# ROBBER FLIES (INSECTA: DIPTERA: ASILIDAE) OF THE MONTANE CORDILLERA ECOZONE

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## **ABSTRACT**

Robber flies are predators that kill other insects with paralyzing saliva injected through the proboscis. Over 7000 species of the family are described worldwide; the Montane Cordillera Ecozone supports about half the Canadian fauna and more species remain to be recorded. A checklist and a systematic overview of the six subfamilies and their 101 species (8 of which are listed as potentially endangered, threatened, or vulnerable) and an analysis of their biogeographic elements are presented. The fauna is overwhelmingly represented by species restricted to the western mountains, plateaus and valleys from the Rocky Mountains westward. Sixty-three species of Cordilleran origin (62%) are recorded. Intermontane species total 18 species (18%) and there are 7 (7%) Boreal species, including two with holarctic ranges. Six species (6%) are Western, 1 (1%) is Transition, and 5 (5%) are Austral. One (1%) is Eastern Beringian. Ecozone habitats are divided into subalpine forest, montane forest and grasslands and the typical species inhabiting each are listed. Stress on robber fly populations is discussed under the headings of grassland destruction, logging, and climate change. Recommendations for inventory and taxonomic research are briefly discussed.

## INTRODUCTION

The Asilidae contains over 7000 described species worldwide (Geller-Grimm 2008), and about 200 in Canada (McAlpine 1979). Our knowledge of the Canadian fauna as a whole is only fair, and for this reason it is difficult to put the fauna of the Montane Cordillera Ecozone into perspective. Although in North America the Asilidae is predominantly a southern family, especially diverse in arid and semiarid environments, over the years specimens have been rather frequently collected in the ecozone. With its dissected physiography and extremes of elevation, the Montane Cordillera contains a wide variety of robber fly habitats, from many in grasslands to those in subalpine forests. The diversity of asilids present reflects this richness of habitats, and the ecozone supports more species than any other in Canada. The species total for the Montane Cordillera now stands at 101, but it is certain that more remain to be recorded. Thus, the Montane Cordillera supports about half the Canadian species of Asilidae.

Nevertheless, little has been published on the robber flies of the Montane Cordillera. Revisions of large genera such as *Cyrtopogon* (Wilcox and Martin 1936), *Efferia* (Wilcox 1966), *Lasiopogon* (Cole and Wilcox 1938; Cannings 2002), and *Dioctria* and related genera (Adisoemarto and Wood 1975) included references to species of the ecozone. The various taxonomic works of Curran, for example, the designation and summary of the genus

Eucyrtopogon (Curran 1923) also are relevant. Foxlee's intensive collecting around Robson in the Columbia Valley of the West Kootenays resulted in specimens (Foxlee 1942) that are still the main source of our knowledge for that region. Adisoemarto (1967), in his overview of the Asilidae of Alberta, included species known from the narrow, mountainous part of the ecozone in that province. Cannings (1994) updated the species list for the region and published (Cannings 1989) an account of the species found in a grassland typical of mesic sites at low elevations in the southern Okanagan Valley. He analysed the geographic variation in Rhadiurgus variabilis over its holarctic range and documented its distribution, including its range in the ecozone. The fauna is now moderately well-known for the Okanagan Valley, where considerable collecting in the grasslands has occurred, but for the rest of the ecozone, especially the northern areas, the family has been little studied.

Asilids are predatory flies that as adults pursue other insects (usually flying ones), seize them, and kill them with paralyzing saliva injected through the hypopharynx (tongue). The liquefied contents of the prey are then sucked up through the proboscis (Wood 1981). The morphology of the adult fly (especially the prominent eyes, the mouthparts, and the raptorial legs) reflects this mode of prey capture and feeding.

In temperate climates, robber flies usually hunt in open areas where there is plenty of light, and are most active in the warmest parts of the day. Overcast skies greatly curtail their activity. Different genera, and often different species within a genus, have different hunting behaviours and preferences for perching sites.

There is usually little obvious difference between the sexes, except for the genitalia (the morphology of which is sometimes striking, as in *Efferia*), although females tend to be larger than males and often have broader abdomens. Colour patterns sometimes differ between males and females; in Montane Cordillera species this is particularly evident in *Cyrtopogon bimacula* (Walker), *C. dasyllis* Williston, and *C. dasylloides* Williston in which the males have prominent, dark marks on the wings. Other secondary sexual characteristics occur in males; some that are displayed in species found in the Montane Cordillera include the expanded silver abdominal apex in *Nicocles*, the striking white abdomens of *Efferia*, the tufted golden abdominal hairs of *Cyrtopogon auratus* and the tarsal ornamentation of some other *Cyrtopogon* species. Males of these latter species signal with their decorated legs during mating displays.

Records of prey taken by Asilidae indicate that they are often opportunistic predators, feeding upon any insect that they can subdue and kill. However, some species show a strong preference for prey from one or two insect orders (Wood 1981). In many instances this may simply reflect the availability of prey in the habitat where the particular robber fly lives.

Detailed life-history studies of robber flies are rare. Melin (1923), studying Asilidae in Sweden showed that in northern species, at least, the larva is the overwintering stage and the pupal stage lasts two to six weeks. He estimated that the life cycle of *Laphria* species was at least three years and that of *Lasiopogon cinctus* (Fabricius) was at least two. Both these genera are common in the Montane Cordillera Ecozone. It is likely that larval growth is faster in warmer regions and many species probably live only one year (Theodor 1980).

Larvae are predators of the eggs, larvae and pupae of other insects in the soil or in rotting wood, although in a few species studied the immature larvae, especially, are ectoparasitic on their hosts (Wood 1981). Knutson (1972) has reviewed the literature on this subject.

The world genera of Asilidae are examined by Hull (1962) and the North American genera are keyed by Wood (1981), although these treatments are out-of-date. Wood (1981) gives a summary of the morphology, biology, and classification of the North American fauna. The higher classification of the family is still in some turmoil, and a lack of phylogenetic studies has hindered understanding of the relationships of taxa at all levels. The tentative scheme of Artigas and Papavero (1988) for the New World fauna was adopted by Fisher and Wilcox (1997) for a draft Nearctic catalogue of the family, and is also used here, although it does not conform to the most recent phylogenetic hypotheses (Dikow, 2009b). More recent systematic treatments of the family have been published (Dikow 2209a, b, Fisher ) but a satisfactory higher classification is not yet established.

A web site on the internet devoted to the Asilidae (Geller-Grimm 2008) covers topics from morphology to behaviour and phylogenetics.

#### **Systematic Review**

A systematic checklist of the 101 species (8 of which are listed as potentially endangered, threatened, or vulnerable) including their biogeographic elements, is included as Appendix 1. A brief review of the major taxa of the ecozone with notes on habits is presented below.

