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HABITAT SELECTION AND ALLOZYME VARIATION IN SOME POPULATIONS OF THE *Saldula pallipes* SPECIES COMPLEX (HEMIPTERA: SALDIDAE) OCCURRING IN ALBERTA AND WESTERN SASKATCHEWAN

BY

DEAN STEFAN MULYK

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

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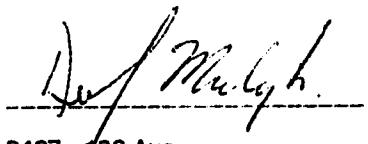

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It was the best of times.
It was the worst of times.

Charles Dickens, A Tale of Two Cities

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled HABITAT SELECTION AND ALLOZYME VARIATION IN SOME POPULATIONS OF THE *Saldula pallipes* SPECIES COMPLEX (HEMIPTERA: SALDIDAE) OCCURRING IN ALBERTA AND WESTERN SASKATCHEWAN submitted by DEAN STEFAN MULYK in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Dr. W.G. Evans

Dr. J.R. Spence

Dr. N. Stacey

I dedicate this thesis to members of the *Saldula pallipes* species complex everywhere.

ABSTRACT

Members of the holarctic *Saldula pallipes* species complex (Hemiptera: Saldidae) are small, well-camouflaged shore inhabiting insects. This complex has defied taxonomic resolution using morphological or life history data so alternative approaches were tried. A detailed catalog of habitats from which specimens were collected, habitat preference trials, and an electrophoretic examination of protein variation were used in this study. As a result, *S. pallipes* from Alberta and western Saskatchewan are now separated into two species; *S. pallipes and S. sodanuma sp. nov.* Several distinct *S. sodanuma* Forms co-occurred at some sites whereas no distinct *S. pallipes* Forms were observed.

The *S. pallipes* are collected on temporary habitats such as sloughs and creeks; but were also found on more stable habitats such as freshwater lakeshores, while *S. sodanuma* are collected on permanent and temporary alkaline shores. Individuals of either species were infrequently collected on shores where the other species was readily collected.

Individuals of Form A, the most common of the several *S. sodanuma* Forms which co-occur at Wells Lake, Saskatchewan, were used in the habitat preference trials. These individuals were attracted to a variety of substrates from different shore habitats in choice chambers but only to volatiles from alkaline shore substrates in the wind tunnel. Individuals of the *S. pallipes* complex mate on the shore substrate and since potential habitats are assessed and selected from a distance, interbreeding does not occur because each species inhabits different types of shore habitats.

Allozyme mobility and frequency were measured for 7 loci (7 enzymes) using vertical polyacrylamide gel electrophoresis. *Saldula pallipes* and *S. sodanuma* were separated by their unique alcohol dehydrogenase and aldehyde oxidase alleles. Continual turnover of temporary shoreline habitats, extreme vagility of adults, multiple matings by a single individual, and multivoltism may explain the genetic similarity of *S. pallipes* across Alberta and western Saskatchewan. Although the relationships between the various Forms of *S. sodanuma* were not fully resolved they represent a natural group because of their structural, habitat preference, and allozyme similarities.

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1. Introduction

Among shore inhabiting animals the shy, diminutive saldid (Heteroptera: Saldidae) is rarely seen by most people. Even able and patient collectors are tasked by saldid camouflage, stealth, and rapid movement. Their common name "shore bug" is both highly appropriate and a misnomer; while most species are found in shore environments, others are not (Brooks and Kelton 1967; Polhemus 1985). Their grace, beauty and speed, combined with the precarious nature of their habitat, makes them a challenge to collect and work with.

1.1 Classification of the North American Saldidae

Saldids belong to the infraorder Leptopodomorpha. There are 297 known leptopodomorphan species; 89 percent of known species belong to the family Saldidae (Schuh *et al.* 1987). Other than Leptopodidae (28 described species), all leptopodomorphans live in some association with a "shore" habitat.

In North America, saldid species are easily separated into two subfamilies by the number of cells in the hemelytral membrane. The subfamily Chiloxanthinae has five hemelytral cells and the subfamily Saldinae four (Cobben 1959). No records exist for any species of Chiloxanthinae in Alberta, but *Pentacora signoreti* (Guérin-Méneville), which occurs in Saskatchewan, may yet be found in Alberta. Two of the three tribes of Saldinae are well represented in Alberta. The tribe Saldini is represented in the province by the genera *Salda* Fabricius, *Lampracanthia* Reuter, and *Teloleuca* Reuter, while the Saldoidini is represented by *Saldula* Van Duzee and *Micracanthia* Reuter. Whether *Micracanthia* is a species group within *Saldula* or the sister-genus to *Saldula* is still disputed (Lindskog 1985; Polhemus 1985). *Saldula (sensu stricto)* is used here following Polhemus (1985) to exclude those species included in *Micracanthia* by Lindskog (1985) and Polhemus (1985). Figure 1.1 illustrates relationships of the above mentioned genera according to Polhemus (1985).

Depending upon the classification scheme, *Saldula* may include as few as 110 (Schuh *et al.* 1987) or as many as 146 species worldwide (Cobben 1960, 1985).

Polhemus (1985) has suggested that after the genus has become better understood several presently recognized species groups should be accorded generic status. Currently, four species groups of *Saldula* (*sensu stricto*) are recognized in North America: *pallipes, saltatoria, opacula*, and *orbiculata* (P. Lindskog pers. comm.). Eighteen Nearctic species are assigned to the *S. pallipes* complex (Lindskog pers. comm.).

Identifying specimens in some species groups, especially within the *S. pallipes* group, can be an exasperating and trying experience. *Saldula pallipes* (Fabricius) is, and has been, a taxonomic wastebasket. This "species" is a paraphyletic assemblage of species whose relationships are unclear. Conflicting synonymies and mis-identifications within the *S. pallipes* species group are rife in the literature. It is little wonder that this group has remained unresolved for 200 years.

Beside nomenclatural problems, saldid systematists are quite sure Nearctic specimens are not conspecific with *S. pallipes sensu stricto* from the Palaearctic. The identity of Old and New World species in the *S. pallipes* complex has been the subject of much discussion (Stock 1979; Lindskog 1981; Polhemus 1985). European populations of *S. pallipes* have served as the basis of comparison when discussing the identity and status of the North American forms. Diagnostic characters such as eunomic series (i.e., sequential variation of light and dark hemelytral coloration, Wagner 1951) and length of setae on the male parameres (Cobben 1960; Wróblewski 1966) were usually based on west European specimens rather than specimens from the entire holarctic range of *S. pallipes*.

Different eunomic series throughout Europe and North America in populations of *S. pallipes* (Cobben 1960; Kamecká 1978; Polhemus 1985) complicate accurate species identifications. An eunomic series for a member of the *S. pallipes* complex from California has been described (Polhemus and Chapman 1979) but no continent-wide studies have been reported. In a study of wing pigmentation in adult *Saldula laticollis* (Reuter), Stock (1980, as *S. palustris*) related an individual's coloration to environmental conditions experienced as a nymph. Lower temperatures or dark substrates induce darker nymphs, and hence adults, while the opposite environmental conditions induce lighter adults (Stock 1980). Studies to fully determine effects of environmental conditions on eunomic series are lacking.

In spite of the above complications, eunomic series can be used if there is no readily observable variation in other morphological characters; in North America, some populations have unique morphological characters. Previous workers considered this to be normal variation within the species (e.g., Schuh 1967), but these specimens can be separated into distinct non-overlapping groups called "morphs" (J. Polhemus pers. comm.). Eunomic variation is lacking in Albertan and Saskatchewan populations which contain these Forms. I use the terms "variety" and "Form" to separate distinct groups and subgroups within Albertan and Saskatchewan populations of *S. pallipes* throughout this thesis. Variety and Form were chosen instead of morph because they do not denote an intraspecific relationship. Varieties were defined as the largest, most readily identifiable group within the *S. pallipes* complex. The tan and black varieties in this study were based on a gross morphological character (i.e., habitus color) which was readily diagnosable in the field with a hand lens. Forms were defined as distinct subgroups within a variety. Forms were based on similarities of finer morphological characters (i.e., pronotal margin color) that were observed with the aid of a microscope in the laboratory. It is not known whether these Forms represent phenotypes of a single species or are distinct species (J. Polhemus pers. comm.). An understanding of the status of these varieties and Forms and their relationship to eunomic series is required before the systematics of the *S. pallipes* complex can be resolved in North America.

1.2 Discussion of the Alberta and western Saskatchewan populations of *S. pallipes* and definition of thesis topic

This study was prompted by the inability of J. Polhemus, the North American specialist on saldids, to identify specimens from Wells Lake, Saskatchewan, sent to him by W.G. Evans. In his letter to W.G. Evans, Polhemus stated the specimens belonged to the *S. pallipes* group which he believes to be the most difficult taxonomic problem he knows of.

My study concentrates on specimens from Alberta and western Saskatchewan because it was not feasible to work with specimens from the entire holarctic range of *S. pallipes*. Further, the techniques I tried required polymorphic populations in distinctly different types of shore habitats. These conditions were satisfied in the selected

geographic area. Some specimens from Ontario and Newfoundland were included for comparative purposes. This delimited geographic area included Wells Lake, Saskatchewan, where the specimens identified as "*S. pallipes* group" by J. Polhemus were collected from, thus providing an "identified population".

Morphology and life cycle studies (i.e., Drake 1950; Hodgden 1942; Lindskog 1981; Polhemus 1967, 1977, 1979, 1985; Schuh 1967; Stock 1979) have not defined the relationships among North American members of the *S. pallipes* group because of high variation (Polhemus 1985), so alternative techniques needed to be tried. I decided to try a detailed examination and cataloguing of the habitats in which specimens were collected, habitat preference trials, and an electrophoretic examination. The information gathered from each technique can be incorporated into the other methods to help resolve this complex.

Since this "species" can be collected from a wide variety of shore habitats it was assumed to be a "single species - habitat generalist" (i.e., Polhemus 1985; Schuh 1967), but no one had used a specific habitat classification scheme (e.g., river: unconsolidated mud shore with some grassy wrack) to try and separate members of this complex. A rigorous classification of shore habitats where specimens were collected may provide insights into possible groupings which were not obvious using the previous assumption of a "single species - habitat generalist".

Shore insects locate new habitats by a variety of cues (e.g., visual, chemical). Volatiles of cyanobacteria and chlorophytic algae have been implicated in the habitat selection process of saldid bugs (Evans 1988) and carabid beetles (Evans 1982, 1983, 1984, 1986, 1988). Different species or ecophenotypes (separate populations of a species adapted to different environmental conditions) of microorganisms present in the habitat emit unique, volatile "chemical signatures" that are recognized by particular insects (W.G. Evans pers. comm.). Seven shoreline carabid species were classified as eurytopic (tolerant of a wide range of habitats) or stenotopic (narrow range of habitats) depending upon their response to allelochemicals from habitats other than those from which they were collected (Evans 1988).

In Alberta, specimens of S. *pallipes* can be collected in almost every shore habitat. Individuals of *Saldula comatula* Parshley and *S. pallipes* respond positively to

habitat allelochemicals from habitats in which they were caught but response to allelochemicals from other habitats was not ascertained (Evans 1988). Therefore, it is not known whether members of the *S. pallipes* species complex are eurytopic or stenotopic. This thesis attempts to address this problem.

An electrophoretic examination of genetic variation in relation to habitat type was also conducted to see if there was any relationship between them. Electrophoretic techniques have been applied to biosystematic problems for >25 yr. and have yielded vast amounts of information regarding species concepts and the genetic structure of populations (Richardson *et al.* 1986). Defining species limits is extremely difficult because of the phenotypic variation observed within and between populations of *S. pallipes* (Cobben 1960; Polhemus 1985; Wróblewski 1966). Also, the presence of distinct Forms within some populations has been assumed to be phenotypic variation (e.g., Schuh 1967), yet no work to prove or disprove this notion has been done. The electrophoretic examination includes six *S. pallipes* Forms found at Wells Lake. I ask if these Forms are different phenotypes of the same genotype or are they genetically distinct populations co-existing in the same habitat?

Chapter 2 is a detailed catalogue of field sites illustrating the variety of distinct shore habitats in Alberta in which *S. pallipes* is found. Chapter 3 presents the results of a limited study of habitat selection in *S. pallipes*. Chapter 4 presents the results of an electrophoretic survey of some members of the *S. pallipes* species complex, including the electrophoretic examination of the six phenotypically distinct Forms of *S. pallipes* found at Wells Lake, Saskatchewan. Chapter 5 presents some concluding remarks about the *S. pallipes* species complex in Alberta and suggestions for future research.

1.3 Biology of *Saldula pallipes*

Saldula pallipes is a hemimetabolous insect having five nymphal instars. Using a saw-like ovipositor the females may oviposit in firm, moist soil or the basal stem area of shoreline plants (Wiley 1922; Polhemus 1985). In the laboratory, females will oviposit in or on damp wads of cheesecloth, paper towel, or filter paper (Cobben 1968). Eggs require high humidity for normal development but are not affected by submersion (Stock and Lattin 1976). Incubation time varies from four days at a constant 30°C (Cobben

1968) to six days at 25°C . Development time from first instar through to adult requires about 23 days at a constant 25°C with each nymphal instar taking roughly four days.

Following eclosion, adults feed for several days prior to mating. Ovarioles in recently eclosed females are undeveloped while in older females they are in various stages of development. Both sexes mate readily and repeatedly during their lives. Copulation in saldids is side-by-side rather than with the male on top as is typical of Gerromorpha (Cobben 1968; Polhemus 1985). A mating pair are attached to each other by special structures on the wing and second abdominal segment and by their genitalia, for more detail see Polhemus (1985). When attached, the female transports the male, and in this state they can jump short distances and feed without disengagement (Hungerford 1919; Polhemus 1985). Laboratory-reared five and six day old females readily mate and deposit fertile eggs.

Females in the laboratory laid an average of 61.3 (± 43.1 S.D.) eggs, usually laid in small batches over a period of several weeks. Adults can live up to 30 days at 25°C or up to 60 days at 8°C in the laboratory. The entire life cycle, from egg through to the next generation of breeding adults, can be completed in approximately 55 days at 25°C; this results in 2 new generations observed per year in central Alberta.

I have observed at least three peaks in the numbers of adults per year in central Alberta. The first peak occurs roughly at the end of April, shortly after the snow has melted in the gallery forests alongside athalassic habitats where the adults of *S. pallipes* overwintered. These overwintered adults die before the adults of the first summer generation (i.e., the second peak observed during the year) eclose from their last nymphal instar in late June. A second summer generation adults (i.e., the third peak observed during the year) are collected after mid August well after the adults of the first summer generation have died. The second generation adults form the overwintering generation in central Alberta.

