distribution and origin in a meaningful way. Today, while the prairie fauna is still comparatively poorly known, information is adequate to allow a zoogeographical analysis. While

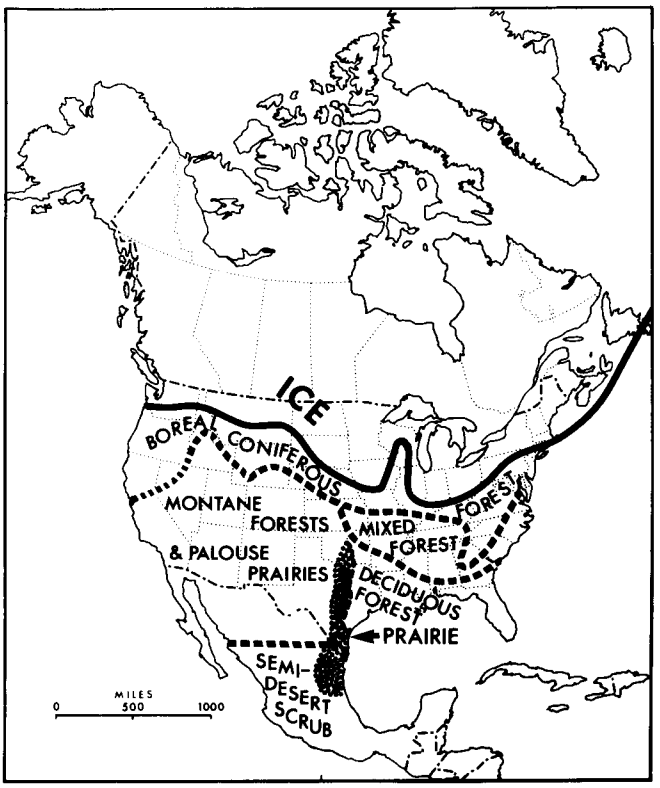


FIG. 1. Probable distribution of biomes and ice front during Wisconsinan maximum, northern refugia excluded. (Modified from Ross, 1970.)

Table I. Past vegetation in areas that are now prairie (adapted from Wright, 1970)

| Date (B.P.) | Place | Event or description |
|---|---|---|
| 16000 | Missouri | Mastodons, spruce forest |
| 11500 | North Dakota | Spruce forest |
| 10500 | South Dakota | Rapid destruction of spruce forest |
| 10000 | Saskatchewan–U.S. border | Spruce forest |
| 10000 | Kansas | Prairie began |
| 8-9000 | South Dakota | Prairie began |
| 8000-4000 | Prairie more widespread than now | |

numerous faunal studies have been completed in recent years and will be cited where appropriate, it is not my objective to present a complete catalog of distributional studies. Rather, I am concerned with the dynamic nature and general pattern of immigration to the prairies. Present day distribution in the prairies can be understood only in terms of an on-going process. Brooks (1958), for example, reports many isolated colonies of grasshopper species in the prairies which are probably survivors of a past favorable period when the range of the species was much greater. Subsequent deterioration of conditions cause widespread extinction except in the isolated colonies. Thus, species are constantly extending their range during favorable periods. It should be stressed that in the prairies, there are no physical barriers in the usual sense of mountains and oceans. An elevation of about 1000–3000 ft above sea level will be encountered, along with a harsh continental climate. Strong, drying

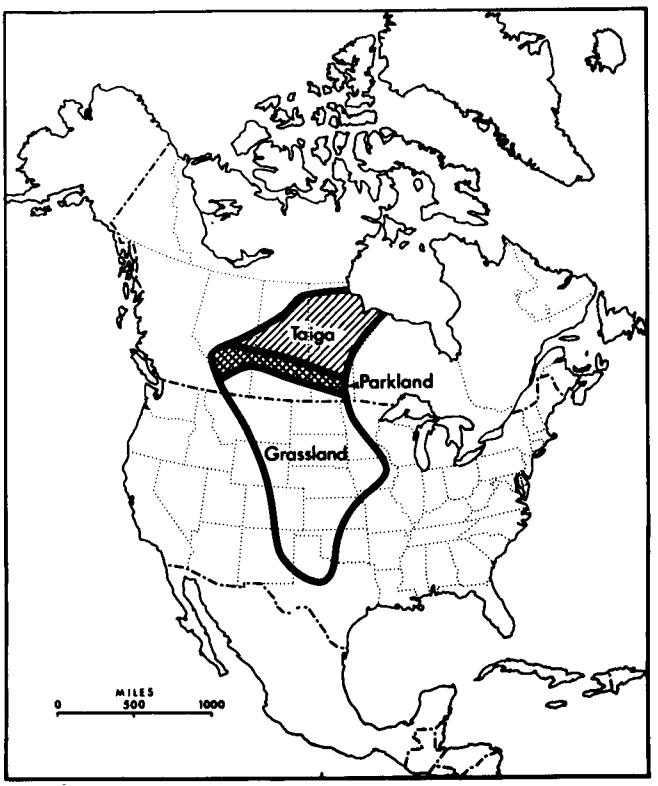


FIG. 2. Outline of present day Canadian "prairie" and distribution of major vegetation types.

winds, periods of drought, and temperatures ranging from +40°C to −40°C are to be expected. Thus during a period of favorable years nothing stops the forward movement of mobile species.

Aquatic organisms face more difficult problems, and what is true of Mollusca in the western interior (Clarke 1973) probably also applies to many insects, especially aquatic insects. Clarke (1973) estimates that among clams and snails, only 21 of 103 species studied now populate all of the area in which they would be capable of reproduction. Thus, we are dealing with a youthful environment that is ecologically only partially filled. The vast distances, the land, and the climate are barriers to many insects which could probably thrive if they could penetrate the area. Mayflies and stoneflies are probably good examples of this. Both have relatively poor dispersal powers, and their paths of immigration via water routes are often easily traced. However, lack of a water route often excludes a species from a potentially suitable habitat.