#### SUBFAMILY LEPTOGASTRINAE (2 species, 2%)

These delicate little flies are represented by two species, *Leptogaster arida* and *L. fornicata*. Both are seldom collected, and their distributions are poorly known. *L. arida* is the more widespread, living across the southern part of the province from Vancouver Island eastward; *L. fornicata* is restricted to Interior valleys. They are extremely slender, long-legged, almost bare species that hover among the grasses of grasslands and dry forests in the southern valleys of the ecozone.

# SUBFAMILY DASYPOGONINAE (9 species, 9%)

The species of Dasypogoninae are distinguished by an enlarged or twisted spine at the apex of the fore tibia. The nine species in the Montane Cordillera are small to medium-sized flies. *Comantella pacifica*, a species known only from mesic grasslands in the Okanagan Valley, is unique in its flight period. For an asilid in Canada, it flies unusually late into the autumn (late October) and is the first species to appear in the spring (late March). There is evidence that adults overwinter in protected places. *Cophura albosetosa, C. brevicornis*, and *C. vitripennis* are small, dark species active on the forest floor of open woods in the southern part of the ecozone. The silvery little *Lestomyia sabulona* sits on the bare ground in grasslands of the southern Okanagan. The genus needs revision, and it appears that the Canadian species is actually undescribed. *Nicocles* is a genus of beautiful flies with brown-spotted wings and in the male, with brilliant silver terminal abdominal segments. *Nicocles canadensis, N. dives, N. pollinosus*, and *N. utahensis* are all species of western montane forests and grassland edges. This genus also sorely requires systematic attention.

# SUBFAMILY LAPHRIINAE (23 species, 23%)

The 23 robber flies of the Laphriinae in the Montane Cordillera are forest species whose larvae develop in rotting wood. Many of them are large and colourful and mimic bees and wasps. Adults perch on leaves or logs, stumps and tree trunks and wait for prey to fly by. Beetles are a

favourite prey of some species. Andrenosoma fulvicaudum is a black and orange fly that ranges across the continent south of the northern forests. It is attracted to forest fires; the females lay eggs in burned trees where the larvae prey on metallic woodboring beetle (Buprestidae) larvae (Fisher 1986). Pogonosoma ridingsi, another black species, is a widespread cordilleran asilid. Laphria is the largest genus in the Montane Cordillera with 21 species. Laphria s. str. is a group of bumblebee mimics with bright fuzzy yellow and black or yellow, red and black bodies. Cordilleran species include L. astur, L. asturina, L. columbica, L. fernaldi, L. partitor, L. sackeni, L. insignis, and L. posticata are boreal species. The rest of the genus can be divided into three other distinctive groups based on genitalic and other characters.

*Laphria asackeni* and *L. vultur* are spectacular, large flies clothed with glowing orange-gold pile. *L. asackeni* is the more common, widespread species, but both are restricted to the western mountains. *L. janus* is a common Boreal species.

A group in which the males bear paired protuberances on the sixth abdominal segment contains the widespread black-bodied *Laphria franciscana*, a Cordilleran species. Two much rarer species, both with golden yellow abdomens, are *L. index*, an Austral species and *L. scorpio*, the only species in the Transitional element in the ecozone.

A third group (*Choerades*) has distinctive lamellae formed from fused bristles in the male genitalia. *Laphria aimatus*, *L. felis*, *L. ferox*, *L. milvina*, and *L. vivax* are restricted to the mountain forests of western North America; *L. sadales* and *L. gilva* are boreal. The latter species is one of two holarctic asilids; it ranges from Scotland to Siberia, from Alaska to Labrador.

## SUBFAMILY STENOPOGONINAE (42 species, 41%)

Species of this subfamily lay their eggs in the soil and the larvae develop there. The group is dominated in the Montane Cordillera by the large holarctic genus Cyrtopogon, with 19 species in the forests of the region. This is 27% of the Nearctic Cyrtopogon fauna, which is overwhelmingly western in distribution. Indeed all, but one, of the Montane Cordillera species is Cordilleran in origin. The exception is C. bimacula, a very common Boreal species with striking dark spots on the wings; in the western mountains it is largely a subalpine species. With their fuzzy yellow and black abdomens, C. dasyllis and C. dasylloides look a bit like Laphria species; the wings of the males have dark brown patches. The mostly subalpine C. auratus and C. aurifex also have thick, tufted, golden hair on the abdomen; the former is widespread in the south, the latter is restricted to the Cascade Mountains in the extreme southwestern corner of the ecozone. The beautiful chocolate-winged C. princeps has a similar range in the Cascades. Cyrtopogon banksi, a small black and grey species of low and mid elevation forests, is a widespread species in the ecozone. Cyrtopogon montanus, densely black haired, is the most often encountered species in the dry forests of low and medium elevations throughout the region; the closely related C. inversus, with its striking white-haired hind femora, appears in Ponderosa Pine and Douglasfir woods in the spring. Cyrtopogon willistoni is common in the moister, higher elevation grasslands across the Montane Cordillera. The male has beautifully decorated legs that it uses in mating displays; the fore tarsi are densely silver-haired and the mid tarsi are tipped with a fanshaped tuft of black setae.

*Eucyrtopogon* contains 12 named grassland and forest species restricted to the West, seven of which live in the Montane Cordillera. It is badly in need of revision and there are certainly a number of undescribed species in the ecozone. The wings are brown-spotted in both sexes. Some species are notable for late or early seasonal activity. For example, *E. calcaratus* has been

collected on 23 November in Vernon and 23 January in Penticton. *Coleomyia hinei, C. setigera, Heteropogon senilis, Holopogon albipilosus, H. stellatus*, and *Callinicus pollenius* are species of forest openings and grassland edges. *Callinicus* is an uncommon, beautifully yellow-banded wasp mimic.

Myelaphus lobicornis lives in intermontane grasslands from southern British Columbia to California and Utah. It is known from only two grassland sites in the Montane Cordillera, one at Penticton, the other at Dutch Creek in the Rocky Mountain Trench. At the Penticton site it flies only around Common Rabbit-brush (Chrysothamnus nauseosus) in June. With its almost hairless body, dark head, thorax and wings, elongate antennae, red abdomen and yellow legs, it resembles a wasp. Dicolonus nigricentrum and Dioctria henshawi are grassland or dry forest edge species at the northern limit of their range and rarely collected in the ecozone. They are known only from the Okanagan Valley. Dioctria pusio and Eudioctria sackeni are tiny species that hunt from leaves and twigs in forest openings and edges at low and mid elevations. The latter is particularly common and widespread across the southern part of the Montane Cordillera and ranges south to California. It has two striking colour morphs; in the male of the more common one the wings are orange basally and grey apically.