Saldula pallipes adults from the second summer generation move to diapause sites in the duff or leaf litter of drier upland areas in early autumn. Migration by adults away from shoreline areas in autumn occurs in many species of *Saldula* (Lindskog 1968; Stock and Lattin 1976; Polhemus 1985). A change in response to humidity from positive to negative may be responsible for migration of adults of *Saldula saltatoria* (Linnaeus) to

higher, drier areas in autumn (Lindskog 1968). Overwintering females from four members of the European *S. pallipes* species complex have undeveloped ovaries (Cobben 1968). The delay observed between collection of overwintered adult specimens of *S. pallipes* in the spring and collection of first or second instar nymphs suggests a similar pattern for Alberta.

Saldula pallipes is positively phototactic and is usually active in the open sunlight areas of the shore. During cloudy weather or at night, nymphs and adults hide in shoreline wrack, gravel, and shrinkage crevices of drying mud deposits. I have collected adults emerging from unconsolidated higher shore sand after a prolonged rainstorm. Movement away from immediate shoreline areas during prolonged periods of inclement weather and between suitable shore habitats appears to be an adult characteristic. Nymphs are restricted to the habitat in which they are developing, while adults can fly between habitats. Nymphs can track minor shoreline changes but gross changes (i.e., rapid increase or decrease in water levels) means that individuals may be stranded. An ideal habitat must satisfy both adult and nymphal requirements otherwise it will not be successfully colonized.

Early instar nymphs are saprophagous, while older nymphs and adults are active predators feeding on surface and subsurface dipteran larvae (Lindskog 1968; Polhemus 1985). Other prey items may include springtails, mites, stranded crustaceans, and annelids. Cannibalism is widespread throughout the Order Hemiptera (e.g., Spence and Cárcamo 1991) and it has been recorded in *Pentacora signoreti* (Hungerford 1919) and *S. laticollis* (as *S. palustris*) (Stock 1976); so it may occur in *S. pallipes*, but it has not been observed.

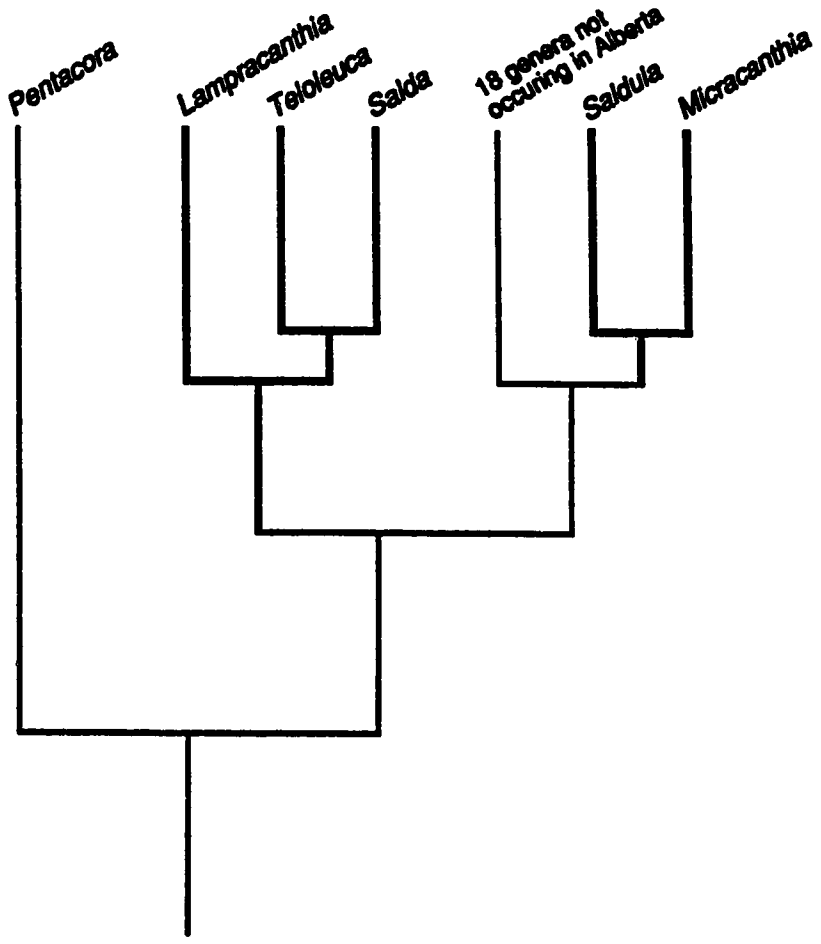


Figure 1.1 Dendrogram illustrating relationships of saldid genera occuring in Alberta and western Saskatchewan. Bold lines indicate sister genera relationships *sensu* Polhemus (1985). *Pentacora* is the only representative of the subfamily Chiloxanthinae; all other genera listed here belong to the Saldinae. *Lampracanthia*, *Teloleuca*, and *Salda* form the tribe Saldini, whereas *Saldula* and *Micracanthia* are the only representatives of the tribe Saldoidini in this region.

2. Saldidae Collection Records and Habitat Descriptions

2.1 Introduction to Shore Habitats

Shore areas are transition zones between terrestrial and aquatic ecosystems. Terrestrial components include the majority of biotic shore elements and the local topography (which is also partially responsible for the type of aquatic component, Bilby 1988). Shorelines are created and eroded by currents and wave action while the biotic composition and structure is influenced by mineral content, pH, and water temperature (among other factors) of the bordering aquatic ecosystem (Bilby 1988). Physical processes which govern both the creation and erosion of marine shorelines have been studied since ancient times. These studies, while not always "scientific", have generated a large body of knowledge regarding processes operating on marine shorelines. The intertidal zone is possibly the best studied marine habitat because of its accessibility and effects on man's activities. Athalassic shore habitats, which are those along riverine, palustrine (i.e., small, shallow, permanent or intermittent water bodies lacking active wave-formed shorelines), and lacustrine (i.e., larger, deeper, permanent water bodies with active wave-formed shorelines) areas, have not been as well studied.

When studied, athalassic shore areas, like their marine counterparts, have unique biotic communities (Evans 1988). Certain groups of shore-inhabiting insects are commonly identified in these surveys. Beetles from several families are prominent members of the shore biota. Heterocerid beetles burrow through saturated sand near the waterline scavenging subsurface organic material. Members of Bembidiini and Elaphrini (Coleoptera: Carabidae) rove the surface preying on smaller animals that occur or have been stranded on the shore. Flies occupy several important places in shore community trophic levels. Ephydrid, canaceid, and coelopid fly larvae feed on algal and vascular plant wrack cast up on the shore by wave action. Larval and adult dolichopodid flies prey on other wrack-inhabiting species. Hemipteran predators (e.g., Saldidae, Gelastocoridae, and Hebridae) are commonly collected on shoreline habitats where they attack both surface and subsurface prey. Collembola feeding on detritus may occur in great numbers. Other non-insectan arthropods (e.g., mites and wolf spiders) are commonly seen foraging in shore areas. In western Canada, shore communities consist

mainly of shore-inhabiting insects living near, on, or in wrack on shores of various size and substrate compositions.

A shore can vary in width from a few centimeters around rocky, steep-banked, small springs to several tens of meters on broad-shored lakes. These areas are affected by their neighboring terrestrial and aquatic ecosystems, so flooding and desiccation hazards are present. After floodwaters (or higher than normal tides on marine shores) recede they may leave deposits (e.g., sediment and/or wrack) that completely cover the habitats of the resident organisms. Other shore habitats are destroyed when their aquatic component subsides during periods of decreased precipitation or water course changes. In cases of flooding or subsidence the shore moves up or down relative to its previous position or the entire shore habitat is destroyed. Water level changes brought about by episodes of flooding or subsidence, plus the effects of currents and waves affect the permanence of the shore.

Permanence of the shore is affected by water level changes, local topography, and the ability of waves and currents to create, modify, or destroy shore areas. Shore alteration may be a gradual or rapid process depending upon the force(s) driving it. Gradual changes are noticeable over longer periods of time (e.g., several years, decades, or centuries). Lake shorelines may have seasonal changes, but rapid, devastating, immediate changes are not common. While the altering processes are continually at work their changes are usually noticed after a longer period of time, giving lakeshore areas a "permanent" appearance. This habitat stability allows for the establishment of long term shore insect populations. In essence, while the beach is slowly changing, the "flavor and character" of the beach remains relatively constant. I apply the term *permanent* to shore habitats (e.g., lakeshores, bogs, and some river shores) whose general structure and biotic community has remained "stable" for several years. For example, water levels at Wells Lake, Saskatchewan (Figure 2.1, Study site #14), have been very gradually subsiding since 1983 due to decreased yearly precipitation, but the general shore structure and biota has not changed greatly. Several years of increased precipitation could raise the water levels back to their 1983 level.

Precipitation can have a greater impact on some shore systems than others. Rapid changes in the water level of a flowing system can cause immediate and catastrophic changes to the shore area. Shore structure in flowing systems is more

ephemeral because of the nature of moving water. Riverine shore habitats can be created, modified, or destroyed in a matter of hours by increased amounts of precipitation or changes in river channel morphology (e.g., stream theft, bedrock resistance, etc.). The "temporary" nature of these habitats may prevent establishment of long term insect populations. I apply the term *temporary* to shore habitats (e.g., vernal sloughs, rivershores, and some lakeshores) whose general structure and biotic communities can change abruptly in a short time span. In mid-June 1986 a sudden and extensive flood altered what had been a relatively stable shore on the Pembina River near Barrhead, Alberta (Figure 2.1, Study site #5). Before the flood, the shore was a large flat expanse consisting of sand overlaid with thick mud deposits. Mud-loving species like *Bembidion interventor* Lindroth (Coleoptera: Carabidae) and *S. pallipes* were collected in large numbers from this site. Only sand-loving carabid species were collected on the steeply terraced "pure" sand beach which was left after the floodwaters receded. Saldids were collected only in small numbers, and only in newly formed silt-covered depositional areas.

2.2 Shore Habitat Classification

People, even in ancient times, were intimately familiar with the tidal cycle of the intertidal area. On marine shores the different tidal heights were named and their periodicity noted because of their economic and/or social importance. Intertidal shores were classified by their basic substrate (i.e., rock or sand), tidal height, and tidal periodicity. Since athalassic systems lack well-defined periodicity, their water levels may rise or fall unpredictably. Unlike intertidal areas athalassic shores are usually named after the aquatic systems they border and not water level periodicity. Problems in defining and classifying athalassic systems (Cowardin *et al.* 1979) have created difficulties for workers studying these shores.

Basic classification terms used for shores (i.e., "stream" *sensu* Evans 1986) do not accurately describe a shore habitat, rather they give the reader a basic idea about what habitat the researcher worked in. Detailed habitat descriptions usually cannot be compared from author to author because author's usually describe habitats from their own perspective. The shore descriptions of Evans (1986) and Zack (1979) have very little

in common, frustrating the synthesizer of their works. If both had followed a common habitat classification system, then had written their habitat descriptions, the similarities and differences between their habitats would be more apparent.

I used the Wetland Classification System of Cowardin *et al.* (1979) to classify the shores I sampled because it is consistent in classifying aquatic systems and their shores. Two independent observers using Cowardin *et al.* (1979) will get the same shore habitat classification. Other classification systems are not rigorous in their definition of habitat types so independent observers can get vastly different results. Wetland classification systems and, by extension, shore classification systems, should be based on hydrologic, geomorphologic, chemical, and biological factors. Most systems use one or two of the above factors to separate aquatic systems (e.g., Martin *et al.* 1953) whereas Cowardin *et al.* (1979) consider all of them. Other systems based on habitat preference(s) of a single species or a small group of species are common (e.g., Deonier 1979; Polhemus 1985). Species-based systems such as Deonier's "Ephydrid Habitat Types" (1979) are usually not applicable to other shore species or geographic regions. Regional differences in naming a system (e.g., prairie slough versus Canadian shield pond) create further difficulties.

Cowardin *et al.* (1979) is a straight-forward, simple-to-apply, hierarchical classification system progressing from SYSTEM to SUBSYSTEM, at the most general levels, to CLASS, SUBCLASS, and DOMINANCE TYPES. The term SYSTEM refers to a complex of habitats that share similar hydrologic, geomorphologic, chemical, and biological factors. Systems are further divided into Subsystems using shared similarities. CLASS describes the general appearance of the habitat by using the dominant plant species or composition of the inorganic substrate. Subclasses are based on finer distinctions in plant species or substrate materials. DOMINANCE TYPE is named for the predominant plant(s) or sedentary or sessile macroinvertebrate(s) species. WATER REGIME, WATER CHEMISTRY, SOIL and SPECIAL are modifiers that define the habitat in precise terms.

2.3 Site Descriptions and Collection Data

Saldid and substrate collection localities are described below. Sites are separated into Lacustrine, Palustrine and Riverine systems for the reader's convenience. The classification hierarchy is given for habitat so the reader can immediately see differences between the described habitats. SUBSYSTEM has been included in the Lacustrine section title as all lakeshore sites are littoral. Subsystems for riverine systems have been included in the locality description as there are different subsystem types present. There are no palustrine subsystems in the classification system of Cowardin *et al.*(1979). CLASS, SUBCLASS, DOMINANCE TYPE, WATER REGIME, and WATER CHEMISTRY descriptors are included for sites as applicable. Also, unless otherwise stated, *S. pallipes* in the following habitat descriptions refer exclusively to the black variety and not to the tan variety (see Appendix 1 for details).

Adult and nymphal saldids, especially individuals of the *S. pallipes* complex, were collected using a vacuum aspirator (modified from Marshall 1982) from numerous shore habitats. Collecting trips started in spring shortly after snow had melted from the diapause sites and were terminated by the first lasting snowfall in autumn. The shore habitats from Alberta and Saskatchewan that are described in Section 2.3 were usually sampled several times per collecting season. Sampling was not done in a standardized quantitative manner because I was looking for obvious similarities and differences in the types of shore habitats that members of the *S. pallipes* complex were associated with. In essence, could a shore classification system be easily used by fellow saldid systematists to recognize species within the *S. pallipes* complex.

While at each site, I attempted to collect as many saldids as possible before the batteries in the vacuum aspirator were discharged (after approximately 0.5 h of continuous suction). Since I had three rechargeable battery packs this allowed for approximately 1.5 h of continuous suction collecting time. However, the aspirator was only briefly turned on while collecting an individual saldid so the amount of time spent at the site often exceeded 1.5 h. The amount of time spent at each site varied depending upon weather conditions (i.e., saldids are active in the open sunlight areas of the shore) and how readily collected the saldids were. Habitats in which saldids were numerous (i.e., >1 individual per m^2) were paid greater attention than those where there was <1 individual per m^2.

Identifying members of *Saldula* requires either a dissecting microscope or hand lens, of sufficient magnification (i.e., 50X). I collected as many specimens as possible and later separated them to species in the laboratory under a dissecting microscope. By collecting in this manner I believe that I was not biased to collect a particular species, variety, or Form from any habitat.