The rarity of endemics is explained by the youthfulness and the instability of the environment. While Nebeker and Gaufin (1967), for the 81 stoneflies of the family Capniidae in the Rocky Mountains, were able to identify six centers of speciation and the barriers which separated the centers, and to list the endemic species in each center, we find nothing similar in the prairies. For many Orders there appear to be no endemic species at all, and for other groups endemics constitute no more than 1 or 2% of the species in the group. While certain "rare" mayflies are common in prairie rivers, there are not endemics, but rather isolated colonies and last survivors of once widespread groups.

In order to obtain an overview of the temporal and spatial distribution of the prairie fauna, it is useful to review some of the major works on the prairie fauna which have appeared in the last 20 years.

Brooks (1960) treats 137 species of 26 genera of Elateridae from southern Alberta, Saskatchewan, and Manitoba. Present-day ecological distributions of species are discussed,

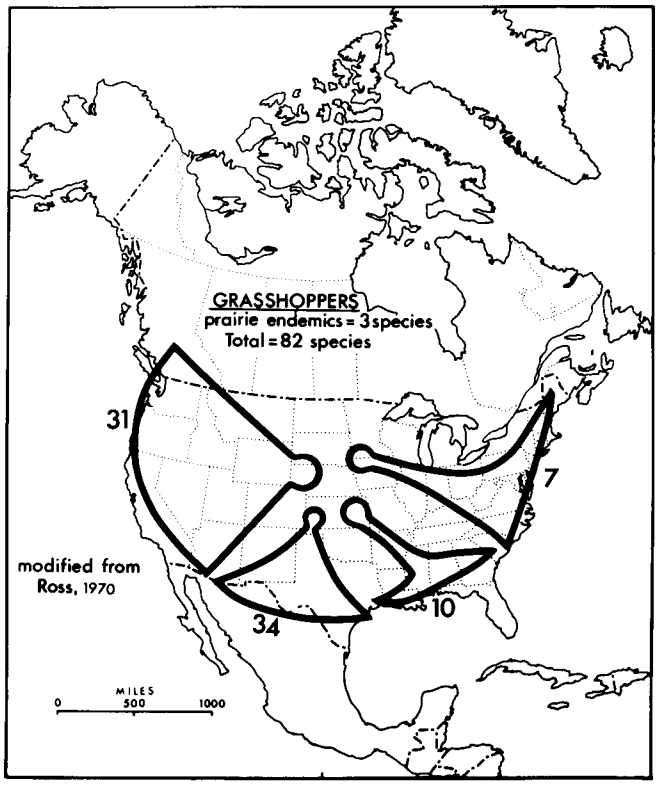


FIG. 3. Distribution of "prairie" grasshoppers, indicating the derived nature of the fauna and the lack of endemics. (Modified from Ross, 1970.)

and he found that distributions coincide closely with vegetation and soil zones. Different species are associated with ecological areas such as Boreal Forest, true prairie, and parkland. Not enough information is contained in this publication to generalize about the origins of the Elateridae of the prairies, but the list of species provides the means for searching the literature if one wished to study the distribution of each species.

Brooks (1958) also studied the grasshopper fauna of the same region. Again, individual species are correlated with characteristic vegetation and soil types. In this case, centers of origin are mentioned. Of the 87 species found in the area, about 20 appear to have originated from the Rocky Mountain region, about 15 are Boreal Coniferous forest species, while about 50 species are eastern or southeastern in affinity. Endemic species are not mentioned and it appears that there are very few or none in the Canadian prairies.

Nimmo (1971) lists several distribution patterns for Trichoptera which are of interest to this discussion. Of 113 species of Limnephilidae and Rhyacophilidae, about 25 species are very widespread and found throughout North America; 7 species range from Alaska southward and east to the prairies; 2 species appear to be prairie endemics; 9 species are eastern in origin. Nimmo's study concentrated on the mountains west of the current study area, and thus covers only a few of the eastern species that are found in the prairies. Smith (1975) found 38 species in 8 families in the Saskatchewan River in Saskatchewan. He postulates that four are of Alaskan-Beringia origin, four are great plains endemics, four are from the western mountains, 15 are of southeastern origin, while three are found throughout the continent.

Dosdall and Lehmkuhl (1979) studied the stoneflies of the entire province of Saskatchewan and found 41 species in 29 genera. Of these, we list three as great plains endemics, three from Alaska-Beringia, 12 from the southeast, and 10 from the western mountains. The

Cypress Hills are a special case, with 10 additional mountain species, most of which are not found elsewhere in the prairies. Dosdall and Lehmkuhl list one species as Sonoran, originating from the Colorado system in Utah. It is among the mayflies that the "Sonoran connection" is most clearly illustrated. Over a dozen species are found in both the Saskatchewan drainage and the Colorado drainage of the southwest interior of the U.S.A. (Lehmkuhl 1970, 1976*a*, *b*). Several mountain species of mayflies are found in the Cypress Hills and an additional three or four mountain or western species are found in the parkland and boreal region. Although the genera *Caenis* and *Callibaetis* are typical of prairie potholes, the species are not endemic to the prairies. Over half of the 50-plus species of Saskatchewan mayflies are eastern or southeastern in origin (Lehmkuhl 1976*b*).

Larson (1975) studied 145 species in 17 genera of Dytiscidae in Alberta, and concluded that most of the Alberta fauna is transcontinental. However, he also recognizes a mountain assemblage, a great basin assemblage, a great plains element (8 species, it is not stated if they are considered endemic), a few eastern species, and some species of possible Beringian origin.

From this brief survey of sources, a pattern emerges. As was stressed previously, the prairies contain few endemic species. Refugia suggested by all or most authors include Beringia (Alaska and Yukon); the Boreal East, the temperate southeast, the Rocky Mountains, and southwest interior. Finally, some species are found throughout the continent. These patterns will now be discussed individually.

**Widely distributed insects**. Among insects there are many species that have been called "good travellers" and "aerial plankton". These species have an extremely wide distribution. Aphids and small diptera can be carried long distances by the wind. Other insects of various sizes, and by various means, are able to travel vast distances by their own powers, and just as important, survive in the newly colonized area. Mason (1978) found that many of the Chironomidae of the Saskatchewan River are very widespread. Generalizations are difficult to make about Chironomidae because of the paucity of species level information, but typical records for a species are "Idaho, California, Saskatchewan, Quebec and Florida". Of the 36 species of the tribe Chironomini found in the Saskatchewan River, at least six are holarctic and one species is recorded from the Ethiopian region.