Stenopogon inquinatus, big and usually rusty coloured, is one of the most common and noticeable species in the Montane Cordillera. Hunting a variety of prey in habitats ranging from arid sagebrush steppe to open Douglas-fir forests, it is always an impressive sight. I have frequently seen it feeding on grasshoppers larger than itself, and in one case, a dragonfly, Gomphus graslinellus, with a mass many times that of the robber fly, had been killed on the ground. A close relative, S. rufibarbis, is smaller and more rufous in colour; it is common and widespread in the moister, upper grasslands. Scleropogon neglectus, grey, and similar in size and shape, is also common on a wide range of grasslands. Much rarer, and known from only a handful of localities in the Okanagan and Thompson valleys, Ospriocerus aeacus is a redabdomened, black-winged, grassland denizen that ranges over western North America and into Mexico. Willistonina bilineata inhabits open woods and grassland borders, but has been collected only two times in the region.

## SUBFAMILY STICHOPOGONINAE (6 species, 6%)

The Stichopogoninae, characterized, among other things, by a broadened face above the antennae, is dominated in the Montane Cordillera by the genus Lasiopogon. These are small grey or brown flies that hunt from the bare ground or from rocks and logs. Larvae develop in the soil. All, but one, of the species in the region are Cordilleran in origin, and all are at home in the mountains of the ecozone, although just to the south in the Columbia Basin several species live in grasslands. Lasiopogon prima is an East Beringian species, being most closely related to the Asian fauna. It ranges through Alaska and the Yukon, reaching the Arctic Ocean, and occurs in the Montane Cordillera only in the eastern foothills of the Rockies in Alberta. Lasiopogon aldrichii and L. monticola are found mostly along trails in spruce and subalpine fir woods across the southern mountains in the ecozone. Lasiopogon cinereus and L. trivittatus are found along streams; the former ranges as far north as the Skeena River, northwest of the ecozone, the latter lives on the eastern side of the Rocky Mountains and spills out onto the prairies. The sole Stichopogon species, S. fragilis, is a tiny silver fly from the sandy Okanagan grasslands at Osoyoos, right on the United States border. Only a single specimen has been collected in Canada. The common Canadian species, S. trifasciatus, widespread across the continent, occurs in southern Alberta grasslands, but has not been collected in the Montane Cordillera Ecozone.

#### SUBFAMILY ASILINAE (19 species, 19%)

In the Montane Cordillera Ecozone the asilines are mostly medium to large, grey, elongate species. Perhaps the most distinctive ones are in the genus Efferia, a common and striking group of flies in grasslands. The males have large club-shaped genitalia; the ovipositors of the females are long and sword-like. These are used to place the eggs in cracks in the soil, in dead plant inflorescences, and so on. The larvae, as in all species in the subfamily, as far as is known. develop in the soil and the ones studied feed on the larvae of scarab beetles (Scarabaeidae). Adult males of all the species have silver-white abdominal segments; in most, only the sixth and seventh segments are white, but in E. benedicti and E. staminea most of the segments are white and clothed with long, white hairs parted along the midline. Efferia albibarbis is widespread right across the United States, but in Canada it occurs only in sandy habitats in the extreme southern Okanagan and on the beaches of Lake Erie in Ontario. In Canada E. frewingi is mainly a species of the southwestern Great Plains, but in the Montane Cordillera it has been found only in the grasslands adjacent to the Columbia and Kootenay Rivers in the Rocky Mountain Trench. Efferia coulei is a spring species, flying mostly in May and early June; E. benedicti flies mainly from mid-June to the end of July. Efferia harvevi is active mostly from August through September. All three are among the most common and distinctive grassland asilids and can be present in high densities. Where they occur sympatrically, their staggered flight seasons allow them to fill similar ecological niches. An undescribed species, closely related to E. coulei, occurs in the Okanagan and Thompson valleys.

Other grassland members of the subfamily are *Dictropaltum mesae*, a small, widespread golden species; *Machimus occidentalis*; *M. vescus*; *Neomochtherus willistoni*; *Proctacanthus milbertii*, and *P. occidentis. Machimus occidentalis* and *Neomochtherus willistoni* are very common species and are also found in open dry forests. However, these two similar species seldom are found together; the former flies mostly in June and is replaced by the latter in late July and August. The two *Proctacanthus* species are the largest robber flies in the Montane Cordillera, reaching a length of about 40 millimetres. *Megaphorus willistoni* is a rare little leaf-cutting bee mimic known from only one specimen in Canada (from the southern Similkameen Valley) and a photograph from Oliver (South Okanagan). The remaining species are forest dwellers, mostly Cordilleran species: *Machimus callidus, M. erythocnemius, Neoitamus brevicomus*, and *Nevadasilus auriannulatus. Rhadiurgus variabilis* is an exception in this list. This species is a member of the Boreal element and is one of only two Holarctic robber flies. It is one of the most northerly dwelling asilids and one of the most common species in the spruce forests of the ecozone, from the Cascade Mountains to the Rockies, from the Okanagan Highlands to the Omineca Mountains.

## **Biogeography and Faunal Elements**

#### **Faunal elements**

Species may be grouped with others that share similar distributions to form what can be termed faunal elements. The majority of the 101 known species are confined to the Nearctic Realm, although two are Holarctic (defined here as species with transcontinental ranges in both North America and Eurasia). This section describes the Nearctic faunal elements pertaining to the fauna of the Montane Cordillera Ecozone (species with Holarctic and Palaearctic-East Beringian distributions are also assigned a North American faunal element). These faunal elements are:

- **1. Boreal** (7 spp., 7%). Species occurring in the northern transcontinental forests dominated by spruce (*Picea*). In general, these species range from the Atlantic Provinces across the northern New England states, Quebec, northern Ontario, parts of the northern tier of mid-western states, the Prairie Provinces north of the Great Plains, and northern British Columbia, often ranging considerably southward in the mountains and plateaus of the Cordillera. Such species ranging south of the central plateaus of British Columbia (south of about 51°N) could be termed Boreomontane species. *Laphria gilva* (Linnaeus), *Laphria insignis* (Banks), *Laphria janus* McAtee, *Laphria posticata* (Say), *Laphria sadales* Walker, *Cyrtopogon bimacula* (Walker), *Rhadiurgus variabilis* (Zetterstedt).
- 2. Cordilleran (63 spp., 62%). Species confined to the western mountain systems and their associated plateaus. Largely confined to subalpine and montane coniferous forests. Cophura albosetosa Hine, Cophura vitripennis (Curran), Nicocles canadensis Curran, N. dives (Loew), N. pollinosus Wilcox, Laphria aimatus McAtee, L. asackeni Wilcox, L. astur Osten Sacken, L. asturina (Bromley), L. columbica Walker, L. felis (Osten Sacken), L. fernaldi (Back), L. ferox Williston, L. franciscana Bigot, L. milvina Bromley, L. partitor (Banks), L. sackeni (Banks), L. vivax Williston, L. vultur Osten Sacken, Pogonosoma ridingsi Cresson, Coleomvia hinei Wilcox and Martin, Coleomyia setigera (Cole), Callinicus pollenius (Cole), Cyrtopogon ablautoides Melander, C. albovarians Curran, C. auratus Cole, C. aurifex Osten Sacken, C. banksi Wilcox and Martin, C. dasyllis Williston, C. dasylloides Williston, C. fumipennis Wilcox and Martin, C. glarealis Melander, C. infuscatus Cole, C. inversus Curran, C. lineotarsus Curran, C. montanus Loew, C. nugator Osten Sacken, C. princeps Osten Sacken, C. sansoni Curran, C. sudator Osten Sacken, C. willistoni Curran, Dioctria pusio Osten Sacken, Eucyrtopogon calcaratus Curran, E. comantis Curran, E. diversipilosus Curran, E. nebulo Osten Sacken, E. punctipennis Melander, E. spinigera Curran, E. varipennis (Coquillett), Eudioctria sackeni (Williston), Heteropogon senilis (Bigot), Holopogon albipilosus Curran, H. stellatus Martin, Lasiopogon aldrichii Melander, L. cinereus Cole, L. monticola Melander, L. trivittatus Melander, Machimus callidus (Williston), M. occidentalis (Hine), M. vescus (Hine), Neoitamus brevicomus (Hine), Neomochtherus willistoni (Hine), Nevadasilus auriannulatus (Hine).
- 3. Intermontane (18 spp., 18%). Species of southern affinity in the western intermontane region, restricted to the valleys and lower elevation plateaus of the southern half of the ecozone. These are mostly grassland species, but this element may intergrade with the Cordilleran element in the open, dry montane forests of Ponderosa Pine and Douglas-fir at low and medium elevations. Some species may extend into adjacent areas of the Great Plains. Leptogaster fornicata Martin, Comantella pacifica Curran, Lestomyia sabulona (Osten Sacken), Nicocles utahensis Cordilleran, Dicolonus nigricentrum Adisoemarto, Dioctria henshawi Johnson, Myelaphus lobicornis (Osten Sacken), Scleropogon neglectus (Bromley), Stenopogon inquinatus Loew, S. rufibarbis Bromley, Willistonina bilineata (Williston), Stichopogon fragilis Back, Efferia benedicti (Bromley), E. coulei Wilcox, E. harveyi (Hine), E. n. sp., Megaphorus willistoni (Cole), Proctacanthus occidentalis Hine.
- **4. Western** (6 spp., 6%). Species of western mountains and associated lowlands, but extending considerable distances eastward, often to the 100th meridian (Mississippi River). *Leptogaster arida* Cole, *Cophura brevicornis* (Williston), *Ospriocerus aeacus* (Wiedemann), *Dicropaltum mesae* (Tucker), *Efferia frewingi* Wilcox, *E. staminea* (Williston).

- **5. Transition** (1 species, 1%). Species generally most common in the southern boreal forests and adjacent montane forests in the West and in the mixed and deciduous forests in the East. *Laphria scorpio* McAtee.
- **6. Austral** (5 spp., 5%). Species ranging from coast to coast south of the boreal and mixed forests. Transcontinental at least in the United States; in Canada only in extreme southern areas. *Laphria index* McAtee, *Andrenosoma fulvicaudum* (Say), *Efferia albibarbis* (Macquart), *Machimus erythocnemius* (Hine), *Proctacanthus milbertii* Macquart.
- **7. East Beringian** (1 spp., 1%). Species originating in the unglaciated areas of Yukon and Alaska and restricted to the eastern (North American) side of the Bering Strait. *Lasiopogon prima* Adisoemarto.

## **Biogeographic Summary**

Although they probably occurred in the region in the late Mesozoic (Cannings 2002) robber flies do not appear in the fossil record in the western Cordillera until the Late Early to the Late Middle Eocene, 52-47mybp (Green River shales of the Utah Eocene) (Wilson 1978). Interestingly, these are specimens of Asilinae, assumed to be the youngest of the asilid subfamilies. The Florissant shales of Colorado (Oligocene, 23.7-36.6 mybp) contain a variety of genera living in the Montane Cordillera today, including *Leptogaster* (Leptogastrinae); *Cophura, Lestomyia*, and *Nicocles* (Dasypogoninae); *Dioctria* and *Holopogon* (Stenopogoninae); *Machimus* (Asilinae). The Florissant fossil site was a subtropical savannah woodland (Cronquist 1978).

Cannings (2002) summarizes some of the major environmental shifts that helped produce a characteristic montane fauna.

"Climatic cooling around the Eocene-Oligocene boundary and the uplift of the Western Cordillera from the late Oligocene through the Pliocene initiated striking modifications to the environments of North America. With the subsequent cooling and drying of the mid-continent the once widespread broadleaved forests shifted eastward and major disjunctions between eastern and western biotas occurred. Most mesophytic temperate floras were isolated in eastern North America and in the West. In the West an arid-adapted flora, including grasslands, developed in the lowlands in the Miocene and mesic conifer forests withdrew to higher elevations. In the Great Basin the flora and fauna had a modern aspect by the Miocene."

For example, the sister species of the widespread Montane Cordilleran *Lasiopogon cinereus*, *L. shermani*, lives in the southern Appalachian Mountains. The divergence of these two species appears to be a typical east/west vicariance, but may have been a rather early one because the two have many morphological differences (Cannings 2002). *L. cinereus* is one of the most variable *Lasiopogon* species. Although the species is rather uniform morphologically throughout the Montane Cordillera Ecozone in Canada, populations living along streams in the coastal hills from Oregon south to northern California are especially different, and were even originally separately described as *L. atripennis* Cole & Wilcox. These populations probably spent at least the Wisconsinan glaciation in the Pacific Coastal refugium, separated from other populations (Cannings 2002).

*L. aldrichii* is another common and widespread *Lasiopogon* in the Montane Cordillera, at least in the southern mountains. It and its close relatives form the aldrichii species group, which is

distinctly northwestern in distribution. It has montane and Pacific coastal components separated by the Cascade Mountains, which reached maximum uplift in the Pliocene and Pleistocene (Lafontaine 1982). One of the species, *L. yukonensis*, is restricted to the southern and central Yukon and distributionally qualifies as an East Beringian species. It appears to be most closely related to the two Pacific coastal species in the group, *L. pacificus* and an undescribed species from the California coast. *Lasiopogon yukonensis* may represent a relict population of a once more widespread southern species that was distributed through the Montane Cordillera and beyond, derived in a similar manner to the southern steppe Noctuidae documented in Beringia by Lafontaine and Wood (1988).