2.3.1 Littoral Lacustrine Habitats

Wells Lake

CLASS	Unconsolidated shore
SUBCLASS	Mud
DOMINANCE TYPE	Algal wrack and/or evaporite deposits
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Alkaline

SITE 2 kilometers west of Marsden, Saskatchewan (Figure 2.1)

Wells Lake has a complex shore habitat due to the shallow slope of the shore. As a result, small changes in water level have a disproportionate effect on exposed shore area. The shore area can be divided into three distinct zones: low, mid, and high. Large sheets of wrack composed of green algae (mainly *Cladophora* spp.) are usually present on the lower beach and to a lesser extent on the salt-encrusted (mainly sodium sulphate, Hammer 1978) mid beach area. Lake water levels fall during some years due to low precipitation in late spring and summer and no extensive algal wracks are formed; under these conditions, small amounts of aquatic grasses are deposited on the immediate shoreline. Specimens of the tan variety of *S. pallipes* occur in large numbers on the low beach; their numbers decrease markedly higher on the beach, and it is only rarely collected in the high beach areas. Specimens of the black variety of *S. pallipes* were infrequently collected at Wells Lake, and then only in the low beach area while those of *Pentacora signoreti* were commonly collected from the mid beach area from late July to mid August. Dense growths of blue-green algae [*Oscillatoria animalis* Adardh and *O. subbrevis* Schmidle; (Evans 1988)] occur in shallow, sometimes water-filled, depressions surrounded by tussocks of beach grass on the high beach. Specimens of *Salda provancheri* Kelton and Lattin were collected only from the high beach zone.

Red Deer Lake

CLASS	Unconsolidated shore
SUBCLASS	Sand
DOMINANCE TYPE	Algal wrack
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Alkaline

SITE 32 kilometers east of Ponoka, Alberta (Figure 2.1)

The lake has a predominantly sand shore with some exposed rocks and patches of algal wrack confined to the immediate beach. Unlike Wells Lake, substantial evaporite deposits are rarely encountered at Red Deer Lake. The large numbers of tan variety of S. *pallipes* occur on the wrack, where they feed upon collembolans (Isotomidae) and ephydrid fly larvae. Due to steep relief the high beach is usually less than three meters from the waterline; in contrast, the high beach at Wells Lake is usually 10 to 40 meters away. Specimens of *Salda provancheri* were abundant among thin stands of beach grass growing around scattered stones of the high beach.

Manito Lake

CLASS	Unconsolidated shore
SUBCLASS	Sand
DOMINANCE TYPE	Sparse green algal wrack
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Alkaline

SITE 7 kilometers southeast of Marsden, Saskatchewan (Figure 2.1)

While Manito Lake is connected to Wells Lake, the shore structure and composition is similar to Red Deer Lake. Specimens of the tan variety of *S. pallipes* were collected on shoreline algal wrack, while individuals of *Salda provancheri* were taken in patches of grass on the high beach.

Calling Lake

	Site 1 (Calling Lake Provincial Park)	**Site 2 (Public Beach)**
CLASS	Unconsolidated shore	Unconsolidated shore
SUBCLASS	Stone and sand	Sand
DOMINANCE	*Typha latifolia* and aquatic grass wrack	Aquatic grass wrack
WATER REGIME	Seasonally flooded	Seasonally flooded
WATER CHEMISTRY	Fresh	Fresh

	Site 3 (Private Sand Beach)
CLASS	Unconsolidated shore
SUBCLASS	Sand
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Fresh

SITE 59 kilometers north of Athabasca, Alberta (Figure 2.1)

Three different shores were examined at Calling Lake: rock with sparse grassy wrack (site 1); sand with sparse wrack (site 2); and a "pure" sand beach (site 3). Specimens of *S. pallipes* from the rock beach were collected only on the numerous large rocks and not on wrack or sand. Very few insects were associated with wrack that had collected in spaces between rocks and up on the higher sandy beach.

Much larger numbers of the black variety of *S. pallipes* than the tan variety of *S. pallipes* were collected on a public sand beach, which had sparse grassy wrack on the immediate shoreline. Green algal cells growing in the interstitial spaces between sand grains of the lower beach gave the light brown sand a slight green tinge. Collembolans, ephydrids, and other shoreline, wrack-inhabiting insects were also collected in this habitat.

The private "pure" sand beach had no grassy wrack or greenish tinge to the sand. Aside from the low numbers of saldids and *Bembidion* spp. (Coleoptera: Carabidae) on this shore, no other shore insects were noted, possibly due to the lack of plant material.

Sylvan Lake

CLASS	Unconsolidated shore
SUBCLASS	Cobble-gravel
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Fresh

SITE 24 kilometers west of Red Deer, Alberta (Figure 2.1)

This man-made shore was created by pouring large rocks into the lake to form a dock. Algal and grassy wrack deposits collected in rock interstices provided resources for developing collembolans, ephydrid flies, and other insects. Both nymphs and adults of *S. pallipes* were present, indicating the shore area is stable. Adult saldids were caught both on wrack and sun-exposed rocks while nymphs were found only on wrack.

Hastings Lake

	SITE 1	SITE 2
CLASS	Unconsolidated shore	Unconsolidated shore
SUBCLASS	Organic	Sand
DOMINANCE TYPE	*Typha latifolia* L.	*T. latifolia* wrack
WATER REGIME	Seasonally flooded	Seasonally flooded
WATER CHEMISTRY	Fresh	Fresh

SITE 28 kilometers east of Edmonton, Alberta (Figure 2.1)

Two distinctly different shore habitats were examined at Hastings lake: *T. latifolia* growing in black chernozemic soil (site 1); and sand covered with wrack (predominantly *T. latifolia*) (site 2). Specimens of *S. pallipes* were collected on algal-soil patches between *T. latifolia* stands. Unfortunately this site was flooded during this study, so another site had to be found on this lake. At the second site, adults and nymphs of S. *pallipes* were collected on or near *T. latifolia* wrack that had accumulated on a sand beach.

2.3.2 Palustrine Habitats

George Lake

CLASS	Emergent wetland
SUBCLASS	Persistent
DOMINANCE TYPE	Sedge stand
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE approximately 16 kilometers west of Busby, Alberta (Figure 2.1)

Specimens of *S. pallipes* were taken on heaps of decomposing vegetation from small open areas within a sedge stand which extended well out into the lake. Despite considerable collecting effort, few specimens were taken, suggesting this may be a marginal habitat for *S. pallipes*.

Sugarloaf Pond

CLASS	Unconsolidated shore
SUBCLASS	Gravel
DOMINANCE TYPE	Grass
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Fresh

SITE 2 kilometers north-east of St. John's, Newfoundland (Figure 2.2)

Saldid nymphs and adults hid in short clumps of grass growing in a shore composed of gravel and sand with some small rocks present. Shoreline vegetation surrounding the pond suggested that variation in water level was slight, indicating a stable shore.

House River Gravel Pit

CLASS	Unconsolidated shore
SUBCLASS	Mud
WATER REGIME	Saturated
WATER CHEMISTRY	Fresh

SITE 52 kilometers north of Wandering River, Alberta (Figure 2.1)

Adults of *S. pallipes* were taken along the muddy edge of a large, shallow, water-filled pit in the older and less frequently used section of a gravel pit operation. No standing vegetation was present around the muddy margin but a slight green algal sheen was present in the near shore mud.

Wagner Natural Area

	Site 1 (Marl flats)	Site 2 (Bog)
CLASS	Unconsolidated shore	Forested wetland
SUBCLASS	Mud	Needle-leaved Evergreen
DOMINANCE TYPE	Feather moss	*Sphagnum* spp.
WATER REGIME	Saturated	Saturated
WATER CHEMISTRY	Alkaline to fresh	Fresh to acid

SITE 7 kilometers west of Edmonton, Alberta (Figure 2.1)

Saldids from the Wagner Natural Area were collected in patches of fen and bog. Specimens of *Salda provancheri* were taken in large numbers but only on marl flats, while those of Saldula *pallipes* were also taken infrequently, also only on marl flats. Individuals of *Lampracanthia crassicornis* (Uhler) and *Micracanthia bergrothi* (Jakovlev) were collected on small sphagnum hillocks in open boggy areas surrounded by black spruce [*Picea mariana* (Mill.)].

Glenn's Slough

	Site 1	Site 2
CLASS	Unconsolidated shore	Emergent wetland
SUBCLASS	Vegetated	Palustrine persistent emergent wetland
DOMINANCE TYPE	Grass and sedge	Duckweed
WATER REGIME	Semipermanently flooded	Semipermanently flooded
WATER CHEMISTRY	Fresh	Fresh

SITE 16 kilometers east of Legal, Alberta (Figure 2.1)

This site is a typical Alberta parkland slough, where the organic component of the soil was developed from mosses, rushes, sedges, and woody materials. Although water levels have changed slowly, the slough has been present for at least forty years (M. Ozipko pers. comm.). Specimens of *S. pallipes* were commonly found on shore, on thick mats of floating duckweed (*Lemna* spp.), and on emergent grass/sedge tussocks, while those of *Saldula opacula* (Zetterstedt) were found exclusively on floating duckweed mats. Individuals of *S. pallipes* were collected in higher numbers than *S. opacula* throughout the field season; however, higher numbers of *S. opacula* were caught in spring and fall.

Pembina Slough

CLASS	Unconsolidated shore
SUBCLASS	Vegetated
DOMINANCE TYPE	Grass
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE approximately 16 km south of Barrhead, Alberta (Figure 2.1)

The shoreline is similar to Glenn's Slough but grasses were close-cropped due to grazing cattle. Specimens of *S. pallipes* occurred in low numbers while those of *S. opacula* were not found possibly because of the scant cover of *Lemna* spp.

Cooking Lake Slough

CLASS	Emergent wetland
SUBCLASS	Persistent
DOMINANCE TYPE	*T. latifolia* stands
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE 22 km east of Edmonton, Alberta (Figure 2.1)

The collecting area is connected by an extensive shallow slough to Cooking Lake proper, which was approximately one kilometer away. Mudflats were formed on the southeastern edge of the slough when water levels dropped in late spring 1989. Adults and nymphs of S. *pallipes* were collected on the muddy surface between tussocks of grass and stands of *T. latifolia*. By late summer, 1989, water levels had risen and covered the mudflats.

2.3.3 Riverine Habitats

Amisk Creek

SUBSYSTEM	Intermittent
CLASS	Streambed
SUBCLASS	Organic
DOMINANCE TYPE	Grass stands and algal filled depressions
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Fresh to acidic

SITE 10 kilometers southeast of Tofield, Alberta (Figure 2.1)

Specimens of *S. pallipes* and *S. comatula* were taken in small numbers from a partially overgrown mudflat formed during the summer of 1988 by receding water levels. No saldid specimens were taken during 1989 and 1990 because this shore area was under water.

Newton Creek

SUBSYSTEM	Intermittent
CLASS	Streambed
SUBCLASS	Organic and mud
DOMINANCE TYPE	Stranded duckweed
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE approximately 16 kilometers west of Busby, Alberta (Figure 2.1)

After a beaver dam was demolished in the summer of 1989, the outflow from George Lake flowed freely again, exposing a large, muddy, duckweed covered shore. Nymphs and adults of *S. pallipes* were taken in large numbers from this temporary habitat. The dam was rebuilt early in the summer of 1990, and shortly thereafter the site was again under water.

Mount Sarrail Campsite Creek

SUBSYSTEM	Lower perennial
CLASS	Unconsolidated shore
SUBCLASS	Vegetated
DOMINANCE TYPE	Moss and *Equisetum* spp.
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE 67 kilometers southwest of Calgary, Alberta (Figure 2.1)

This site was a small unnamed creek that joined the southern end of Lower Kananaskis Lake to Upper Kananaskis Lake due east of Mount Sarrail Campsite. The shore had a diverse saldid fauna. Specimens of *Micracanthia bergrothi* and *Teloleuca bifasciata* (Thomson) were readily collected while those of S. *pallipes*, and *S. bouchervillei* (Provancher), and *Salda* nr. *alta* Polhemus were present in much lower numbers. Two weeks after initial collection, this site was visited again. It was found to be underwater but the same species could still be collected along the new shoreline.

Pembina River

SUBSYSTEM	Lower perennial
CLASS	Unconsolidated shore
SUBCLASS	Sand and mud
WATER REGIME	Seasonally flooded
WATER CHEMISTRY	Fresh

SITE approximately 15 kilometers south of Barrhead, Alberta (Figure 2.1)

From 1984 to early 1986, specimens of *S. pallipes* were found in open areas of sand overlaid by silt near the water's edge. In mid-June, 1986, an extensive flood altered the beach and created a "pure" sand shore. Changes in the carabid beetle fauna and distribution of *S. pallipes* were noted. *Saldula pallipes*, in very small numbers, were found only in a small, isolated, *Equisetum*-covered patch of silt and sand on the depositional shore. Since the flood, alluvial silt deposits have been building up in shallow depressions along the immediate shore. Saldids have been collected in these exposed depositional zones. The presence of saldid nymphs in 1989 indicated breeding populations had again been established after being "wiped-out" in 1986.

North Saskatchewan River

SUBSYSTEM	Lower perennial
CLASS	Unconsolidated shore
SUBCLASS	Sand or mud-organic
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE below Groat Road Bridge in Edmonton, Alberta (Figure 2.1)

Large, sediment-scoured shore areas appear after spring runoff, but unusual weather conditions (e.g., above or below average precipitation) can have profound immediate effects and changes which affected collecting success. Specimens of *S. pallipes* were never collected on lower shores but were collected in older, overgrown, exposed river channels.

House River

SUBSYSTEM	Upper perennial
CLASS	Unconsolidated shore
SUBCLASS	Gravel
WATER REGIME	Semipermanently flooded
WATER CHEMISTRY	Fresh

SITE 51 kilometers north of Wandering River, Alberta (Figure 2.1)

Individuals of *S. pallipes* were found in small numbers along the rocky, relatively vegetation-bare, sand shores of this river running through the boreal forest of northern Alberta.

2.3.4 Ontario Habitats

I have no first-hand observations of these sites as saldids were sent to me by a colleague. Descriptions of the shore may not be accurate as detailed descriptions or photos were not included with the specimens. Shore material inadvertently gathered with the saldids allows me to make crude descriptions.

Rondeau Provincial Park

SYSTEM	Lacustrine
SUBSYSTEM	Littoral
CLASS	Unconsolidated shore
SUBCLASS	Sand
DOMINANCE TYPE	Algal wrack

SITE on Lake Erie, Kent County, Ontario (Figure 2.2)

Forty-five specimens of S. *pallipes* were collected on a sandy, wrack-covered shore.

Medway Creek

SYSTEM	Riverine
SUBSYSTEM	Lower perennial
CLASS	Unconsolidated shore
SUBCLASS	Mud

SITE London, Middlesex County, Ontario (Figure 2.2)

Individuals of *S. pallipes* were collected on the silt banks of Medway Creek below the University of Western Ontario.