Extensive records are available for the bug *Lygus lineolaris*, a species distributed from coast to coast and from Alaska to Central America (Fig. 4). As part of another study (Steeves *et al.*, 1979) we have recorded the lacebug *Corythuca cydoniae* and the Negro bug *Corimelaena pulicaria* from the Canadian prairies, and while published records are more sparse than for the *Lygus* bug, it is probable that these species would fall in the "widespread" category.

There are probably dozens if not hundreds of prairie species with this widespread type of distribution, although the general impression gained during this review would indicate that the total would be less than 10% of the fauna.

**Colonizers from the southeast**. If one examines a distribution such as that for *Sialis velata* (Fig. 5) and compares it with the biome and glacial front map (Fig. 1) for the period of glacial optimum, it seems clear that such species survived the glacial period in the southeastern United States. *S. velata* at present does not penetrate far into the true prairies, and is absent from the pacific northwest of the United States (Evans 1972). The species is widely distributed in the eastern U.S.A. It can be assumed that as the glacier retreated, *S. velata* moved from the southeast to the north and northwest, eventually reaching Manitoba, Saskatchewan, Alberta, and British Columbia.

This type of pattern is one of the most common for insects of the Canadian prairie, and it is generalized in Fig. 6. As previously mentioned, the pattern is well known for mayflies, stoneflies, grasshoppers, and caddisflies. It is probably safe to say that the greatest percentage of the fauna of the prairies is southeastern in origin. These species are typically inhabitants of parklands and transition zones, or in the case of aquatic insects, the Saskatchewan River, including areas where it courses through the arid prairies. A few insects from the southeast inhabit very dry situations in the prairies. Of the three species of ant lions in Saskatchewan, all of which seek out arid areas or sand deposits, one is from the southeast (*Cryptoleon*

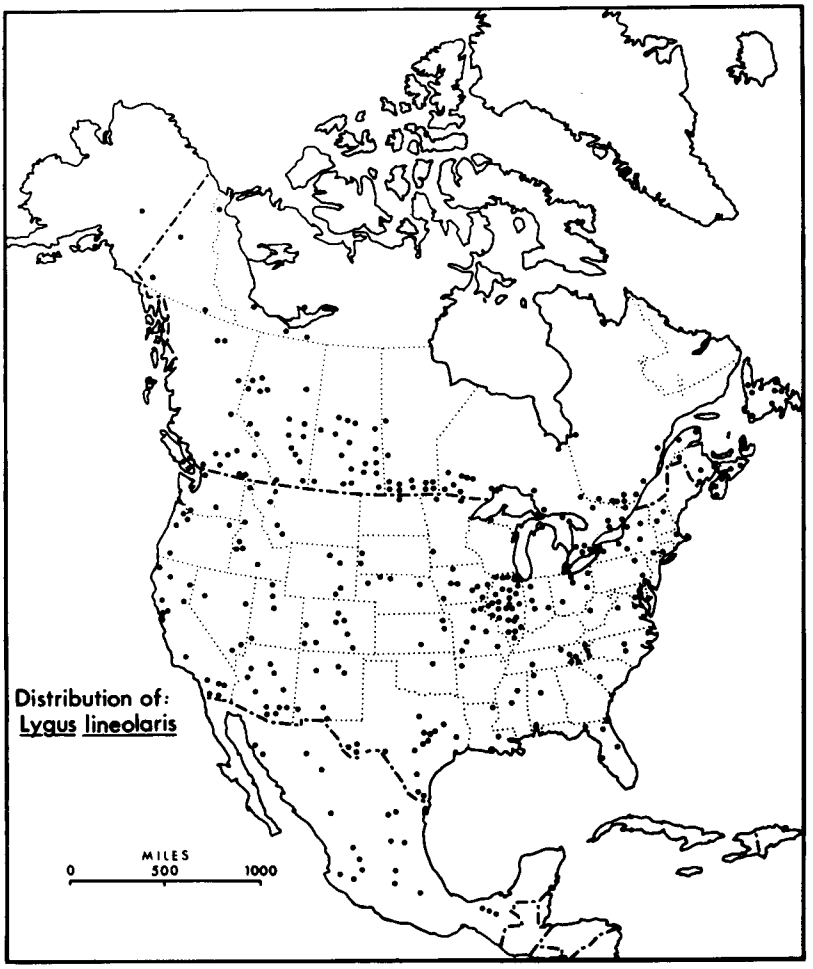


FIG. 4. A widespread type of distribution as illustrated by the true bug, *Lygus lineolaris*. (After Kelton 1975.)

*signatum*), one is from the southwest and south (*Hesperoleon nigrilabris*), and one is temperate transcontinental (*Hesperoleon abdominalis*) (Banks 1927).

Among aquatic insects such as mayflies and stoneflies which have poor powers of dispersal, the route from the southeast takes on another aspect. Figure 7 shows a distribution in the Saskatchewan drainage and the Mississippi drainage that is typical of a community of aquatic species, and also the present day barrier that exists between the drainages. Colonization of the Saskatchewan system by these poor travellers is explained by glacial river patterns. The Saskatchewan drainage once curved south and flowed into the Mississippi system, and at this time a community of mayflies presumably invaded the Saskatchewan drainage. Subsequently the Saskatchewan drainage turned north to Hudson Bay, and now the two populations are isolated (Lehmkuhl 1972).