The robber fly fauna of the Montane Cordillera Ecozone is overwhelmingly represented (81%) by species restricted to the western mountains, plateaus and valleys from the Rocky Mountains westward. These are the 81 species of the Cordilleran and Intermontane elements. The faunal elements are represented in the Montane Cordillera Ecozone as follows:

Sixty-three species of Cordilleran origin (62%) are recorded. Intermontane species total 18 species (18%) and there are 7 (7%) Boreal species, including two with holarctic ranges. Six species (6%) are Western, 1 (1%) is Transition, and 5 (5%) are Austral. One (1%) is Eastern Beringian.

Two species, Laphria gilva and Rhadiurgus variabilis, are holarctic, ranging around the Northern Hemisphere. Possibly, these species have had these wide distributions since before the last glacial age, living in the circumboreal forests that linked the continent. During the Pleistocene in North America, they could have lived south of the ice sheets. The Beringian glacial refugium has influenced the distribution of Montane Cordilleran asilids to only a small extent. The large and widespread holarctic genus Lasiopogon contains the only Beringian fauna in the Asilidae (Cannings 1997). Three species (L. hinei, L. canus, and L. prima) are closely related to Eurasian forms; they or their ancestors entered North America through ice-free Beringia, L. prima is the sole species that reaches the Montane Cordillera, ranging south from the Yukon and northern British Columbia into the foothills of the Rocky Mountains in central Alberta. It is the eastern representative of a species pair that is separated by the Bering Strait. In the Yakutskaya, Magadanskaya, and Amurskaya regions of eastern Siberia and Far-eastern Russia its sister species, L. septentrionalis Lehr, is widespread (Cannings 2002). The distribution of this species pair, far to the northwest of the rest of their close relatives, suggests mid-Tertiary uplift of the northern Rockies was responsible for the vicariance of their ancestor from the rest of the lineage. The species are primarily inhabitants of taiga, and L. prima, at least, has followed treed river valleys to the Arctic coast. It also has expanded its range southward along the mountains into Alberta and eastward into Saskatchewan since the last glaciation. The species pair is likely at least 3 million years old, and its ancestor was probably a Nearctic species. Sister species from the taiga in East and West Beringia represent a vicariance pattern that results from Pliocene separation of forest habitats in Beringia after climatic cooling (Lafontaine and Wood 1988) or by the initial Pliocene formation of the Bering Strait itself (Matthews and Telka 1997). This is seen in a number of taxa, but is perhaps best documented in the noctuid moths (Lafontaine and Wood 1988).

Thirty-five percent of 20 Yukon species are of Boreal origin (Cannings and Cannings 1997); in the Montane Cordillera this boreal component is reduced to 7 percent. This reduction is the result of the overwhelming influence of more southerly species, because all of the Yukon's seven boreal species range south into the Montane Cordillera and only one additional boreal species

(*Laphria sadales*) is included in the ecozone's much larger total fauna (five times larger than that of the Yukon). All, but one (*Laphria posticata*), of the seven species in the Boreal element of the Montane Cordillera range south of 51°N along the mountains and plateaus of the Cordillera. These also could be termed boreomontane species.

Robber flies apparently are seldom introduced to non-native habitats. Accidental introductions of larvae in soil would not be impossible, although densities are usually low. Purposeful introductions for biological control of insect pests would be impracticable because asilids are generalist predators and are difficult to rear. Nevertheless, two species have been introduced to eastern North America from Europe; the mode of introduction is unknown. No non-native species live in the Montane Cordillera Ecozone.

## Robber Fly Habitats in The Montane Cordillera

The habitat requirements of most species of robber flies in the Montane Cordillera are known in only a most general way. Habitats are grouped here into three broad categories (Biogeoclimatic Zones in parentheses):

- 1. Subalpine forests and other spruce dominated forests: These spruce forests generally occur above 1200m in the south and 1000m in the north and on northern plateaus (Engelmann Spruce/Subalpine Fir, Montane Spruce, and Subboreal Spruce zones). In general, the dominant trees are Engelmann Spruce (*Picea engelmanni*) in the southern mountains and White Spruce (*Picea glauca*) in the north, with wide swaths of hybrids in the central regions. Some asilids found in the meadows of these spruce forests may periodically appear above tree-line in the Arctic-Alpine Zone. In many areas, especially in drier areas affected by fire, Lodgepole Pine (*Pinus contorta*) can dominate. Large areas of pine forests in the ecozone have been killed by the Mountain Pine Beetle (*Dendroctonus ponderosae*) in the last decade. Typical robber flies are *Laphria columbica*, *L. gilva*, *L. janus*, *L. milvina*, *L. posticata*, *L. sadales*, *Cyrtopogon bimacula*, *C. dasyllis*, *C. glarialis*, *Lasiopogon aldrichii*, *L. fumipennis* (Cascade Mtns.) *L. monticola*, and *Rhadiurgus variabilis*. These are species of both the Boreal and Cordilleran elements. Some Cordilleran species living in subalpine habitats, such as those in the genus *Lasiopogon*, are restricted to the southern part of the ecozone.
- 2. Montane forests. These are warmer forests growing below the spruces in the valleys and hillsides of the Montane Cordillera, mainly south of about Williams Lake. They are dominated by Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) (Ponderosa Pine and Interior Douglas-fir zones). These forests have also been seriously affected by unusually extensive pine beetle attacks. In wetter areas such as the Shuswap and Kootenay regions, Western Hemlock (*Tsuga hetrophylla*) and Western Redcedar (*Thuja plicata*) predominate (Interior Cedar-Hemlock Zone). Much of the understorey of the open dry forests is similar to that of adjacent grasslands and the robber fly species characteristic of forests and grasslands often intermingle.

The forest fauna is dominated by the large genera *Laphria* and *Cyrtopogon. Laphria* larvae tunnel in rotting wood searching out beetle larvae and other prey. Species characteristic of low and mid-altitude woodlands include *Leptogaster arida*, *Cophura albosetosa*, *C. brevicornis*, *Nicocles dives*, *Andrenosoma fulvicaudum*, *Laphria aimatus*, *L. columbica*, *L. felis*, *L. fernaldi*, *L. ferox*, *L. franciscana*, *L. gilva*, *L. insignis*, *L. janus*, *L. sadales*, *L. vivax*, *Pogonosoma ridingsi*,

Coleomyia hinei, Callinicus pollenius, Cyrtopogon auratus, C. banksi, C. glarealis, C. inversus, C. montanus, Dioctria pusio, Eucyrtopogon calcaratus, E. nebulo, Eudioctria sackeni, Heteropogon senilis, Holopogon albopilosus, H. stellatus, Stenopogon inquinatus, Lasiopogon aldrichii, L. cinereus, L. monticola, Machimus callidus, M. erythocnemius, M. occidentalis, Neoitamus brevicomus, Neomochtherus willistoni, Nevadasilus auriannulatus.