2.4 Results and Discussion

The examined species of saldids were generally collected in a certain type of habitat (Table 2.1). Individuals of *P. signoreti* were collected on permanent alkaline shores while those of *S. opacula* were collected only on floating mats of *Lemna* spp. Specimens of *S. provancheri* were collected from a wider variety of habitats whose shores tended to be permanent. Individuals of the tan variety of *S. pallipes* were usually collected on permanent alkaline shores while specimens of the black variety were usually collected on temporary freshwater shores. Alkaline shores occur predominantly in the *Saline Lakes Limnological Region* of the prairie provinces (*sensu* Northcote and Larkin 1966). The absence of saline habitats in the *Forest Zone of Freshwater Lakes* (*sensu* Northcote and Larkin 1966) suggests this may be the northern limit for the tan variety. Individuals of the black variety were collected on a variety of temporary and permanent freshwater habitats. These habitats occur all over the province but are especially predominant in the northern half of the province of Alberta (Northcote and Larkin 1966). Freshwater corridors through the *Saline Lakes Limnological Region* are provided by rivers

(Northcote and Larkin 1966) thus allowing the black variety of *S. pallipes* into the *Great Plains Area* (*sensu* Allen 1892). Therefore, although the two varieties occur in the same geographic area of central Alberta and Saskatchewan they were generally collected in markedly different habitats which maintain their separation. Individuals of either variety were infrequently collected at sites where the other variety was more readily collected.

Although individuals of either variety infrequently co-occurred in the same habitat the relative abundance of the rarer variety did not equal its abundance in habitats where it was more readily collected. For example, individuals of the tan variety were not similarly abundant at Calling Lake and Red Deer Lake (Table 2.1) while individuals of the black variety were not similarly abundant at Wells Lake and Glenn's Slough (Table 2.1).

The presence and abundance of a species in a habitat in itself does not suggest that it is the preferred or required habitat. The absence of one species may be the result of competition with another, or the species for other reasons has not been able to colonize that habitat. While my data suggests there was a fundamental difference between the kind of habitats that either variety of *S. pallipes* was collected in, it does not prove that these varieties represent non-interbreeding groups nor that these observed differences have an ecological and/or behavioral basis. Other methods must be used to determine if the observed habitat collection data reflect the distinctness of the two varieties of *S. pallipes*.

Knowing that individuals of *S. pallipes* respond to allelochemicals from the habitat they were collected from (Evans 1988),I wanted to determine the habitat specificity of each variety. By determining habitat specificity, questions regarding the frequency individuals of both varieties co-occur and possible interbreeding can be answered.

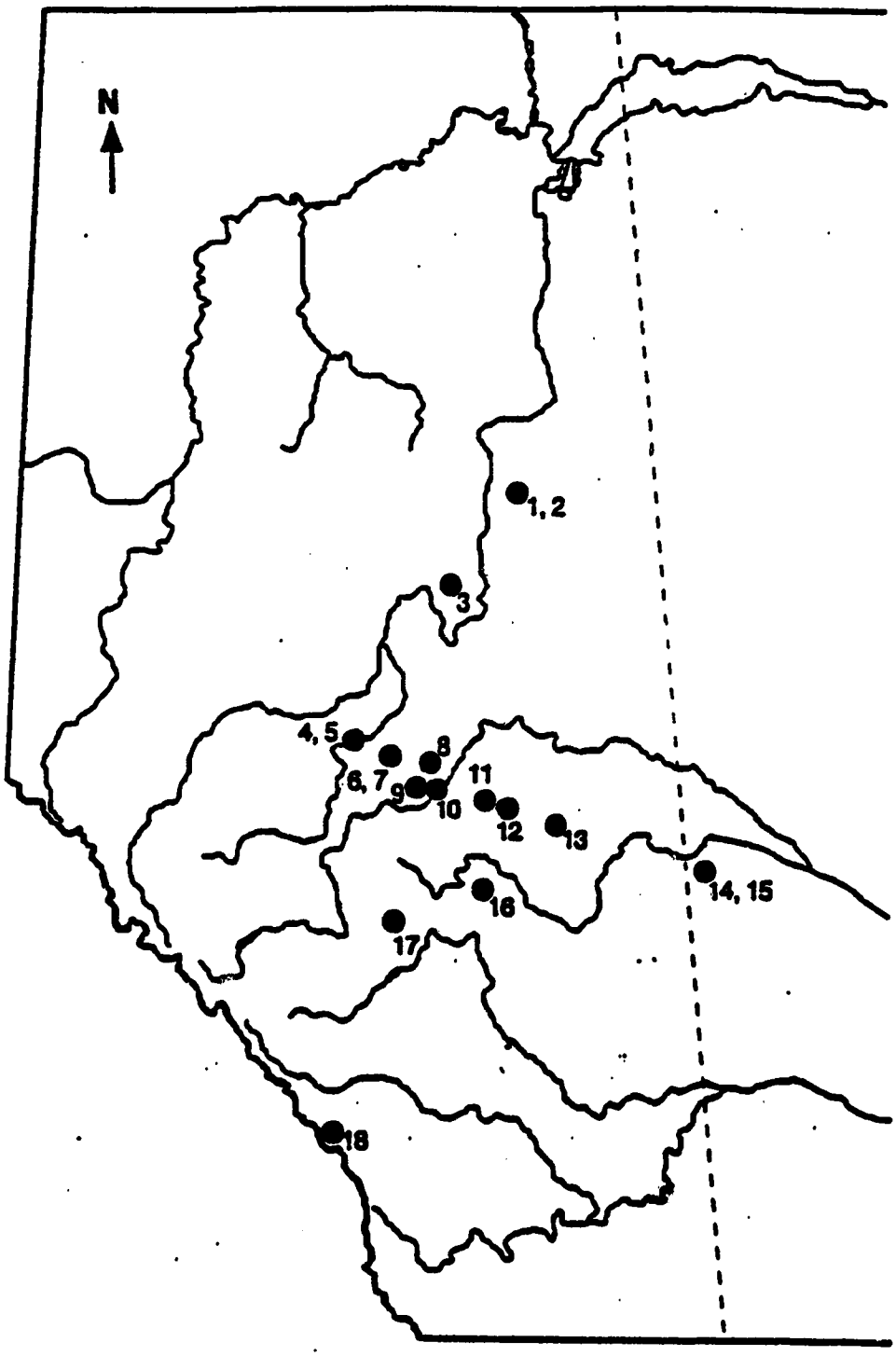


Figure 2.1 Field sites in Alberta and western Saskatchewan.
1. House River; 2. House River Gravel Pit; 3. Calling Lake; 4. Pembina Slough; 5. Pembina River; 6. Newton Creek; 7. George Lake; 8. Glenn's Slough; 9. Wagner Bog; 10. North Saskatchewan River; 11. Cooking Lake; 12. Hastings Lake; 13. Amisk Creek; 14. Wells Lake; 15. Manito Lake; 16. Red Deer Lake; 17. Sylvan Lake; 18. Mount Sarrail Campsite Creek.

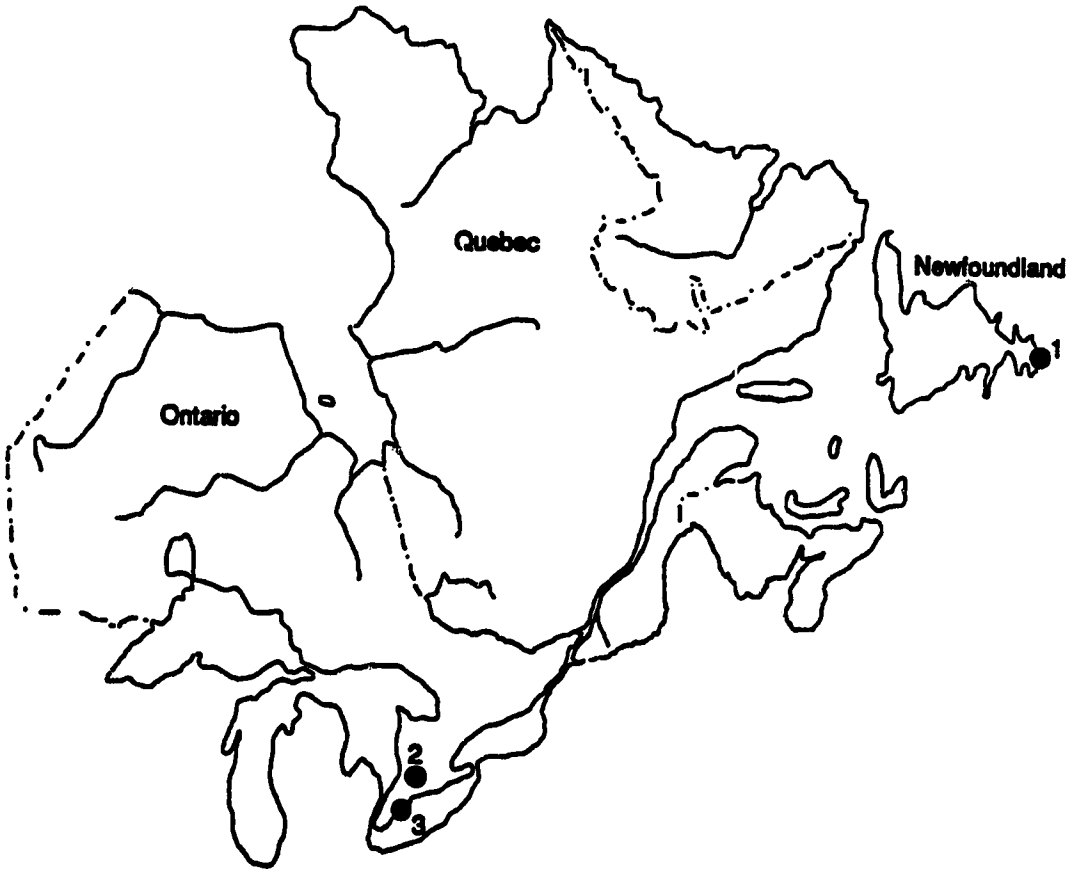


Figure 2.2 Eastern Canada field sites. 1. Sugarloaf pond, Newfoundland; 2. Medway Creek, Ontario; 3. Rondeau Provincial Park, Ontario.

Table 2.1 Approximate numbers of four species of saldids collected at field sites.

SITE	BLACK *Saldula pallipes*	TAN *Saldula pallipes*	*Saldula opacula*	*Salda provancheri*	*Pentacora signoreti*
Wells Lake, Sask.	10	50000	0	150	100
Red Deer Lake, Alta.	10	30000	0	700	0
Manito Lake, Sask.	5	5000	0	50	0
Calling lake, Alta.	100	10	0	10	0
Sylvan lake, Alta.	75	0	0	0	0
Hastings Lake, Alta.	60	0	0	0	0
George Lake, Alta.	40	0	0	10	0
Sugarloaf Pond, Nfld.	40	0	0	0	0
House River Gravel Pit, Alta.	50	0	0	0	0
Pembina Slough, Alta.	50	0	0	0	0
Wagner Natural Area, Alta.	20	0	0	5	0
Glenn's Slough, Alta.	200	0	50	0	0
Cooking Lake Slough, Alta.	50	0	0	0	0
Amisk Creek, Alta.	50	0	0	0	0
Newton Creek, Alta.	150	2	0	0	0
Mount Sarrial Campsite Creek, Alta.	20	0	0	0	0
Pembina River, Alta.	250	0	0	0	0
North Saskatchewan River, Alta.	100	5	0	0	0
House River, Alta.	35	5	0	0	0
Rondeau Park, Ont.	45	0	0	0	0
Medway Creek, Ont.	35	0	0	0	0

3. Chemically-mediated habitat selection of *Saldula pallipes*

3.1 Introduction

All insects live in a habitat. Do they hatch or move there or are they somehow transported there? Female insects usually oviposit in the appropriate juvenile microhabitat (Albert 1991; Thompson 1988) and, when developing individuals become adults, do they move out of their juvenile habitat site and look for a "new" (at least to that individual) habitat site? If so, how do they do this? By using a variety of cues, which are perceived and interpreted by the dispersing insect's nervous system, the appropriate response (e.g., klinokinesis, anemotaxis) is coded for by the disperser's nervous system (Dethier 1982) thus enabling it to move towards the required resource (i.e., potential mates, food).

Olfactory cues are used by a wide variety of insects to locate mates (Cardé and Baker 1984; Tobin and Bell 1986), plant and animal hosts (Vinson 1984; Roland *et al.* 1989) and habitats (Evans 1982, 1984, 1988; Hoffmann *et al.* 1984). Shoreline carabids perceive and orient upwind to habitat allelochemicals blown over them (Evans 1984). These carabids also responded to habitat allelochemicals in choice chambers where there is no directional information; therefore these insects use the allelochemicals, which act as arrestants (Dethier *et al.* 1960), as short-range cues for microhabitat identification. Similarly, *S. pallipes* responds in choice chambers to allelochemicals from habitats in which they were caught (Evans 1988).

Saldula pallipes moves among shore habitats because adverse weather conditions may cause episodes of flooding or desiccation. Ecological succession may arise from terrestrial encroachment (i.e., from a large open lake to a swamp) or simple shore processes such as silt deposition on a sandy rivershore. Adults of *Saldula* must locate shore habitats after diapausing in the leaf litter of drier, upland, forested areas. These diapause areas are at least several meters from the shore habitat and possibly up to several kilometers away. Individuals of *S. pallipes* have been collected from flight intercept traps set up in forested areas several kilometers away from shore areas during the summer (pers. obs.), indicating that long distance dispersal is not unusual. Suitable new shore habitats are rapidly colonized by adults of *S. pallipes* (pers. obs.) suggesting they are very efficient at finding shore areas.

Aside from Evans' (1988) limited work there are no published records of chemically mediated habitat selection experiments in the Saldidae even though many authors have commented in their species descriptions and/or regional keys as to what kind of habitat members of certain saldid species are most commonly collected. The *habitat preferences* (*sensu* Polhemus 1985) of some species are quite well known (e.g., *P. signoreti*, inland alkaline and intertidal- sediment shores, Polhemus 1985), but the habitat preferences for some other species were assumed to be rather broad because they have not been examined in detail. Yet, when species descriptions and collection records of the various species of saldids are examined certain trends are noticed (pers. obs.). Most species have been collected in very few types of habitats, some are restricted to only one habitat while others are collected in habitats that very closely approximate each other. I find it surprising that other saldid workers have not noticed this trend and have not tried to separate *S. pallipes* on the basis of what type of habitat the specimens were collected in. Essentially, habitat specificity differences among members of the *S. pallipes* group may reflect actual species level differences. These differences in habitat specificity can be (at least partially) determined by observing how insects respond to "cues" from the habitat.