**Boreal and northern transcontinental.** Related to the previous pattern is that of boreal species. While not necessarily restricted to a specific boreal host plant, the insects are nonetheless dominantly boreal. The heavy line in Fig. 8 is meant to represent a "best fit" for this type of pattern. Many authors (e.g. Brooks 1958) recognize "boreal" species which are associated with spruce dominated forests and differentiate them from temperate species such as shown in Figs. 5 and 6. The records south of the heavy line in Fig. 8 probably

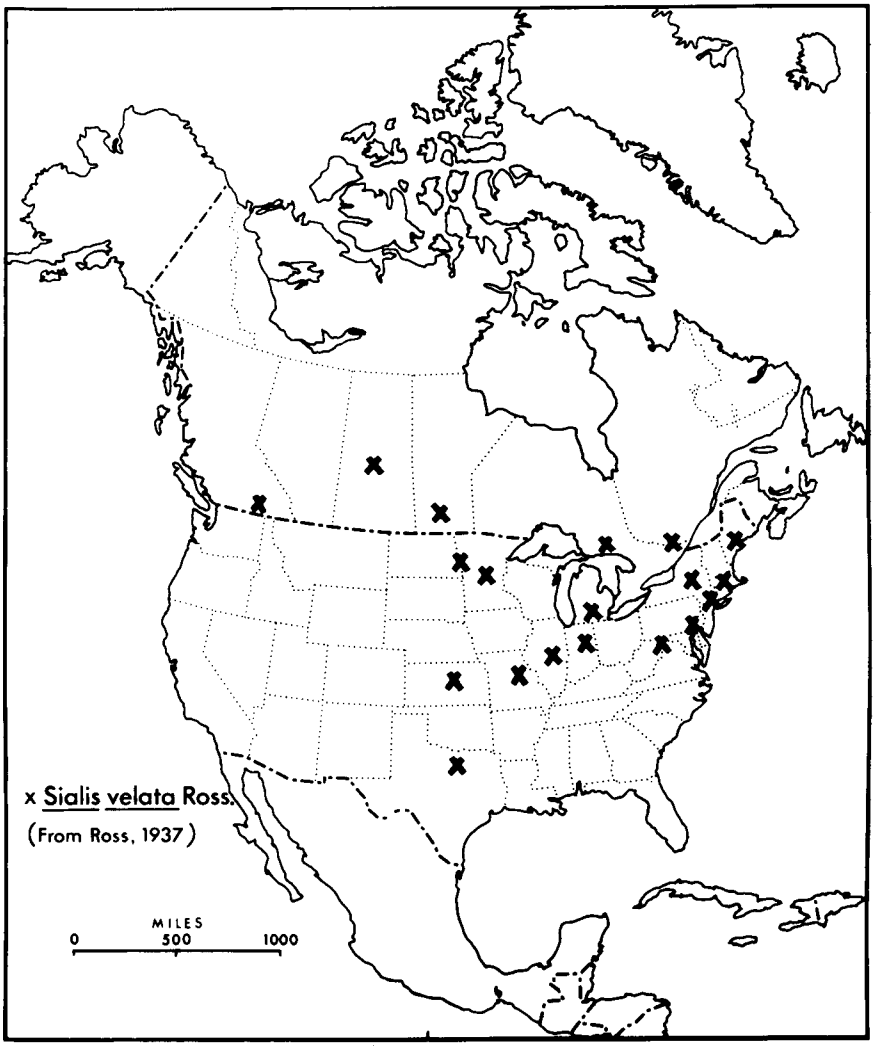


FIG. 5. Distribution of *Sialis velata*, a species with a southeast origin. (Data from Ross 1937.)

represent isolated relict populations (e.g. the record from the Black Hills of South Dakota, an area of Boreal type forest surrounded by arid prairie). A number of common prairie ant species (e.g. *Formica podzolica*, *Formica sanguinea subnuda*) appear to be boreal transcontinental (Gregg 1963), as are many aquatic beetles (Larson 1975). *Lygus rubidorsus* and *L. rubroclarus* (Fig. 8), while recorded from the U.S.A., fall primarily inside the heavy line.

In many cases where a distribution is transcontinental, it appears that east-west species pairs, or at least recognizable morphs, have differentiated, presumably when eastern and western populations of boreal species were isolated by advancing ice from the north and unsuitable non-boreal habitat to the south. This has been mentioned by Ricker (1946) for stoneflies and Larson (1975) for beetles and is well illustrated by the mayfly *Hexagenia limbata* in Saskatchewan (Fig. 9). In the Saskatchewan River at Lemsford Ferry and other sites, a clearly marked morph is almost identical with the form known from Utah and other southwestern regions. In the boreal forest of Saskatchewan, notably from the La Ronge region, the markings are those of an eastern form. These have variously been recognized as valid species or subspecies, but since intergrades are known, they are now viewed to be a