3. Grasslands: The dry intermountain grasslands or steppes in the southern valleys and plateaus of the Montane Cordillera are dominated by various bunchgrass species and occur in three biogeoclimatic zones (Bunchgrass, Ponderosa Pine, and Interior Douglas-fir zones). Lower elevation grasslands, below about 500 metres, are characterized by an arid community of plants dominated by Bluebunch Wheatgrass (*Agropyron spicatum*) and Big Sagebrush (*Artemisia tridentata*). In sandy soils Antelope-brush (*Purshia tridentata*) may replace sagebrush as a shrub, especially in the extreme south Okanagan. Middle grasslands on northfacing slopes in the main valleys and in areas such as the Nicola Valley generally lack sagebrush. Sandberg Bluegrass (*Poa secunda*) dominates with Bluebunch Wheatgrass and other species. The Upper Grasslands lie above about 800 or 1000 meters on hillsides and on the southern plateaus. Various species of fescues (*Festuca*) usually dominate the cover, although wheatgrass and needlegrasses (*Stipa*) are common and prevail in such regions as the Cariboo and Chilcotin plateaus.

Of the three habitat types, grasslands have the best known asilid fauna because the habitats are relatively restricted in size and are readily accessible to researchers. They are also frequently visited by collectors because their fauna has special and unusual species from the south. Some robber flies prefer specific grassland habitats relating to elevation, soil type and vegetation composition and structure; others are more widespread across different grassland types. Some species range into open Ponderosa Pine or Douglas-fir woods because much of the understorey of such habitats is similar to that of adjacent grasslands.

Widespread species include Scleropogon neglectus, Stenopogon inquinatus, Efferia benedicti, Efferia harveyi, Proctacanthus milberti, Machimus occidentalis, and Neomochtherus willistoni. Examples of others that occur in grasslands and adjacent open forests in the extreme southern part of the ecozone, but are rather rare are Leptogaster fornicata, Nicocles utahensis, Dicolonous nigricentrum, Ospriocerus aeacus, and Willistonina bilineata.

In low elevation, sandy, xeric habitats characteristic species are *Stichopogon fragilis*, *Efferia albibarbis*, and *Proctacanthus occidentalis*. In silty soil where Big Sagebrush flourishes, *Efferia benedicti* is common. If forbs are abundant, the rare *Megaphorus willistoni* may occur. *Efferia staminea* and an undescribed *Efferia* prefer Bluebunch Wheatgrass in well-drained sites.

Middle and higher grasslands dominated by Festuca grasses support species such as Comantella pacifica, Lestomyia sabulona, and Myelaphus lobicornis (only where Common Rabbit-brush [Chrysothamnus nauseosus] grows) in the south. Species typical of the central plateaus tend to be widespread grassland species: Stenopogon inquinatus, Scleropogon neglectus, Dicropaltum mesae, Efferia coulei, E. harveyi, and Machimus occidentalis.

#### Analysis of trends in species occurrence and abundance

#### 1. Grassland destruction

The most serious historic anthropogenic stress on robber fly populations has been the destruction of grassland habitat. The elimination of grasslands, usually at low and medium elevations in the southern valleys, for agriculture and housing, has undoubtedly reduced populations of robber flies, especially Intermontane species. Only about 10 percent of the original grasslands in the Okanagan Valley remain in a relatively natural state and many are considerably disturbed. The Antelope-brush steppe in the extreme south of the valley is one of the most endangered habitats in Canada; it contains one of the richest assemblages of southern species in the nation. Only 40 percent of the original habitat remains, and only nine percent of that is undisturbed. Overgrazing by cattle, disturbance by vehicles, and introduced weeds (Cheatgrass (*Bromus tectorum*) and Diffuse Knapweed (*Centaurea diffusa*) are perhaps the most noxious) in many remaining grasslands may have an effect on populations, but no studies have been undertaken in the ecozone that show this. Some overgrazed sites have dense and healthy populations of *Scleropogon neglectus, Stenopogon inquinatus, Efferia benedicti*, and *E. harveyi*.

## 2. Logging

The extensive logging that has occurred in the ecozone has probably reduced the populations of forest species in both the mid-elevation Montane forests and the subalpine forests at higher altitudes. The suppression of forest fires, largely because of the interests of the forest industry, perhaps has had some negative effect on species such as *Andrenosoma fulvicaudum*, which depends on fires to create habitat for its wood-boring beetle prey (Fisher 1986). Suppression of fire has also allowed the invasion of pines and Douglas-firs into the grasslands. In the Rocky Mountain Trench, for example, the forest has taken over about 30 percent of the grasslands since 1960 (Cannings and Cannings 1996), perhaps altering the makeup of the robber fly assemblage there. However, the extensive attacks of Mountain Pine Beetle on pine forests in the ecozone (described below) will probably reduce this invasion of grasslands by trees. Salvage harvesting of beetle-killed trees will have to be carefully planned to maximize the heterogeneity of habitats and minimize the negative effects on wildlife in general (Klenner 2006).

#### 3. Climate change

Climate change may significantly affect present asilid distributions if grasslands increase in extent and forest types shift in altitude and coverage. Hebda (1982, 1995) revealed that grassland-steppe vegetation was much more prevalent in the southern part of the ecozone during warmer climatic regimes in the early to mid-Holocene than today. Arid grassland asilids such as *Lasiopogon albidus* Cole and Wilcox and *L. chaetosus* Cole and Wilcox now ranging as far north as the Columbia Basin in Washington State could readily enter the Canadian Montane Cordillera if xeric habitats proliferate. Likewise, components of the rich asilid fauna of the Cascade Mountains and montane forests of the Great Basin may move northward as the climate warms.