Shore insects use a variety of cues (e.g., visual, chemical) to locate shore habitats. Saldids (Evans 1988) and carabid beetles (Evans 1982, 1983, 1984, 1986, 1988) respond to volatiles of cyanobacteria and chlororphytic algae found in the shore habitat. Different species or ecophentypes of microorganisms present in the habitat emit unique, volatile "chemical signatures" that are recognized by the appropriate insect members (W.G. Evans pers. comm.). Seven shoreline carabid species were classified as eurytopic or stenotopic depending upon their response to allelochemicals from habitats other than those from which they were collected (Evans 1988).

Individuals of *Saldula comatula* Parshley and *S. pallipes* respond positively to habitat allelochemicals from habitats in which they were caught but response to allelochemicals from other habitats was not ascertained (Evans 1988). In Alberta, specimens of S. *pallipes* can be collected in almost every shore habitat. It is not known whether members of the *S. pallipes* species complex are eurytopic or stenotopic. If individuals of *S. pallipes* are stenotopic then habitat collection data could be used to aid in the separation and classification of the various species in this complex.

Insects diagnosable as *S. pallipes* from Alberta and western Saskatchewan came in at least two distinct commonly-encountered varieties, black and tan. Individuals of the black variety were collected on temporary habitats such as sloughs, ponds, creeks, and rivers, but were also found on more stable habitats such as freshwater lakeshores. Individuals of the tan variety, while being found in the same geographic area as the black variety, were collected on permanent and temporary alkaline shore habitats. Individuals of either variety were rarely collected at shore habitats where the other variety was commonly collected.

In this study I examine whether habitat allelochemicals are used by individuals of *S. pallipes* to identify and distinguish shore habitats. Adult response to habitat allelochemicals from a variety of shore habitats may indicate whether or not reproductive isolation is occurring among populations of *S. pallipes* inhabiting Alberta and western Saskatchewan. This information could aid in the separation of the species in this complex. I also address how the allelochemical presentation method (i.e., wind tunnel or choice chamber) affects the response of individual *S. pallipes* to a habitat's allelochemicals. This is extremely important because an insect goes through a hierarchy of cues in the wild to locate the correct habitat, patch, and/or resource unit (Bell 1990). In essence, at long range the insect uses one set of cues while at a shorter range it may use the same and/or a different set of cues. For example, short range and contact cues may be similar in different shore habitats but if the long range cues are different, the insect will never be in a position where it is using these similar short range and/or contact cues to select a habitat that it is not normally associated with.

3.2 Materials and Methods

3.2.1 Collection, Handling, and Maintenance of Saldids

While specimens of *S. pallipes* can be collected from most shore environments in Alberta and Saskatchewan, they reach their highest densities on alkaline lakeshores. Individuals of *S. pallipes* from Wells Lake, Saskatchewan (Site #14, Figure 2.1), and to a lesser degree, Red Deer Lake, Alberta (Site #16, Figure 2.1) were chosen as the populations for experiments. Several distinct tan Forms of *S. pallipes* co-occur at Wells Lake, Red Deer Lake, and other alkaline shore habitats in Alberta and western

Saskatchewan (for full discussion of Form variation see *S. sodanuma* species description in Appendix 1). For the habitat selection experiments I used the Form, hereafter referred to as "Form A", that was the most abundant in the *S. pallipes* populations at Wells Lake and Red Deer Lake. This was done because I was unsure whether these Forms (which may represent different species or phenotypes of the same species) would respond differently to habitat allelochemicals.

Adult and nymphal *S. pallipes* were collected using a vacuum aspirator (modified from Marshall 1982). Captured saldids were placed in a large plastic holding container, with dampened paper towels (to prevent desiccation) and returned to the laboratory for sorting.

Specimens were gently shaken into a deep-sided glass dish sitting in a tray of ice. All the collected nymphs were placed in 21 litre Hagen aquariums lined with moistened crushed dolomite and fed freezer killed adults of *Sarcophaga bullata*. Fresh food was added every two to three days, after dead saldids and "old foodstuffs" were removed. Substrate dampness was checked three to four times each week and deionized water was added if required. These terrariums were housed in a Conviron 8601 Incubator set at 18 hours light, 20°C : 6 hours dark, 14°C; nymphs require synchronized temperature and photoperiod conditions for maximum rearing success (Stock and Lattin 1976). Rearings from each collection were retained as vouchers for subsequent morphological evaluation.

Individual Form A adults were separated from other co-occurring Forms and further divided by sex. Each sex was maintained in separate terrariums similar to the rearing terrariums but these were placed in a Precision Incubator at 6°C set for a 18 light : 6 dark hour photoperiod. These Form A adults were used in the choice chamber and wind tunnel tests. Most of the habitat selection tests were done using specimens from Wells Lake because they were readily collected in greater numbers. Limited experiments with Form A individuals from Red Deer Lake were also conducted. Voucher specimens of all Forms were preserved in 70% ethyl alcohol for later morphological evaluation.

Individuals of *Saldula* spp. unlike other hemipterans [e.g., *Rhodnius* spp. (Reduviidae), *Gerris* and *Limnoporous* spp. (Gerridae), *Oncopletus* spp. (Lygaeidae), *Geocoris* spp. (Lygaeidae)] do not fare well in laboratory cultures. The various attempts

at mass rearing and maintaining wild caught individuals were an extremely frustrating series of experiences. The rearing and maintenance methods outlined in the previous two paragraphs worked the best. It should also be noted that nymphal mortality even with this rearing method often approached 95%. The field obtained adults became debilitated after only a week in the lab and perished shortly thereafter. Only healthy individuals which were a few days removed from the field were used in the choice chamber and wind tunnel experiments.

3.2.2 Collection of Habitat Allelochemicals

Habitat allelochemicals were collected by placing filter papers on the habitat substrate to adsorb volatiles (Evans 1982). Filter papers were placed at Hastings Lake (Field Site 12, Figure 2.1) on algal-mud substrate between invading *T. latifolia* tussocks because I was unable to scrape off the uppermost layer of substrate for use in the choice chamber or wind tunnel.

Previous to these filter papers (Whatman No. 2 filter papers, 5.5 cm diameter) being placed on the substrate they were prewashed in a Soxhlet apparatus containing a 1:1 mixture of chloroform and methanol to remove most inorganic and organic manufacturing contaminants. Washed filter papers were removed from the Soxhlet and allowed to dry in a fumehood. Filter papers were then placed in airtight, quart-sized, glass jars until needed. Between 100 and 150 individual filter papers were pressed down on the microhabitat substrate with clean forceps to absorb volatiles. Filter papers were retrieved and stored in 250 ml airtight glass jars after remaining in the field for at least three days. Small jars were used to minimize glass surface adsorption of habitat volatiles. Papers collected in the field were transported to the laboratory in a cooler. Jars were stored (at -35°C in a walk-in freezer) until filter papers were needed for choice chamber experiments.

Habitat substrate was collected from field sites where the filter paper technique was not appropriate due to possible human interference, habitat permanence, and/or substrate structure. The uppermost layer of substrate was scraped or peeled off and tightly packed in airtight 250 ml glass jars. Evaporite deposits, low-shore wrack, and mud scrapings were collected from the mid and low beach of Wells Lake. Sand containing

interstitial green algae was collected from low beach areas of Manito Lake (Field Site 14, Figure 2.1) and Calling Lake (Field Site 3, Figure 2.1). Wet mud was collected alongside the Red Deer lakeshore. Substrate samples were transported to the laboratory in a cooler and stored (at -35°C in the walk-in freezer).

3.2.3 Testing for Habitat Specificity

Habitat allelochemicals invoke specific behavioral responses that are dependent on the nature of the signal. At long distances from the habitat, allelochemicals may induce an anemotactic response (i.e., movement upwind to an odor source) which can be observed in a wind tunnel (Bell 1990). At shorter distances habitat allelochemicals induce searching and arrestment behaviors (i.e., movements that allow an insect to remain within its resource patch, Bell 1990). Choice chambers were used because insects can actively distinguish between two conditions and choose a particular condition (e.g., damp preferred over dry).

3.2.3.1 Choice Chamber Bioassays

Open bottomed choice chambers (Figure 3.2) were selected because they allow for tarsal and antennal contact with the substrate. The possibility that the distribution of an individual saldid would affect other saldids in the testing chamber and possible pooling fallacy errors (i.e., treating repeated measurements of the same subject as though they were independent, Machlis *et al.* 1985) prompted me to change the experimental procedure of Evans (1988). Two filter paper halves (Whatman #2, 5.5 cm diameter) untreated or treated with habitat volatiles or substrate were placed on the bottom of the choice chamber. A single saldid was placed in a choice chamber which was then placed inside a large opaque container that eliminates external visual influences. Five times at 2 min. intervals the side the saldid was on was recorded. Sexes were tested separately to determine if there were any sexually-based differences in response to habitat allelochemicals. Possible pooling error was eliminated by averaging the observations for a single individual so "n" percent of the observations were spent on the habitat-exposed filter paper. After averaging, the data for all individuals was

summed and analyzed using χ^2 goodness of fit test for observed to expected ratios of 1:1 (χ^2, Zar 1984).

3.2.3.2 Wind Tunnel Bioassay

A wind tunnel designed by Evans (1984) was used for discerning odor-mediated anemotactic responses in saldids. Wrack from the low shore of Wells Lake, and from sand scrapings from Calling Lake were presented to both sexes of Form A *S. pallipes* from Wells Lake. Volatiles either from mud scrapings collected alongside Red Deer Lake or from low-shore wrack from Wells Lake were presented to both sexes of Form A *S. pallipes* from Red Deer Lake.

Operating Procedure for Wind Tunnel

A Braun slide projector/viewer placed directly above the "working section" of the wind tunnel (see Evans 1984) was used to project a 10 cm diameter circle, divided into twelve 30° sectors (radiating from the center), onto a thin stainless steel plate set horizontally in the working section (see Evans 1984). The first sector represents 345° to 15° with 0° facing directly upwind, the second from 15° to 45°, and so forth to the twelfth sector representing 330° to 360°. A light intensity of 31 lux illuminated the circle (Evans 1984). Windspeed was measured with a tubular anemometer probe (TSI, Inc. St. Paul, MN) and set at 0.75 m s^{-1} with a variable transformer.

Odor injection procedures differed slightly from Evans (1984). Instead of using treatment and mixing chambers (see Evans 1984, Figure 1), habitat volatiles were injected directly onto the mixing fan. Volatiles were obtained by placing habitat substrate in two glass tubes 20 cm long x 5.5 cm ID. A male 55/50 ground glass joint on the end of one tube connected with a female joint on the other tube, forming a sealed tube. The other ends were tapered to 8 mm OD x 7 cm tubing. Swagelok fittings capped these ends, sealing the tube. The Swagelok caps were removed just prior to tapping odors from the tube. A length of surgical rubber tubing attached the glass tube to a 50 ml syringe mounted on a Fisher Burette Dispenser (Model 395). The volatile-laden air was

sucked into the 50 ml syringe on the downstroke of the dispenser unit. Odor was injected into the wind tunnel at a rate of 6.4 ml $min.^{-1}$ when the dispenser was running.

A test insect was dropped from a beaker into a glass funnel, whose flattened base rested on the stainless steel arena in the center of the projected circle. After 5 s the pump injecting treated or untreated air into the wind tunnel inlet was turned on. The insect was released into the airstream 7 s later by lifting the funnel out of the working section and sealing the working section with the "lid". The insect was given 35 s to walk or run out of the illuminated circle of the arena. The sector the insect chose to leave was recorded. After roughly fifteen bugs had been tested, they were retrieved from the drawers into which they had fallen. The data obtained is a circular distribution (Batschelet 1981; Zar 1984). They were analyzed to obtain mean angle(θ), confidence limits of the mean angle (δ), the goodness of fit between observed and uniform distributions (χ^2), and the significance of θ (Rayleigh's R).

3.3 Results

3.3.1 Choice Chamber Trials

If both sides of the choice chamber had the same treatment (e.g., dry versus dry) there were no significant departures from the expected 1:1 ratio (Table 3.1). Both sexes preferred the damp side when given the choice between damp and dry filter paper halves (Table 3.1). Possible humidity bias was eliminated by keeping both filter papers damp during the habitat substrate and habitat-exposed filter paper trials.

Both wrack from the low shore area and surface mud scrapings from Wells Lake (Table 3.2) were attractive to individual Form A *S. pallipes* from Wells Lake. This Form was also attracted to Hastings Lake filter papers (Table 3.2). Sand scrapings from Manito and Calling Lakes were neither attractive nor repulsive to individual Form A *S. pallipes* from Wells Lake (Table 3.2). The absence of a reaction to Manito Lake sand was unexpected as this Form was commonly collected at the site. Individual Form A *S. pallipes* were infrequently collected at Calling Lake, possibly explaining the absence of a reaction.

3.3.2 Wind Tunnel Trials

Form A adults from Wells Lake showed no statistically significant forward directionality when exposed to moving untreated air (Figures 3.2 and 3.3). An anemotactic response in *S. pallipes* was usually noted by the following behavioral sequence. The insect would perch back on its metathoracic legs bringing the head and antennae up into the airstream. The antennae would then vibrate up and down (no lateral movement was noted, but viewing angle may have obscured this), presumably sampling the habitat volatiles for a few seconds and then the insect would run into the wind. There was a marked forward directionality when saldids from Wells Lake were exposed to wrack allelochemicals from the low shore area of Wells Lake (Figure 3.2). Although wind-borne allelochemicals from the Calling Lake sand may be attractive to adult females of Form A *S. pallipes* from Wells Lake, the effect was not statistically significant (Figure 3.3). This, however, may reflect the rare occurrences of this Form on the shores of Calling Lake.

Individual female Form A adults from Red Deer Lake were repelled by untreated air, but displayed a marked forward directionality when exposed to wind-borne volatiles from mud scrapings collected at Red Deer Lake and wrack from the low shore of Wells Lake (Figure 3.4).

3.4 Discussion

The results suggest that Form A adults of *S. pallipes* were attracted to alkaline silt shores that have a large organic component and, to a much lesser extent, permanent freshwater lakeshores that possess fine sediments combined with organic matter. Form A adults of *S. pallipes* were commonly collected at alkali lakeshores, rarely at freshwater lakes, and almost never at temporary habitats (e.g., rivers, creeks, ponds). I propose that this Form is somewhat specific to alkali habitats but whether it interbreeds with the black variety of *S. pallipes* at non-alkali sites cannot be determined from these results.

Individuals of Form A were attracted to habitat allelochemicals from non-alkaline sites only in choice chambers, because some allelochemicals may be the same or similar to those found in alkaline shore habitats (W.G. Evans pers. comm.). This suggests that these chemicals may be acting as arrestants but not as the longer range attractants because if they were attractants then these insects would be collected on non-alkaline shores in greater numbers than they actually are. The wind tunnel data suggests that potential habitats are chosen at a much longer distance. Determination of habitat suitability from a long distance would benefit migrating individuals by eliminating the energetic cost to get to a site that was then determined to be an unsuitable habitat. There would be a selective advantage for individuals who are able to detect and evaluate shore habitats from longer distances. These individuals would be selected over time because they would be more efficient at locating suitable shore habitat than an "arrestant-based" individual.