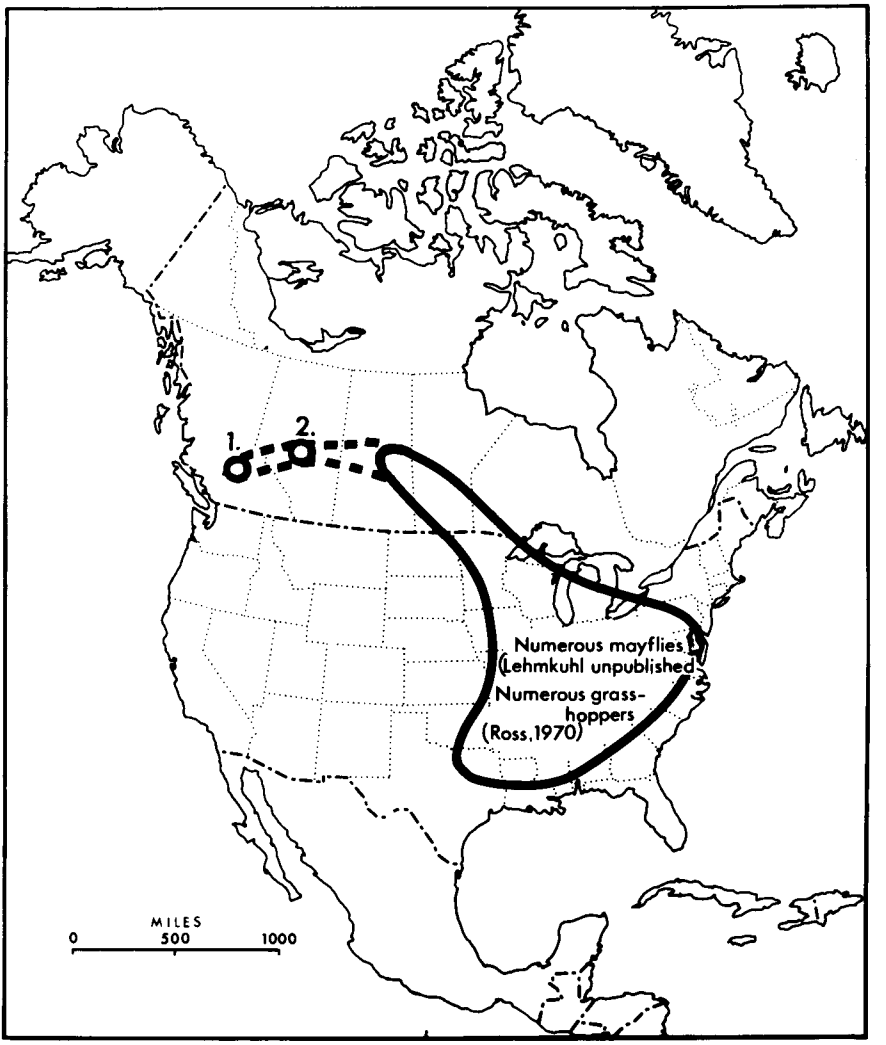


FIG. 6. Generalized distribution of colonizers from the southeast, one of the most common patterns in the prairies. 1. *Sialis velata*; 2. *Siphlonurus alternatus*.

single species. While the species name must be the same for both morphs, a knowledge of past origins and glacial history aids in understanding the taxonomy of the species.

**Insects with a northern origin**. Also ranging into the prairie region are a number of species which are northern and holarctic. In North America, these species are sometimes transcontinental with a distribution resembling Fig. 8, just discussed. For these species there is reason to believe that they passed the glacial period in the Alaskan-Beringia refugium (Wood, pers. comm.). Larson (1975) mentions examples among the Dytiscidae which may be of this type. The mayflies *Metretopus borealis* and *Ephemerella aurivilli*, and several stoneflies, probably also spread from the Beringia refugium, as indicated in Fig. 10. These species just mentioned are found in the Saskatchewan River system. Examples among the Trichoptera can be found in Lehmkuhl and Kerst (1979).

**Western mountain origin**. A number of species from the western mountains range into suitable habitats in the prairies. Most notable is the fauna of the Cypress Hills, a range of

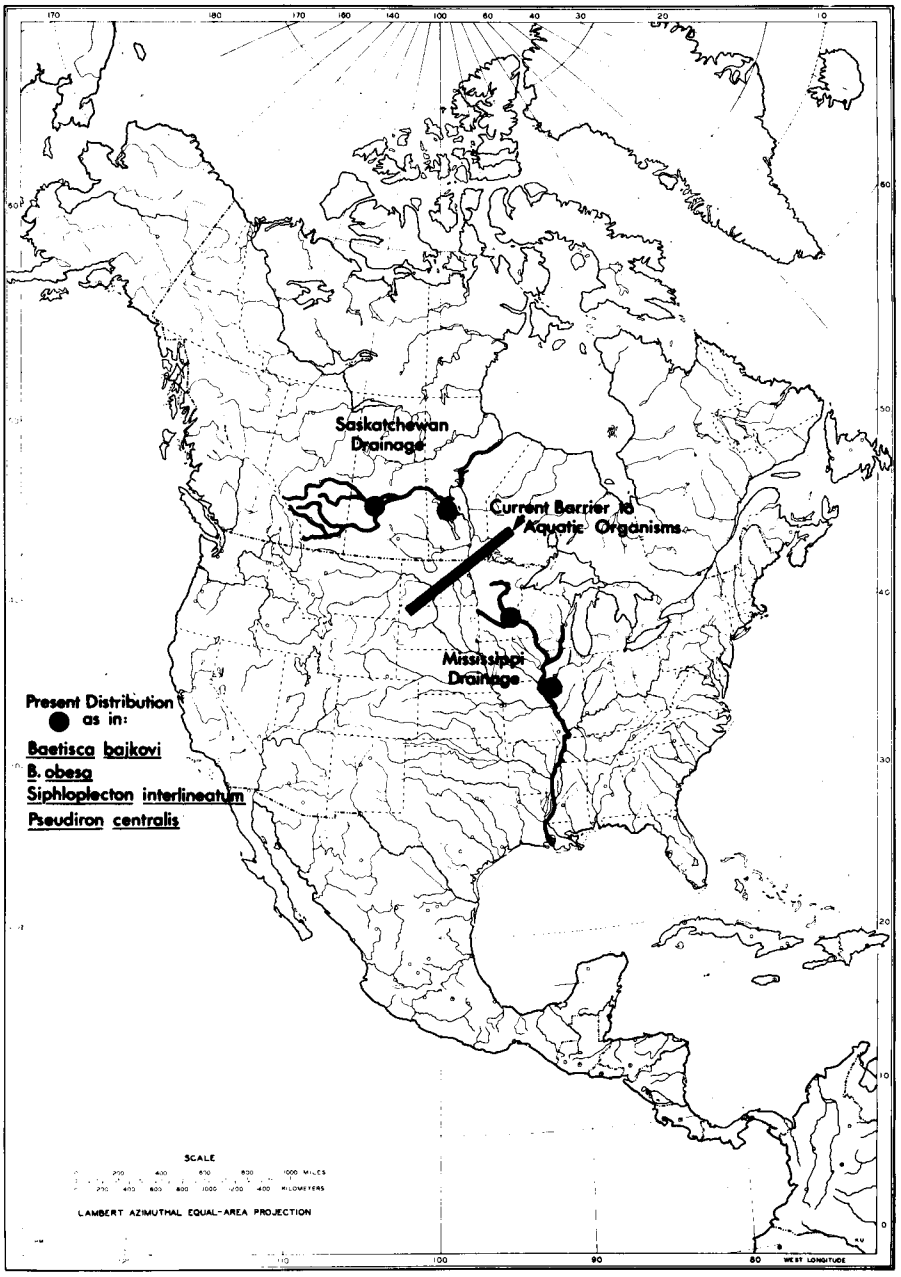


FIG. 7. Disjunct distribution of mayflies in the Saskatchewan and Mississippi drainages.

high hills in southwestern Saskatchewan and southeastern Alberta. These hills were not ice covered during the last glaciation. Dosdall and Lehmkuhl (1979) found 10 species of stoneflies (Table II) in the Cypress Hills, and all but the very widespread *Zapada cinctipes* have a distribution resembling one of those shown in Fig. 11. Some Rocky Mountain species extend into boreal Saskatchewan and southern Manitoba.