The recent widespread death of Lodgepole and Ponderosa pines in the BC interior owing to unprecedented Mountain Pine Beetle attacks has changed the character of much of the ecozone's woodland. According to most foresters, these widespread beetle kills result from a combination of climate warming and an unnatural bias towards susceptible mature trees, the result of aggressive fire suppression. By 2007, almost 50 per cent of the merchantable Lodgepole Pine in the province was killed (Walton *et al.* 2008). The resulting fluctuations in populations of prey

species may affect some asilid species. For some years to come there will be unusual quantities of dead wood for the development of species of Laphrini; it is unclear if this will produce a significant increase in the abundance of any of these species. The removal of much of the forest canopy may also result in drier forest soils, which may affect the development of robber fly species that develop in the soils of these habitats. Certainly, the widespread, at least temporary, retreat of pine forests in BC will aid the spread of species adapted to drier, more open environments, such as those adapted to grasslands.

## Recommendations for Future Inventory, Research and Monitoring

There has never been any significant systematic inventory of asilid flies in the Montane Cordillera. Knowledge of the distribution and status of the species on the list in Appendix 1 has come from sporadic collecting over many years and analysis of specimens in the Royal B.C. Museum, Victoria; Spencer Entomological Museum, University of B.C., Vancouver; and the Canadian National Collection, Agriculture and Agri-Food Canada, Ottawa. The only detailed study of the fauna of one locality was by Cannings (1989), who published an annotated list and biogeographic outline of the species collected in a *Festuca* grassland at Penticton over several years. Even in the southern valleys, much more work is necessary.

Outside the Okanagan drainage no formal inventories have been made anywhere in the zone. High priorities for future inventories are the species-rich, lowland valleys of the Kootenay and Thompson regions and the grasslands and dry forests of the Chilcotin Plateau. For clarifying the ranges of northern species, intensive work in the Cariboo, Omineca and Rocky Mountains; the Bulkley Valley, and the Babine Upland is required.

Increased inventory efforts would especially improve our knowledge of the species that might range widely across the zone, but are known from few localities: for example, *Leptogaster arida*, *Laphria index*, *L. milvina*, *L. scorpio*, *Callinicus pollinosus*, *Cyrtopogon lineotarsus*, *Eucyrtopogon punctipennis*, *E. comantis*, *Willistonina bilineata*, *Dioctria pusio*, *Machimus callidus*, *M. erythocnemius*, and *Neoitamus brevicomus*. *Cyrtopogon falto* Walker, one of the most common robber flies in eastern North America, ranges west sparsely in the transition forests of the Great Plains and appears again in the Skeena Valley of west-central British Columbia. It probably occurs across the northern part of the Montane Cordillera, but has never been recorded in the zone; further inventory in the north would answer this and other distributional questions.

Other species are apparently truly rare and their status needs to be elucidated. Among these are the grassland/dry forest species *Leptogaster fornicata*, *Nicocles utahensis*, *Dicolonus nigricentrum*, *Dioctria henshawi*, *Ospriocerus aeacus*, and *Willistonina bilineata*. *Megaphorus willistoni* and *Stichopogon fragilis*, each known only from one specimen in the arid grasslands of the South Okanagan/Similkameen, require study to assess their potentially threatened status.

Taxonomic work is required to clarify the identity and presence of species in a number of genera in the region. *Leptogaster, Lestomyia, Nicocles, Eucyrtopogon*, and *Machimus* especially are in need of revision. There are undescribed species in all these genera. A detailed examination of some of the larger genera in the ecozone, such as *Cyrtopogon* and *Laphria*, will also result in a better understanding of species limits and the description of new species.

No studies examining the effects of human activity on robber flies (e.g. the effects of overgrazing; the removal of coarse woody debris in logging operations) have been done in the ecozone, and no long-term monitoring studies are in place that could detect changes in species composition and abundance of asilid populations. Our knowledge of the habitat requirements of most species is nonexistent and more autecological studies would be helpful.

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Figures 1-4. 1. Efferia benedicti female, sage flats, Chopaka, B.C., June 15, 1982. 2. Efferia coulei male, West Bench, Penticton, B.C., June 9, 1982. 3. Proctacanthus milbertii, female, West Bench, Penticton, B.C., August 31, 1983. 4. Laphria felis female, West Bench, Penticton, B.C., June 9, 1982. Photos by Robert A. Cannings and Brent Cooke, Royal British Columbia Museum.

#### **SUMMARY**

by Robert A. Cannings

## What are Robber Flies? (Diptera: Asilidae)

Robber flies are predatory flies that as adults pursue other insects (usually flying ones), seize them, and kill them with paralyzing saliva injected through the hypopharynx (tongue). The liquified contents of the prey are then sucked up through the proboscis. The prominent eyes, the piercing mouthparts, and the spiny legs reflect the predatory habits of these flies. Larvae are predators of the eggs, larvae, and pupae of other insects in the soil or in rotting wood.

In the Montane Cordillera, robber flies range in size from 5mm to 40mm long, The largest, grassland species called *Proctacanthus*, are the largest flies in Canada. Some asilids, called *Laphria*, are fat, fuzzy yellow, red and black flies that resemble bees and wasps. Others have patterned wings, colourful abdomens or decorated legs.

#### Where do I find robber flies?

In Canada, robber flies usually hunt in open areas where there is plenty of light, and are most active in the warmest parts of the day. Overcast skies greatly curtail their activity. Different kinds of robber flies have different hunting behaviours and preferences for perching sites. Open, sandy areas and grasslands are good places to find robber flies, and in these habitats, many species sit on the ground waiting for prey. Forest species perch on leaves or logs and tree trunks. In the Montane Cordillera robber flies live in most habitats from lowland grasslands and dry forests all the way up to treeline in the mountains.

# What is the Robber Fly species diversity of the Montane Cordillera Ecozone?

- 101 species known
- all species are native
- The Montane Cordillera Ecozone supports about half of all Canadian species.

## What species are at risk?

Robber flies are not well enough known in the Montane Cordillera to allow us to determine if they are endangered or threatened. More extensive collecting will probably show that some species are much more widespread than is known today. However, in some rather well collected areas such as the Okanagan grasslands, some species do appear to be truly rare. Many of these habitats have been destroyed by agricultural and urban expansion, and others are threatened. Thus, rare grassland species such as *Myelaphus lobicornis*, *Willistonina bilineata*, *Stichopogon fragilis*, *Efferia albibarbis*, and *Megaphorus willistoni* can be considered at risk.

#### What are the human impacts on robber flies?

The elimination of grasslands for agriculture and housing, particularly at low and medium elevations in the southern valleys, has undoubtedly reduced populations of robber flies, especially Intermontane species. About ten percent of the original grasslands in the Okanagan Valley remain intact, and many are considerably disturbed. Overgrazing by cattle, disturbance by vehicles, and introduced weeds in many remaining grasslands may have a negative effect on populations, but no studies have been undertaken in the ecozone that show this. Some overgrazed sites appear to have dense and healthy populations.