The black variety of *S. pallipes* occurs in a variety of permanent and temporary habitats in very low to medium numbers. This variety is found on slough, bog, fen, creek, river and lakeshores, most of which are temporary in nature. The black variety moves around a great deal more than tan variety individuals at permanent alkali lakes because of the ephemeral nature of its habitats (pers. obs.; D.S. Mulyk in Pollock *et al* 1991). Collecting the large numbers (i.e., < 50 individuals) of black variety individuals from one site during a single collecting trip for wind tunnel and choice chamber tests is nearly impossible. Should this data ever be collected I hypothesize that individuals of the black variety would be attracted to a variety of shore habitats (both non-alkaline and alkaline) in the choice chambers but only to non-alkaline habitat allelochemicals in the wind tunnel. In essence a similar pattern of long range habitat selection probably occurs in individuals of the black variety.

The fact that all organisms have some form of habitat selection mechanism when studied (Orains and Whittenberger 1991; Bazzaz 1991) reinforces the importance of the correct habitat to an organism. Organisms monitor their habitat for perceptible changes in its quality. These changes may prompt the organism to escape from the habitat. Sessile organisms display temporal habitat selection (i.e., active only when certain conditions are present, Bazzaz 1991) while motile organisms display spatial habitat selection (i.e., migration between suitable habitats). Insects, in general, are highly motile organisms that display both types of habitat selection (i.e., Andersen 1970, 1978, 1985;

Bell 1979, 1990; Boer and Hanson 1987; Danks 1987; Dethier 1982; Evans 1982, 1984, 1988; Hoffmann *et al.* 1984; Jaenike 1988; Kennedy 1977; Steinly 1986; Tauber *et al.* 1986; Vinson 1984). Habitat selection, in insects, is a behavioral cascade that uses a variety of perceived cues (i.e., olfactory, gustatory, auditory, visual, tactile) and internally-derived information (Bell 1991). Insects locate their habitats by readily switching from one modality and or search mode to another depending on the information perceived from their internal and external environments (Bell 1991).

Insects that specialize in ephemeral habitats tend to be very mobile as their habitats appear and disappear in both spatial and temporal dimensions (Parsons 1983). Saldids escape changes in their shore habitats by migration or diapause. Migrating saldids probably use a variety of cues to locate shore habitats. After observing saldids, both in the field and the laboratory, I suggest that visual and olfactory cues are used to locate habitats from a distance because tactile and gustatory cues are perceived by contact with the substrate. Auditory cues do not seem to be used in habitat selection (Polhemus 1985).

Most insects use visually perceived information somewhere in a specific behavioral cascade that has evolved to locate a host, mate, and or habitat. Migrating saldids may be similar to aquatic and semi-aquatic Heteroptera that detect water while in daytime flight apparently from its reflective surface (Anderson and Wallace 1984). Saldids may recognize the apparent border between the land and water thus locating the shore area. Strict reliance on visual cues to locate distant habitats may not be effective because reflected light travels in a straight line from the source of the reflection and the insect must place itself in a position to perceive it, possibly placing the insect in a dangerous position (Bell 1991). Reflected light, when present, provides a directional cue for the insect to follow. In its absence however, a visually orienting insect cannot determine the direction it should go to locate the habitat usually resulting in a random direction being chosen (Bell 1991). Further, visual cues may suggest the presence of a habitat but they may not indicate the type (e.g., lake, slough, or river) or state (i.e., declining, as perceived by the insect) of the habitat therefore additional long distance cues are probably used to locate and assess distant shore habitats.

Olfactory cues provide information that visual cues cannot. An odor *plume* provides directional information when the habitat is not visually apparent. Habitat

allelochemicals have been implicated in the habitat selection mechanisms of insects which specialize in ephemeral habitats (Dindonis and Miller 1980; Evans 1982, 1984, 1988; Hoffmann 1984; Jaenike 1988; Spivak *et al.* 1991; Vinson 1984). Different types of shore habitats emit different habitat allelochemical mixtures (W.G. Evans pers. comm.) so not only would a shore insect perceive the existence of the habitat but its type and quality. Adults of Form A *S. pallipes* reacted differently (i.e., attraction or no reaction) to habitat allelochemicals from the different habitat types in the wind tunnel.

Possibly, the ability to assess habitat suitability from a long distance using olfactory cues may explain why saldids seem to be habitat specific. This is reflected by collection records that confirm most species are only collected on a certain type of shore habitat (i.e., *P. signoreti* on alkali silt and sand shores). Habitat specificity was recognized in many other saldid species but this concept was not applied to the *S. pallipes* complex. Previous workers (i.e., Schuh 1967; Hodgden 1942; Polhemus 1985) believed *S. pallipes* to be catholic in its habitat preferences because they did not separate this complex on the basis of the habitats in which their specimens were collected. My observations, however, suggest that the tan and black varieties of *S. pallipes* were collected in different types of shore habitats and that habitat selection, in at least in Form A individuals, is in part based on habitat allelochemicals. In essence I believe that either variety's association with different types of shore habitats may reflect their habitat preferences. These preferences were not fully demonstrated for both varieties but if they exist they will have direct effects on speciation events within the *S. pallipes* complex.

The models of Bush and Diehl (1982), Diehl and Bush (1989), and Zwölfer and Bush (1984) have shown that small habitat preference differences can have profound effects if assortative mating is present. Habitat preference is linked to genes and experience so slight differences in gene frequencies would become more important if mating occurs in the habitat (Diehl and Bush 1989). In essence if the two, or more, *races* (*sensu* Diehl and Bush 1989) mate in separate habitats the resulting assortative mating may lead to the formation of habitat races and possibly separate species. Assortative mating has been proposed as the driving force in the formation of several insect species complexes (*e.g., Rhagoletis pomonella* (Bush 1969, 1974), *Muscidifurax* spp. (Legner 1969, 1987), *Drosophila silvarentis* and *D. heedi* (Kaseshiro *et al.* 1973), and *Enchenopa binotata* (Wood and Guttman 1982, 1983). Habitat-associated assortative mating is displayed by individuals of both varieties of *S. pallipes*. Male and female adults mate

only on the shores of habitats to which they have migrated, thus further promoting the hypothesized habitat specificity differences.

Whether the tan and black varieties are single eurytopic species or a complex of species (stenotopic or eurytopic?) cannot be completely answered using only habitat specificity methods. Thus the decision was made to use electrophoretic methods which may answer questions regarding the distinctness of these two varieties, genetic variation between populations of the black variety, and finally the relationships between the different tan Forms found at some field sites (e.g., Wells Lake).

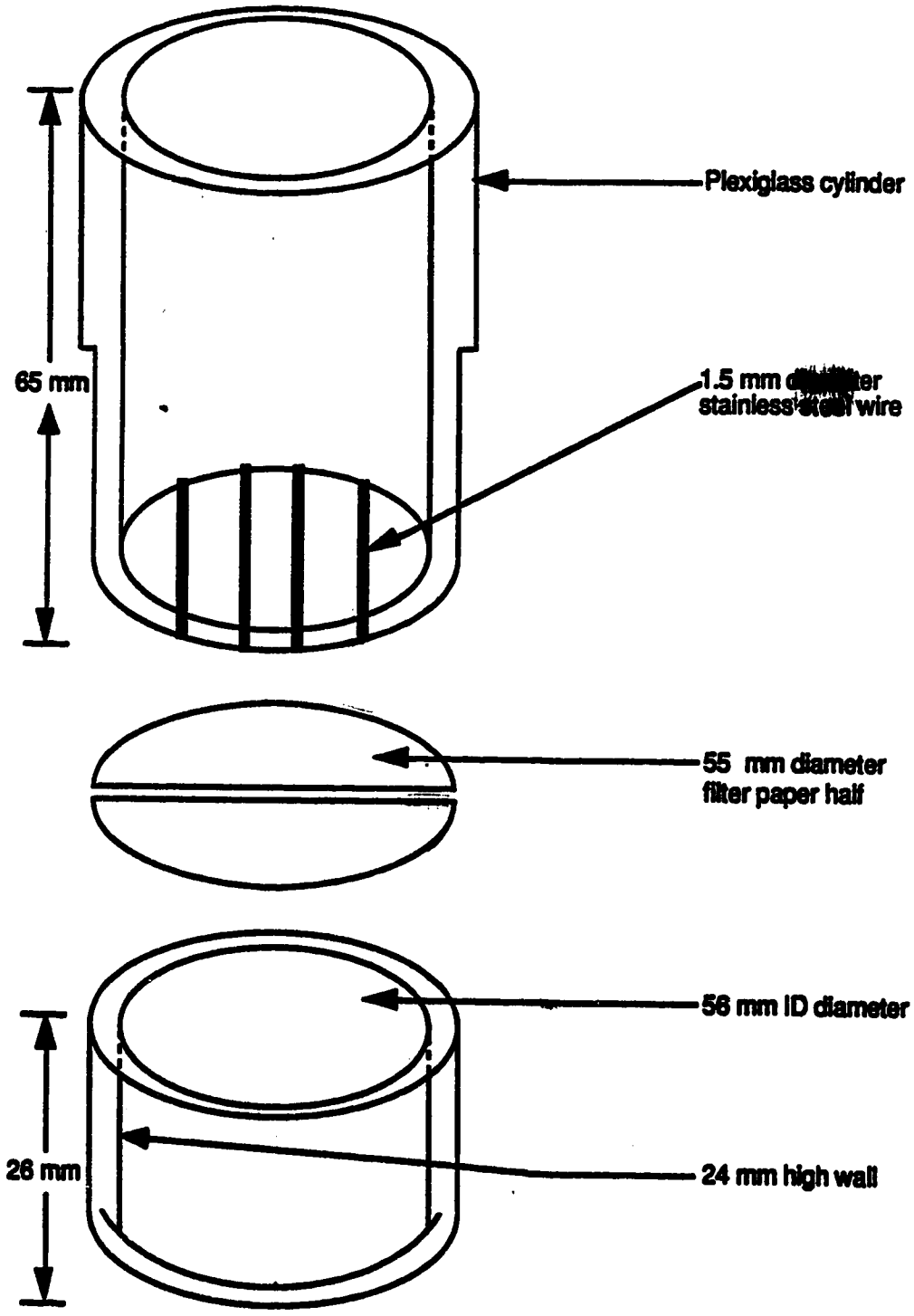


Figure 3.1 Plexiglas choice chamber for testing response to habitat allelochemicals by adults of *Saldula pallipes*.

Table 3.1 Chemically mediated responses of individual Form A *S. pallipes* from Wells Lake, Saskatchewan, to various control substrates.

TESTS	Averaged number/side		χ -square	
	Male	Female	Male	Female
Dry	12.2	8.2		
vs.			0.007, NS	0.142, NS
Dry	11.8	9.8		
Dry	6.6	3.4		
vs.			4.86, P<0.05	12.327, P<0.001
Damp*	17.4	20.6		
Damp*	9.8	12.6		
vs.			0.81, NS	0.060, NS
Damp*	14.2	11.4		

* dampened using distilled water

Table 3.2 Chemically mediated responses of individual Form A *S. pallipes* from Wells Lake, Saskatchewan, to various habitat substrates and to filter papers exposed to habitat volatiles.

TESTS	Averaged number/side		χ-square	
	Male	Female	Male	Female
Damp*	9.6	6.0		
vs.			83.20, P<0.001	23.20, P<0.001
Wells Lake Mud Scrapings	26.4	30.0		
Damp*	14.8	11.4		
vs.			7.05, P<0.01	13.23, P<0.001
Wells Lake Wrack	33.2	36.6		
Damp*	22.0	21.4		
vs.			0.333, NS	0.563, NS
Manito Lake Sand Scrapings	26.0	26.6		
Damp*	24.8	22.4		
vs.			0.053, NS	0.213, NS
Calling Lake Sand Scrapings	23.2	25.6		
Damp*	10.8	18.4		
vs.			5.47, P<0.02	14.52, P<0.001
Hastings Lake Filter Papers	37.2	35.6		