A similar type of distribution is known for the mayflies *Ameletus oregonensis* and *Epeorus longimanus* (the latter ranging to the Black Hills of South Dakota) (Lehmkuhl unpub.) and the bugs *Lygus convexicollis* Reuter, *L. shulli*, and *L. desertinus* (Kelton 1975).

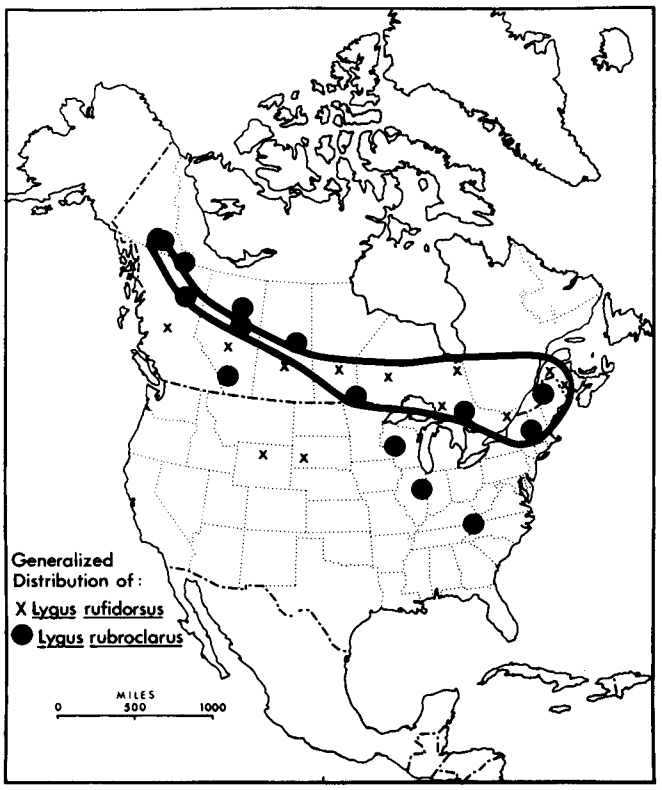


FIG. 8. Boreal transcontinental type of distribution.

It seems clear that at the time of maximum glaciation these species were pushed south in the western mountains, and moved north and east as the glacier retreated.

**The sonoran element**. A faunal association that is most intriguing is the community shared by the Saskatchewan River and the Green River of the Colorado drainage in Utah. Dosdall (1975) and Larson (1975) mention examples among stoneflies and dytiscid beetles, and the association is well illustrated by the mayflies (Lehmkuhl 1970, 1976*a*) and Fig. 12. Mayflies have poor powers of dispersal, yet the present day communities are separated by nearly 1000 miles of arid land. It appears that the Saskatchewan and Green River communities are survivors of a once much wider distribution of these species. That the species involved were once found throughout the many interlying tributaries of the Missouri system is supported by recent collections by Newell (personal communication) from the Yellowstone River.

**Prairie endemic species**. For insects the list of species that have evolved in the prairies and are restricted to them appears to be very short. For example mayflies that are typical of prairie potholes, members of the genera *Callibaetis* and *Caenis*, are very widespread and adaptable forms, and certainly not endemic. While Smith (1975) and Dosdall and Lehmkuhl (1979) mention two caddisflies and three stoneflies respectively that are great plains endemics, this interpretation may not withstand critical examination since these species are from large, warm, silty rivers and are not vitally linked to the prairies. Figure 13 shows the distribution of two *Lygus* spp. that might be considered "prairie species". Examination of the map shows that these insects are found in parklands, coniferous forests, and even mountain foothills as well as the prairies. Other data show that the distribution of the *Lygus* bugs in Fig. 13 are determined more by the host plant distribution than by an affinity for the prairies. Thus, the search for true prairie endemic insects has met with little success.

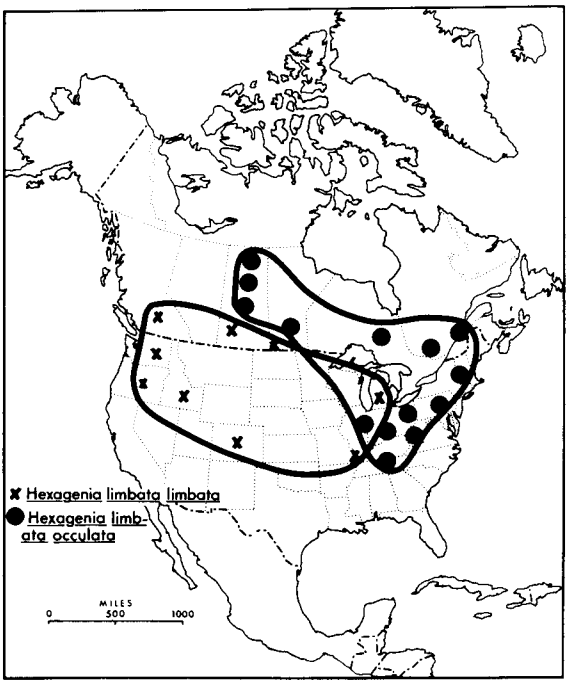


FIG. 9. Distribution of "species pairs" in the prairie species of *Hexagenia*.