Extensive logging has probably reduced the populations of forest species. The suppression of forest fires perhaps has had some negative affect on species such as *Andrenosoma fulvicaudum*, which depends on fires to create habitat for its wood-boring beetle prey. Fire control, along with climate warming, has also been a factor in the widespread death of pine forests in BC, resulting in the accumulation of an unusual amount of dead wood in these forests. Species of *Laphria*, which develop in dead wood, especially may initially profit from this, although other species, whose larva e live in the soil, may find the drier soil conditions a problem. The death of so much pine forest may encourage range extensions in grassland asilids in the ecozone.

#### Trends in robber fly populations

Case History 1 -- Rare species and loss of habitat

Megaphorus willistoni and Stichopogon fragilis, both at the extreme northern edge of their range, and each known only from one specimen in the arid grasslands of the South Okanagan/Similkameen, require study to assess their potentially threatened status. The habitat of these species has shrunk drastically in the last century, having been cleared for agriculture and building, and the future of these species in the ecozone depends on the maintenance of remaining fragments of grassland.

# Appendix 1: Checklist of Asilidae of Montane Cordillera Ecozone

Taxonomic arrangement based on Fisher and Wilcox (1997). Total is 101 species. \* Species of management concern: endangered, threatened, or vulnerable.

## Subfamily Leptogastrinae (2 species, 2%)

Leptogaster arida Cole Western
Leptogaster fornicata Martin Intermontane

## **Subfamily Dasypogoninae** (9 species, 9%)

Comantella pacifica Curran Intermontane Cophura albosetosa Hine Cordilleran Cophura brevicornis (Williston) Western Cophura vitripennis (Curran) Cordilleran Lestomyia sabulona (Osten Sacken) Intermontane Nicocles canadensis Curran Cordilleran Nicocles dives (Loew) Cordilleran Nicocles pollinosus Wilcox Cordilleran Nicocles utahensis Cordilleran Intermontane

# Subfamily Laphriinae (23 species, 23%)

Andrenosoma fulvicaudum (Say) Austral Laphria aimatus McAtee Cordilleran Laphria asackeni Wilcox Cordilleran Laphria astur Osten Sacken Cordilleran Cordilleran Laphria asturina (Bromley) Laphria columbica Walker Cordilleran Laphria felis (Osten Sacken) Cordilleran Laphria fernaldi (Back) Cordilleran Laphria ferox Williston Cordilleran Laphria franciscana Bigot Cordilleran

Laphria gilva (Linnaeus)

Boreal (also Holarctic)

Laphria index McAtee **Boreal** Laphria insignis (Banks) **Boreal** Laphria janus McAtee **Boreal** Laphria milvina Bromley Cordilleran Laphria partitor (Banks) Cordilleran Laphria posticata (Say) **Boreal** Laphria sackeni (Banks) Cordilleran Laphria sadales Walker Boreal Laphria scorpio McAtee **Boreal** Laphria vivax Williston Cordilleran Laphria vultur Osten Sacken Cordilleran Pogonosoma ridingsi Cresson Cordilleran

#### **Subfamily Stenopogoninae** (42 species, 41%)

Coleomyia hinei Wilcox and Martin Cordilleran

Cordilleran Coleomyia setigera (Cole) Cordilleran Callinicus pollenius (Cole) Cyrtopogon ablautoides Melander Cordilleran Cyrtopogon albovarians Curran Cordilleran Cyrtopogon auratus Cole Cordilleran Cyrtopogon aurifex Osten Sacken Cordilleran Cyrtopogon banksi Wilcox and Martin Cordilleran Cyrtopogon bimacula (Walker) **Boreal** Cyrtopogon dasyllis Williston Cordilleran Cyrtopogon dasylloides Williston Cordilleran Cyrtopogon fumipennis Wilcox and Martin Cordilleran Cyrtopogon glarealis Melander Cordilleran Cyrtopogon infuscatus Cole Cordilleran Cyrtopogon inversus Curran Cordilleran Cyrtopogon lineotarsus Curran Cordilleran Cyrtopogon montanus Loew Cordilleran Cyrtopogon nugator Osten Sacken Cordilleran Cyrtopogon princeps Osten Sacken Cordilleran Cyrtopogon sansoni Curran Cordilleran Cyrtopogon sudator Osten Sacken Cordilleran Cyrtopogon willistoni Curran Cordilleran Intermontane \*Dicolonus nigricentrum Adisoemarto Dioctria henshawi Johnson Intermontane Dioctria pusio Osten Sacken Cordilleran Cordilleran Eucyrtopogon calcaratus Curran Cordilleran Eucyrtopogon comantis Curran Eucyrtopogon diversipilosus Curran Cordilleran Eucyrtopogon nebulo Osten Sacken Cordilleran Eucyrtopogon punctipennis Melander Cordilleran Eucyrtopogon spiniger Curran Cordilleran Eucyrtopogon varipennis (Coquillett) Cordilleran Cordilleran Eudioctria sackeni (Williston) Heteropogon senilis (Bigot) Cordilleran Holopogon albipilosus Curran Cordilleran Cordilleran Holopogon stellatus Martin \*Myelaphus lobicornis (Osten Sacken) Intermontane \*Ospriocerus aeacus (Wiedemann) Western Scleropogon neglectus (Bromley) Intermontane Stenopogon inquinatus Loew Intermontane Stenopogon rufibarbis Bromley Intermontane \*Willistonina bilineata (Williston) Intermontane

# Subfamily Stichopogoninae (6 species, 6%)

Lasiopogon aldrichiiMelanderCordilleranLasiopogon cinereusColeCordilleranLasiopogon monticolaMelanderCordilleran

Lasiopogon primaAdisoemartoEast BeringianLasiopogon trivittatusMelanderCordilleran\*Stichopogon fragilisBackIntermontane

# Subfamily Asilinae (19 species, 19%)

Dictropaltum mesae (Tucker) Western \*Efferia albibarbis (Macquart) Austral Efferia benedicti (Bromley) Intermontane Efferia coulei Wilcox Intermontane Efferia frewingi Wilcox Western Efferia harveyi (Hine) Intermontane Efferia staminea (Williston) Western \*Efferia n. sp. Intermontane Machimus callidus (Williston) Cordilleran

Machimus erythocnemius (Hine) Austral Machimus occidentalis (Hine) Cordilleran Cordilleran Machimus vescus (Hine) \*Megaphorus willistoni (Cole) Intermontane Neoitamus brevicomus (Hine) Cordilleran Neomochtherus willistoni (Hine) Cordilleran Nevadasilus auriannulatus (Hine) Cordilleran Proctacanthus milbertii Macquart Austral Proctacanthus occidentalis Hine Intermontane

Rhadiurgus variabilis (Zetterstedt) Boreal (also Holarctic)