* dampened using distilled water

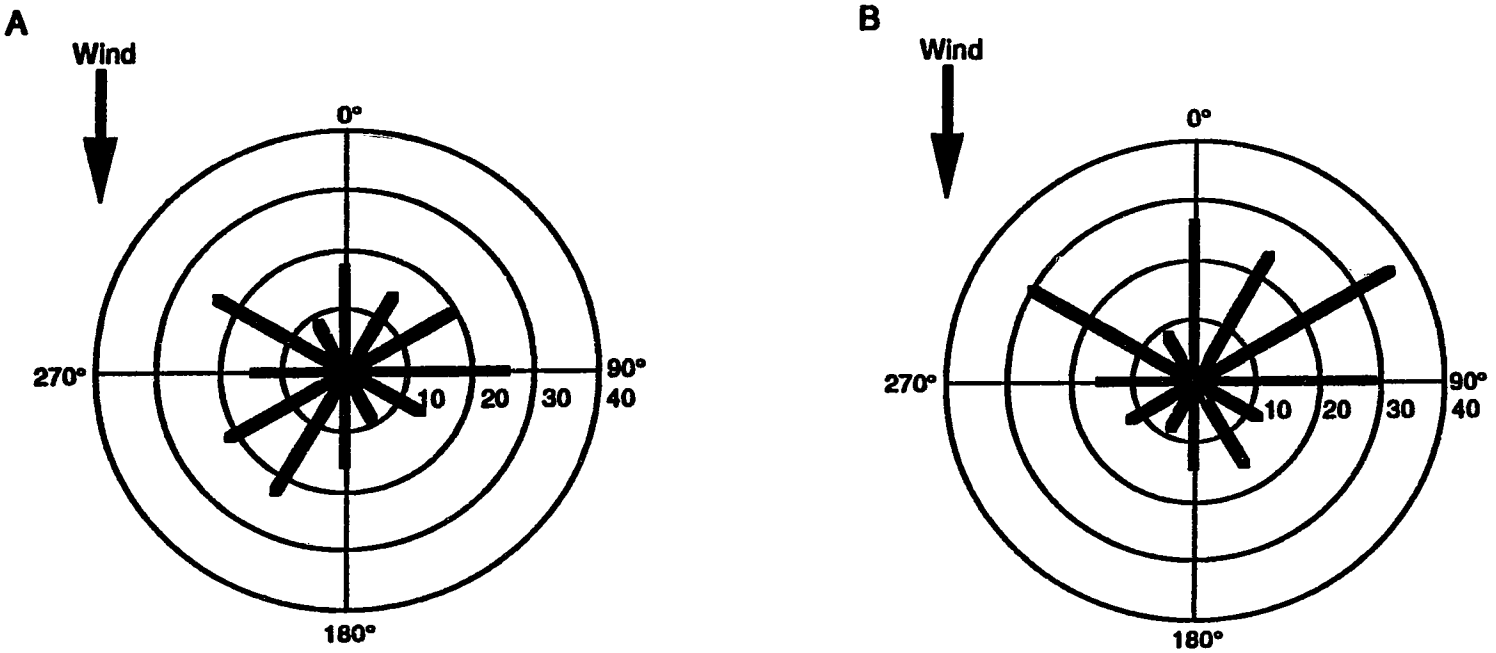
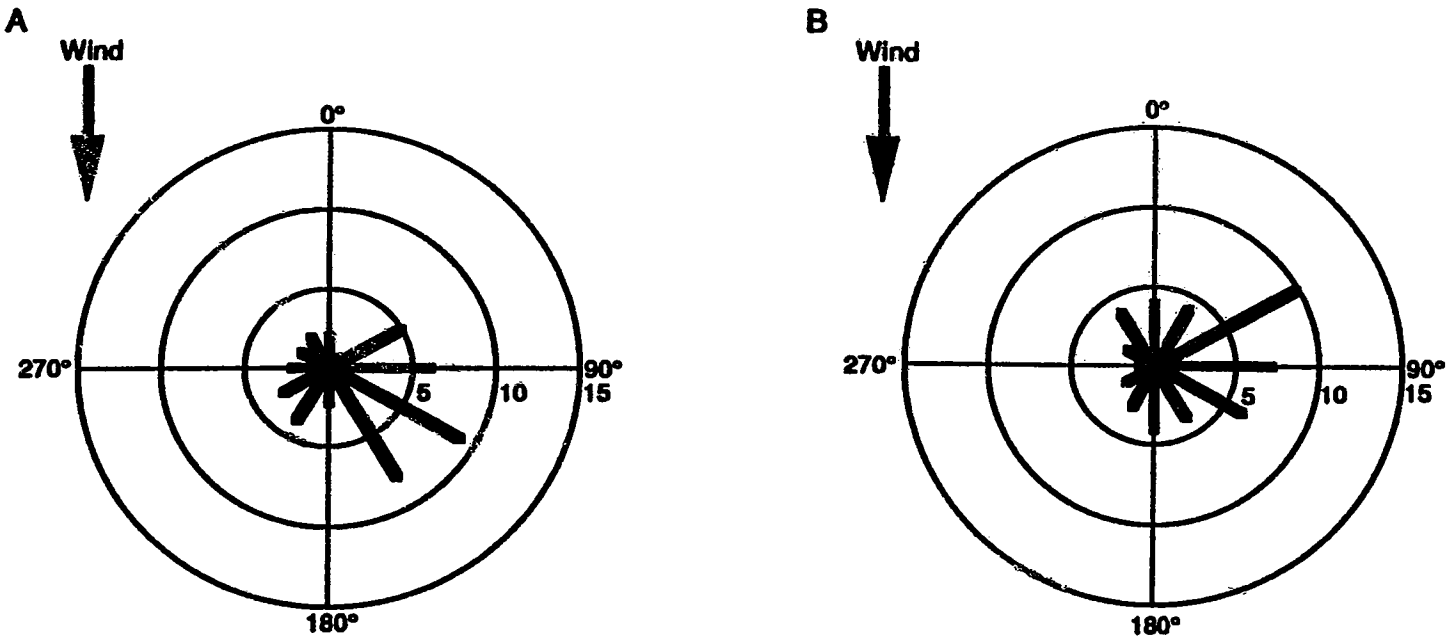


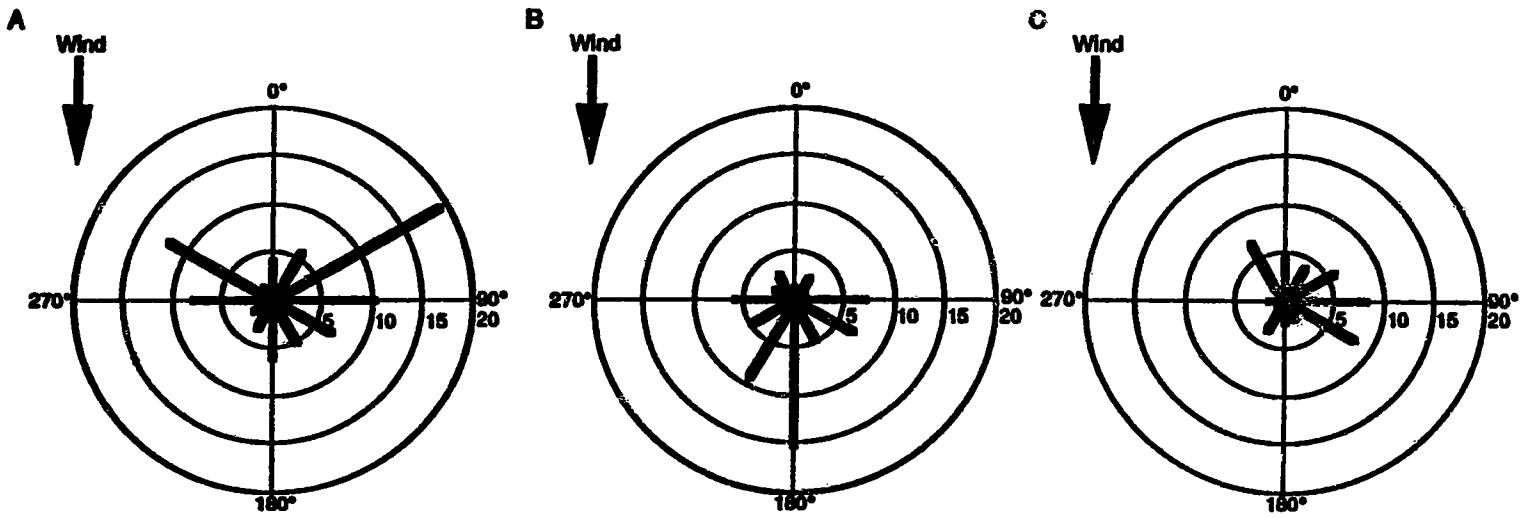
Figure 3.2 Vectors representing numbers of Form A adult *Saldula pallipes* from Wells Lake leaving 30°-wide sectors of a circle projected in the center of an arena in a wind tunnel. A. Responses to wind alone. B. Responses to Wells Lake low shore wrack.



θ±δ = 127.8° ± 64.5°
n = 46
χ^2 = 19.73, n.s.
R = 16.81, P < 0.002

θ±δ = 80.4° ± 66.0°
n = 51
χ^2 = 15.59, n.s.
R = 17.13, P < 0.005

Figure 3.3 Vectors representing numbers of Form A female adults *Saldula pallipes* from Wells Lake leaving 30°-wide sectors of a circle projected in the center of an arena in a wind tunnel. A. Responses to wind alone. B. Responses to Calling Lake sand.



$\theta \pm \delta = 59.7° \pm 71.1°$
$n = 84$
$\chi^2 = 37.14, P < 0.001$
$R = 17.83, P < 0.05$

$\theta \pm \delta = 180.3° \pm 61.3°$
$n = 63$
$\chi^2 = 37.71, P < 0.001$
$R = 26.43, P < 0.001$

$\theta \pm \delta = 65.3° \pm 66.5°$
$n = 49$
$\chi^2 = 18.84, P < 0.1$
$R = 15.99, P < 0.005$

Figure 3.4 Vectors representing numbers of Form A adult *Saldula pallipes* from Red Deer Lake leaving 30°-wide sectors of a circle projected in the center of an arena in a wind tunnel. A. Responses to Red Deer Lake mud scrapings. B. Responses to wind alone. C. Responses to Wells Lake low shore wrack.

4. A preliminary electrophoretic survey of some populations of *Saldula pallipes*

4.1 Introduction

Identifying specimens in the *Saldula pallipes* species complex can be an exasperating and trying experience because species limits have not been fixed for most members of the complex. Defining species limits is extremely difficult because of the phenotypic variation observed within and between populations of *S. pallipes* (Polhemus 1985; Cobben 1960; Wróblewski 1966). Previous workers have described species on the basis of specimens collected from a single site or within a small geographic area (e.g., Drake and Hottes 1955; Distant 1909). Later workers declared these "geographic species" junior synonyms of *S. pallipes*, claiming they represent further examples of the diverse nature of the species (Polhemus 1985). Also, the presence of distinct Forms within some populations has been assumed to reflect only phenotypic variation (e.g., Schuh 1967), but there are no data to support this notion.

The black and tan varieties of *S. pallipes* found in Alberta and western Saskatchewan occur mainly in distinct habitats. Individuals of the black variety were collected on the shores of temporary habitats such as sloughs, ponds, creeks, and rivers but were also collected from more stable habitats such as freshwater lakeshores, while the tan variety, which was found in the same geographic area, was collected on the shores of both permanent lakes and temporary ponds with high alkalinity. My observations at shore habitats, and the habitat selection experiments discussed in Section 3.4 demonstrate that these 2 varieties may sometimes co-occur in the same habitat. A complicating factor is the presence of several distinct Forms in populations of the tan variety. Do these Forms represent different phenotypes of the same genotype or are they genetically distinct species, co-existing in the same habitat?

The status of these two varieties (black and tan) and the several Forms of the tan variety have not been resolved. Other methods (i.e., comparative morphology) which were applied have failed to resolve these entities of the *S. pallipes* species complex. Electrophoretic techniques were used to resolve this problem because they have been applied to biosystematic problems for >25 yr. and have yielded vast amounts of information regarding species concepts and the genetic structure of populations (Richardson *et al.* 1986).

By comparing the genetic composition and variability within and among populations of *S. pallipes,* predominantly from Alberta and western Saskatchewan, I attempt to answer several questions. First, are the black and tan varieties the same species? Second, is the black variety a single species or a morphospecies? Third, what is the proper status of the six Forms of the tan variety found at Wells Lake, Saskatchewan (and other field sites)?

4.2 Materials and Methods

4.2.1 Collection of Specimens

Saldids were collected as outlined in Chapter 3.2.1 at >30 localities in Alberta, Saskatchewan, Ontario, and Newfoundland during 1989 and 1990. From these collections, ten localities were chosen based on the number of individuals collected (usually >20 specimens per site) and their geographic distribution (generally within the aspen parkland ecotone where the ranges of these two varieties of *S. pallipes* overlap). Locality information is given in Table 4.1 and Figures 2.1 and 2.2. Material of more than one species was present in some localities. Individuals of *Pentacora signoreti, Salda provancheri,* and *Saldula opacula* were collected and assayed for comparison with specimens of the *S. pallipes* complex. After adult specimens were identified they were stored in 500 ml Fisher Microcentrifuge tubes at -70° C. Specimens stored for two years still gave interpretable results.

Adult and, if present, nymphal specimens from each locality were retained as vouchers for subsequent morphological examination. Voucher specimens from this study will be deposited in the Strickland Museum (University of Alberta) and the author's private collection.

4.2.2 Electrophoresis

Just prior to homogenization, the abdomen and wings of the individual were removed and preserved in a 1:1 ethyl alcohol and glycerine solution for subsequent study. The head and thorax were then homogenized in 0.1 ml of homogenization fluid

(0.03 M Tris-H_3PO_4, pH 6.7, containing 1.6 mM nicotinamide adenine dinucleotide phosphate (NADP), 8.0 mM DL-dithiothreitol, and 3.5% polyvinylpyrolidine). After centrifugation (8,000 g for 10 min.) subsamples of 0.02 mL of homogenate were electrophoresed in 7 or 9 % vertical polyacrylamide gels (Tris-HCl buffer, pH 8.9), under the conditions outlined in Rolseth and Gooding (1978) and Sperling (1987). By pouring 0.5 mm thick gels instead of the thicker 1.5 mm gels of Rolseth and Gooding (1978) I was able to maximize homogenate use because thinner gels, although much more delicate, do not require as much homogenate for an equivalent amount of staining as do the thick gels. Also, by decreasing the amount of homogenate used per gel, I could assay each individual for a greater number of loci.

Five to 180 individuals from each population were assayed for the following enzymatic proteins: (Enzyme Commission numbers from Nomenclatural Committee of the International Union of Biochemistry 1984) alcohol dehydrogenase (ADH, EC 1.1.1.1), aldehyde oxidase (AO, EC 1.2.3.1), arginine phosphokinase (APK, EC 2.7.3.3), glucose-6-phosphate dehydrogenase (G6PD, EC 1.1.1.49), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), hexokinase (HK, EC 2.7.1.1), and phosphoglucomutase (PGM, EC 5.4.2.2). These 7 enzyme systems consistently produced interpretable bands from the 31 staining methods attempted. Banding patterns suggested that 4 loci (ADH, APK, HK, and PGM) were monomers, 1 locus (GPI) was a dimer, and 2 loci (AO, G6PD) produced undetermined multimers, and that none of these 7 loci were sex-linked.

Stain recipes were standard modifications of Brewer (1970) and Shaw and Prasad (1970). Cellulose acetate overlays were used instead of filter paper when assaying for APK variants using Sperling's and Spence's (1990) method.

The 24 other staining methods which were tried using the recipes of Brewer (1970), Shaw and Prasad (1970), May *et al.* (1979), and Herd and Fenton (1983) either did not produce bands or the bands were uninterpretable (see Table 4.2).

Electrophoretic data were analyzed using the computer program BIOSYS-1 (Version 1.7, Swofford and Selander 1981) which generated the allele frequency tables, tests for Hardy-Weinberg equilibrium, the genetic similarity and distance measures, the UPGMA phenograms, and the Wagner trees.

Several genetic identity and distance measures were used to analyze the electrophoretic data. Nei's (1972) genetic identity and distance measures were used because they are the most widely employed measure, and thus may be used for comparative purposes. That however is their sole use in this thesis. I do not believe they are the best way to measure genetic identity or distance because they have assumptions about the processes leading to the observed divergence and the biological meaning of the results (Richardson *et al.* 1986; Weir 1990). Because this distance measure is derived from the probability of identical alleles being picked from 2 different populations it cannot be converted to metric distance so therefore it is not strictly mathematically correct to apply to UPGMA phenograms (Brussard *et al.* 1989).

Both UPGMA and Wagner Distance phenograms were constructed because each method has different assumptions regarding the rates of evolutionary divergence. The UPGMA algorithm assumes that rates of evolutionary divergence are relatively homologous across the phyletic lines whereas the Wagner Distance algorithm assumes each phyletic line has its own rate of evolutionary divergence. Since their basic assumptions about dendrogram construction are different, the trees derived from each method can be compared with each other for similarities and differences.

Slatkin's (1985) analysis for rare alleles was performed on all populations to determine "relative amounts" of gene flow between populations (computer algorithm written by B. Rolseth). Slatkin's (1985) frequency of rare alleles was used instead of F-statistics (Wright 1951, 1969) to analyze gene flow among populations because it does not require that all populations be of equal size (Weir and Cockerham 1984).