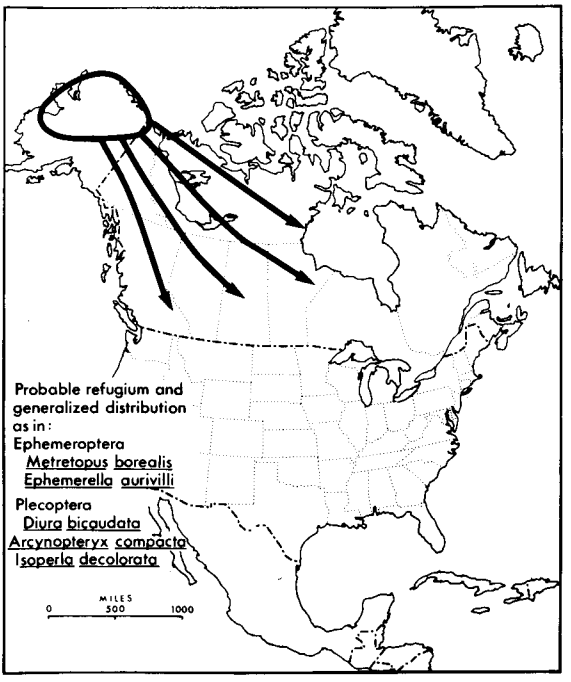


FIG. 10. Species found on the prairies which invaded from the Beringia refugium.

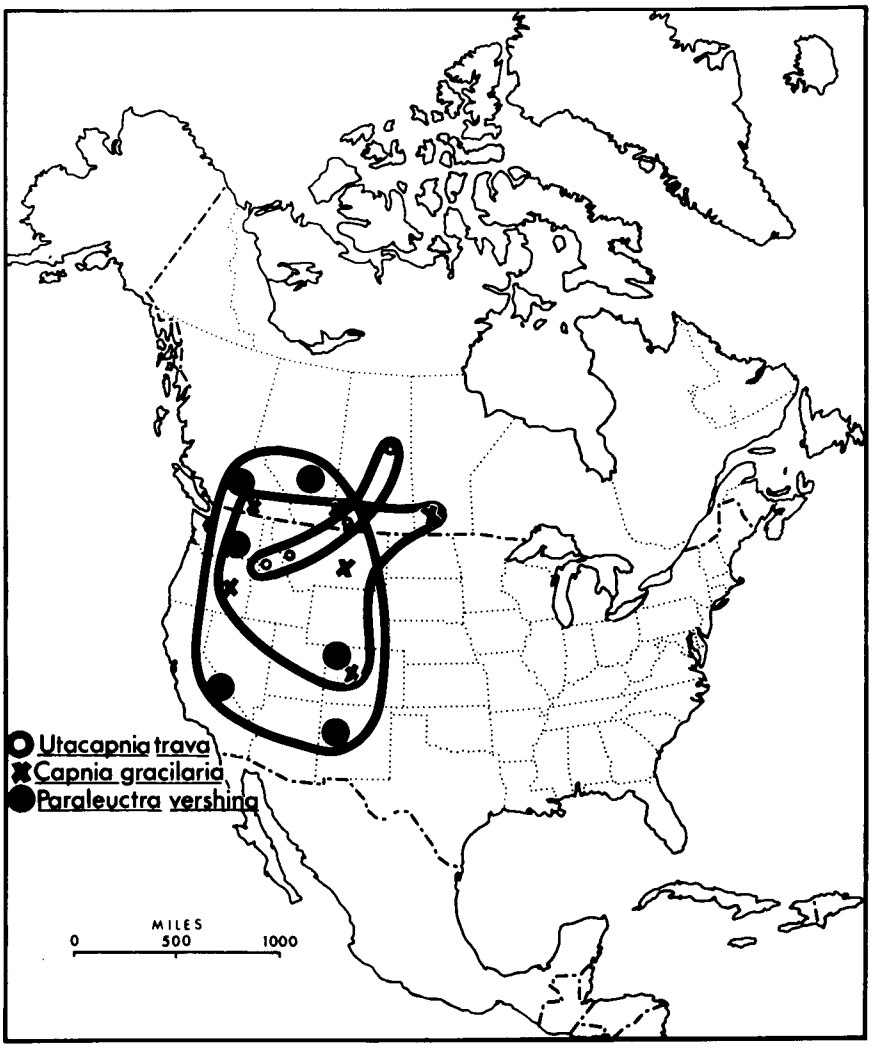


FIG. 11. Western and mountain species which range into the prairies as illustrated by the Plecoptera.

## Discussion

Munroe (1956) in his review of Canada as a habitat for insects pointed out that although extensive collections had been made in the prairie, there was little knowledge of the detailed distribution and composition of the fauna. He felt at that time that for most groups both collecting and taxonomy were inadequate to undertake a detailed analysis of distribution and zoogeographical origin. Much progress has been made since that time, and we now have much more information than can be included in a paper such as this. This paper does not attempt to do more than suggest basic patterns supported by selected examples.

Because of the history of the prairies, particularly the relatively recent glaciation, it appears that the best approach to prairie zoogeography is to consider colonization to be a dynamic and flowing process that even now is actively in progress. Therefore it is probably best to search for patterns of movement rather than static categories or types of distribution.

Finally, one must question the concept of "Canadian Prairies" as to whether they are too artificial a unit to give rise to meaningful generalization. It has been stated that this is a transition region, ranging from true prairie to coniferous forest. Therefore, how valid are

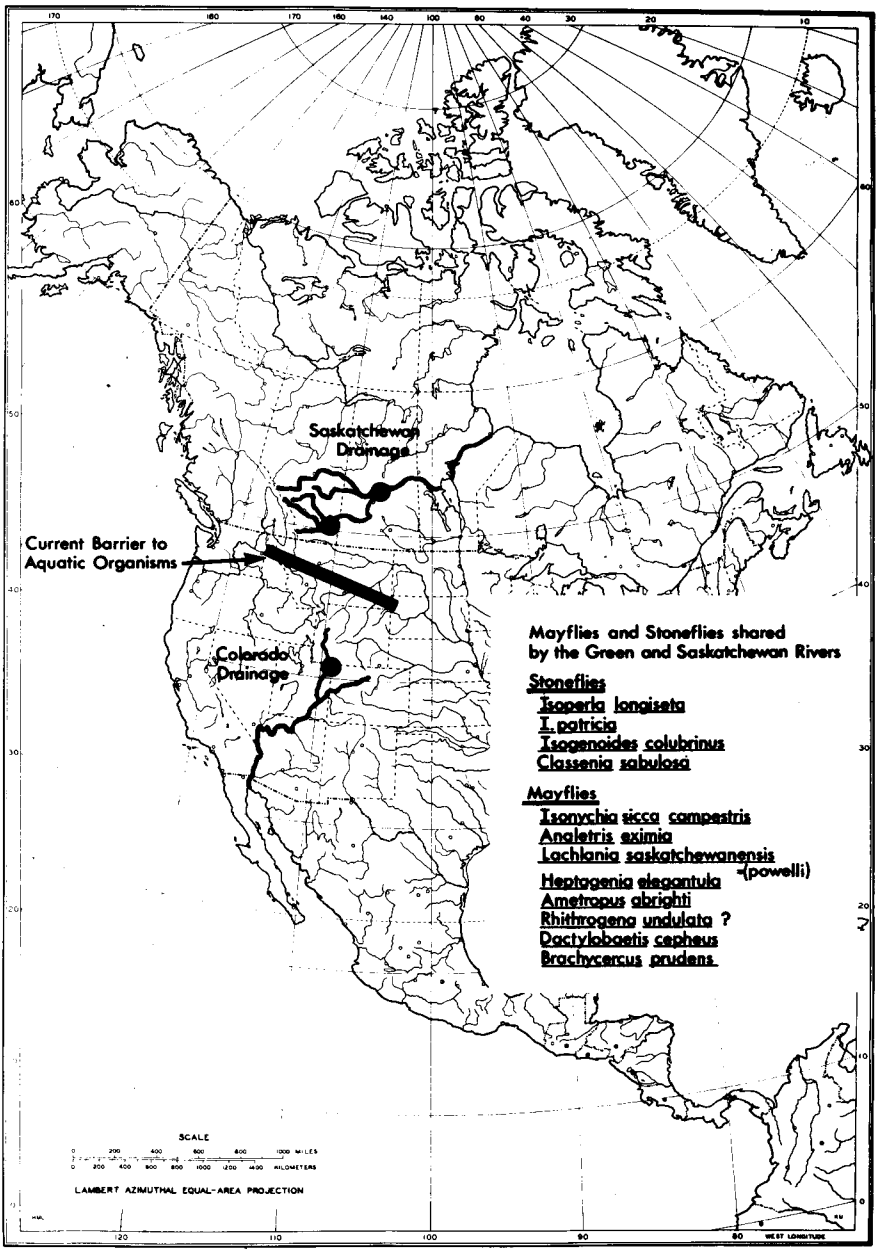


FIG. 12. Disjunct distribution of mayflies and stoneflies in the Saskatchewan and Colorado drainages.

the conclusions in this paper? To check, comparisons have been made with two studies which dealt with regions of true prairies to the south: Ross (1970) for grasshoppers in the Central Great Plains of the U.S.A. and Wheeler and Wheeler (1963) for the ants of North Dakota. After examining their conclusions, there appears to be no reason to modify the views on the zoogeography of the Canadian prairies as expressed here. In all cases, there was a lack of endemic species and a recent post-pleistocene recruitment of species from refugia to the east, west, and north.

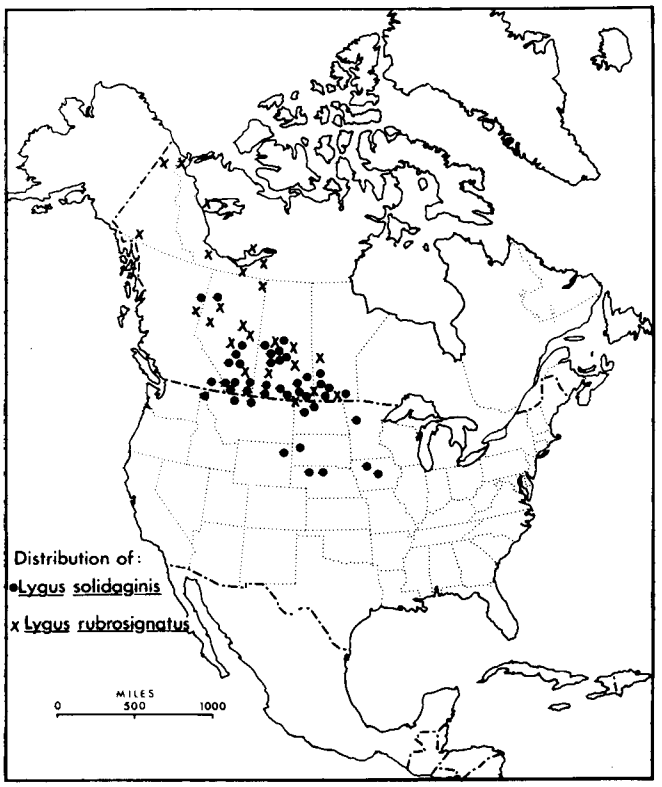


FIG. 13. Distribution of two "prairie" species, showing that they range into many habitats and are not true prairie endemics.

Table II. Stoneflies of the Cypress Hills, southwestern Saskatchewan (from Dosdall and Lehmkuhl 1979)

| Cypress Hills | Boreal Saskatchewan | Other distribution |
|---|---|---|
| *Capnia gracilaria* | No | British Columbia, Manitoba, Oregon, Montana, Utah |
| *Isocapnia missourii* | No | Utah, Montana |
| *I. crinita* | No | Colorado, Utah, Montana |
| *Utacapnia trava* | Yes | Montana, Idaho |
| *Podmosta delicatula* | No | British Columbia, California, Colorado, Utah |
| *Zapada cinctipes* | Yes | Alaska to California, Manitoba, S. Dakota, Ohio, Montana |
| *Paraleuctra vershina* | No | British Columbia, Alberta, California, Washington, Colorado, Montana, Utah |
| *Suwallia lineosa* | No | British Columbia, Alberta, Colorado, Montana, Oregon, Washington, Wyoming |
| *Hesperoperla pacifica* | No | British Columbia, California, New Mexico, Alberta, South Dakota |
| *Skwala parallela* | Yes | British Columbia, Oregon, California, Utah |

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