4.3 Results

4.3.1 Population Structure

I evaluated 31 enzyme systems for consistent and scorable banding patterns in *S. pallipes*. As a guide for future investigators the enzyme systems which did not stain or produced uninterpretable results are listed in Table 4.2. Seven enzyme systems exhibited considerable variation among populations but produced banding patterns which could not be readily interpreted as Mendelian variation (Table 4.2). Seven enzyme

systems (comprising 7 putative loci) gave consistent and interpretable results (Table 4.3). Five loci (AO, GDO, GPI, HK, and PGM) were polymorphic. Two loci (ADH and APK) were essentially monomorphic (most common allele frequency > 0.95) for all populations sampled. A single variant of APK appears to characterize the *S. pallipes* complex because no alleles were shared between this complex and the other species examined. The tan and black varieties of *S. pallipes* were readily separated by their unique AO and ADH alleles. Because as no individuals heterozygotic for ADH were observed within and between populations of either variety, I believe these 2 varieties are different species. This contention is further supported by habitat collection records and the preliminary habitat selection work done in the previous chapter.

Significant deviations from Hardy-Weinberg equilibrium were observed for all polymorphic loci and for at least one locus in every saldid population studied (e.g., AO locus in population 2, Table 4.3). Heterozygote deficiencies were noted in most loci not in Hardy-Weinberg equilibrium.

4.3.2 Genetic Variability

Measures of genetic variability, including mean number of alleles per locus, percentage of polymorphic loci, and unbiased heterozygosity are presented for each population in Table 4.4. The generally higher levels of heterozygosity observed in *S. pallipes* populations suggest that this species is more genetically variable than the other saldid species. The mean number of alleles per locus varied from 1.4 to 2.7 over 6 loci in the sampled populations of *S. pallipes*. The percentage of polymorphic loci was higher in the populations of *S. pallipes* than the other species examined, except for that of *S. opacula*. Unlike the other species which were examined, only one population of *S. opacula* was electrophoresed so a detailed comparative analysis with either variety of *S. pallipes* is premature at this time. However, it is interesting that members of *Saldula* generally have higher percentages of polymorphic loci than other species of saldids (D.S. Mulyk unpublished data) which may be related to their greater number of species (> 110) than other genera of saldids (generally <5 species).

4.3.3 Genetic Differentiation

A matrix of Nei's (1972) genetic distance and identity measures between populations is given in Table 4.5. Distance values range from 8.00 to 0.02 and identity values from 0.00 to 0.99. *Salda provancheri* and *Pentacora signoreti* were the most distant from all the other species by a substantial margin (I = 0.00 - 0.05) which was expected considering their distant relationship to *Saldula*. *Saldula opacula* was more similar to the black variety (I = 0.21 - 0.44) than the tan variety (I = 0.02 - 0.06) of *S. pallipes*. For I, intraspecific comparisons ranged from 0.86 - 0.99 for the tan variety and 0.67 - 0.93 black variety of *S. pallipes*.

UPGMA phenograms constructed from all similarity and distance coefficients available in BIOSYS (Swofford and Selander 1981) had similar topologies, in which all the Forms collected at Wells Lake (populations 4 - 9) clustered together quite separately from the other populations of *S. pallipes*. This is clearly illustrated in the dendrogram using Cavalli-Sforza and Edwards (1967) chord distance (Figure 4.1).

The dendrogram produced for the sampled populations using the Wagner Distance method and modified Rogers Genetic Distance coefficient (Wright 1978) is presented in Figure 4.2. All the populations from Wells Lake cluster together quite separately from the other populations of the *S. pallipes* complex regardless of Form and variety. Also, western Canadian populations of *S. pallipes* (including Wells Lake) cluster together quite separately from eastern Canadian populations of *S. pallipes*. The other three comparative species form a distinct cluster that is distantly related to the *S. pallipes* complex.

4.3.4 Slatkin's Rare Allele Analysis

A matrix was produced using Slatkin's (1985) frequency of rare alleles (Table 4.6). There was little, if any, gene flow between any pair of species. Gene flow values between the various tan Forms of *S. pallipes* were quite high (e.g., populations 8 and 9), as were some values between populations of the black variety (e.g., populations 10 and 11). Gene flow was practically non-existent between the black and tan varieties (e.g., populations 4 and 12) further confirming that these varieties were separate species.

4.4 Discussion

Limited earlier attempts to interpret and quantify the observed protein variation in saldids were unsuccessful (Polhemus 1985). Polhemus (1985) suggested, based on the results of Saxena *et al.* (1965) with other Heteroptera, that the electrophoretic analysis of specific tissues or organs may be the best way to discriminate the genera or species of saldids. However, I successfully measured genetic variation in saldids using standard allozyme electrophoresis techniques on homogenates of whole heads and thoraces. Since my work cannot be compared to other saldid studies I can only compare it to other allozyme studies in the Heteroptera (e.g., Leslie and Dingle 1983; Sperling and Spence 1990; Zera 1981; Varvio-Aho *et al.* 1978).

The average number of alleles per locus was similar to values found in *Limnoporus* spp. (Sperling and Spence 1990; Zera 1981) and *Gerris lacustris* (Varvio-Aho *et al.* 1978). Saldids do however seem to have a greater number of polymorphic loci than other groups of Heteroptera however this may be an artifact of the loci I examined. Mean heterozygosities, over all examined loci, in the Gerridae range from 0.086 (Sperling and Spence 1990) to 0.289 (Varvio-Aho *et al.* 1978) so although the observed range 0.11 - 0.4 in saldids seems slightly high but it again is probably an artifact of the loci examined. The genetic distances which were observed in the saldids cannot be accurately compared with other Heteroptera because the number of loci I examined is much lower than the other studies which directly affects the calculation of genetic distance. However, it is interesting to note that the *I* values observed for congeneric pairings were low compared to other Heteroptera but values within species of saldids were well within the accepted range (0.85 - 1.00).

An outstanding difference between saldids and other hemiptera was the frequent occurrence of heterozygote deficiencies. All the species of saldids examined have similar heterozygote deficiencies (D.S. Mulyk unpublished data). Until further electrophoretic work is done I am unsure if this is a genuine characteristic of this family or simply an artifact of the loci examined.

Heterozygotes of both sexes were observed for all loci suggesting that none of the loci were sex-linked. Members of the *S. pallipes* complex usually have 36 autosomes

and a X0 + m(2) sex chromosome mechanism, for more detail see Ueshima (1979). Because saldids usually have large numbers (>18) of chromosomes (Ueshima 1979), the frequency of sex-linked genes is probably lower.

Genotype frequencies at all loci differed significantly from Hardy-Weinberg expectations. The deviations were reflected by a deficiency of heterozygotes, but heterozygotes were observed for all polymorphic loci. Possible reasons for heterozygote deficiency were sampling errors, the presence of null alleles, severe selection against heterozygotic individuals, the Wahlund effect (i.e., an apparent panmictic population was in fact composed of several subpopulations; Wahlund 1928), and the presence of fixed alleles in particular populations. Sampling error may be an important factor in some of the smaller samples of *S. pallipes* (e.g., Sugarloaf Pond, Newfoundland) but for larger samples (e.g., *Salda provancheri*, Red Deer Lake, Alberta) this seems unlikely. Both the large number of null alleles, several per species examined, required to account for the observed deficiencies and the severity of selection against heterozygotes are alone untenable. The Wahlund effect may explain some of the observed heterozygote deficiencies in polymorphic populations (e.g., tan variety) of *S. pallipes*. If an organism's genetic constitution is largely fixed in the homozygous condition a sampled population of such organism's would appear heterozygote deficient (Fontdevila 1989).

When all the gene frequencies for the various tan Forms from Wells Lake were pooled, they were still not in Hardy-Weinberg equilibrium. Four of the tan Forms can be placed into two distinct groups which were supported by data from the shape of the facial callosities (large versus small, Figure 3.1 A and B), number of wingspots (2 versus 0, Figure 3.1 E and G), Nei's genetic distances and identities (Table 4.5), the UPGMA phenogram (Figure 4.1), the Wagner cladogram (Figure 4.2), and the Nm values (Table 4.6). The first group consists of the A and B tan Forms while the second group consists of the E and F Forms. The C and D Forms of the tan variety cannot be readily assigned to either group. Form C was not placed in either group because it had one wingspot (Figure 3.1 F), several allele frequency differences (i.e., G6PD, GPI, and HK), the lack of shared alleles (e.g., lacks alleles 0.473 and 0.484 for PGM locus), and both the UPGMA phenogram (Figure 4.1) and Wagner cladogram (Figure 4.2) placed it as the outgroup to the other Forms of the tan variety. Form D was problematical because it has some morphological (i.e., tan ground color and 2 wingspots) and shared allele similarities (e.g.,

HK) to the A and B Forms, but the different facial callosities (Figure 3.1 A and B) and genetic similarities (Table 4.5) belie this.

Although the relationships among the various Forms of the tan variety cannot be definitively stated I believe they represent a natural group. This is supported by the presence of a shared, unique, monomorphic allele (i.e., ADH), low genetic distances and high similarities (Table 4.5), and the high gene flow values (Table 4.6). The presence of distinct Forms in some populations has been assumed to be phenotypic variation (e.g., Schuh 1967). Individuals of all these Forms were collected during the entire field season, in approximately the same ratios (D.S. Mulyk unpublished data), suggesting they were stable polymorphisms. These Forms could be separated by small niche differences such as food preference and positioning on the shore. Future work may further elucidate how these Forms were maintained in the tan variety.

Heterozygote deficiencies reminiscent of those in the tan variety were observed in the sampled populations of the black variety of *S. pallipes* and the other species of saldids. Sampling error may be an important factor in the small samples but not the larger samples. When possible null alleles were included gene frequency calculations were still not in Hardy-Weinberg equilibrium. Severe selection against heterozygotes seems untenable considering the markedly different ecological conditions each species lives under. The genetic distance and similarity (Table 4.5) and Nm values (Table 4.7) suggest there is limited geneflow through-out populations of the black variety of *S. pallipes* in Alberta and western Saskatchewan which would reduce the Wahlund effect. Saldids may have their genetic constitution largely fixed in the homozygous state. Genetic homogamy has been noted in other species which colonize ephemeral habitats (Carson 1958; Dobzhansky 1957; Fontdevila 1989; Lanzaro *et al.* 1990).

Athalassic shore habitats are continually in a state of flux because their water levels are constantly rising or falling. At any given time within a geographic area some shores are being created while others are being altered or destroyed. This state of flux results in some proportion of an area's total black variety of *S. pallipes* population being forced to migrate. Whether these migrants join another existing population or establish a new population and are joined by migrants from other collapsing populations, there is the potential for interbreeding. The multiple matings by a single individual and multivoltinism would further contribute to gene flow having an homogenizing effect on the various

populations of the black variety of *S. pallipes* in that geographic area. It was observed that allele frequencies were slightly different but all the alleles for each locus were present in populations which were distant from one another thus suggesting there is gene flow over a large geographic area.

Diagnostic allozymes have been used for identification of a number of species complexes in *Aedes* mosquitoes (e.g. Munstermann *et al.* 1982; Munstermann 1988; Bloem 1991). *Saldula pallipes* complex members can be separated from other species of saldids by their unique monomorphic APK allele. Further, members of either *S. pallipes* variety (black or tan) can be readily separated by their respective ADH and AO alleles. Future studies of the *S. pallipes* complex over its entire range will clarify the distribution of these 2 putative species and may provide insights into the mechanism by which they differentiated. Further electrophoretic studies may elucidate the various species within the *S. pallipes* complex.

The allozyme data presented above indicated high genetic identities between the 5 presumptive taxa (*P. signoreti, S. provancheri, S. opacula,* tan *S. pallipes,* and black *S. pallipes*). Brussard *et al.* (1985) reviewed genetic identities at various taxonomic levels within the insects and concluded that they had surprisingly similar values between an essentially random sample of insects. Brussard *et al* (1985) presented the following range of *I* values: 0.2 - 0.42 for genera within the same subfamily, 0.35 - 0.83 for non-sibling species, 0.57 - 0.95 for sibling species, and 0.85 - 1.00 for local populations. Nei (1976) presents a generalized scale of genetic distance based on electrophoretic data from a number of organisms: 0.01-0.05 for races, 0.02-0.2 for subspecies, and 0.1-2.0 for species. While such scales cannot be used alone for determining taxonomic rankings they does serve as a useful guidelines for evaluating electrophoretic data.

The observed *I* value of *Salda - Saldula* falls well below the range given by Brussard *et al.* (1985) for genera within the same subfamily. Both genera are considered to be the most apotypic representatives of their tribes so the low *I* value may not be unusual. A similar pattern of low *I* values is observed when *S. opacula* is compared separately to both varieties of *S. pallipes.* The separate species groups to which *S. opacula* and *S. pallipes* belong are not considered to be sister groups (P. Lindskog pers. comm.) so low *I* values may not be unusual. If the sibling species genetic identity range given is an accurate estimate the two varieties of *S. pallipes* fall well below the expected

range suggesting they are not sibling species. Identity values are in the expected range when local populations within each variety of *S. pallipes* are compared confirming each variety is a separate essentially panmictic unit. My conclusion that each variety is a separate species is in agreement with the ranges of *I* observed by Brussard *et al.* (1985) for other insect species.

However, when Nei's (1976) scale is used, the 2 varieties of *S. pallipes* are still different species but some populations within each variety are considered to species or subspecies also. The distance data supports my contention that the two varieties are actually two distinct species while also suggesting several subpopulations in the tan variety should be raised to species status. I do not support latter point because these "populations" are subpopulations. Further these subpopulations of the tan variety form a natural group which is supported by the presence of a shared, unique, monomorphic allele and high gene flow values.

Table 4.1 Locality data for the saldid species and populations sampled during the study.

Species sampled and assigned population number	Locality	Collection Date(s)
Pentacora signoreti		
1	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989 and Jul. 26, 1990
Salda provancheri		
2	Red Deer Lake, Alta. (Site #16, Figure 2.1)	Jun. 18, 1989
Saldula opacula		
3	Glenn's Slough, Alta. (Site #8, Figure 2.1)	Apr. 30, 1989
Saldula pallipes		
4 Form A	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989 and Sept. 27, 1989
5 Form B	Wells Lake, Sask. (Site #14, Figure 2.1)	Sept. 27, 1989
6 Form C	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989
7 Form D	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989
8 Form E	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989
9 Form F	Wells Lake, Sask. (Site #14, Figure 2.1)	Aug. 3, 1989
10	Pembina River, Alta. (Site # 5, Figure 2.1)	Jul. 4, 1989
11	Pembina Slough, Alta. (Site #4, Figure 2.1)	Jun. 1, 1989 and Jul. 4, 1989
12	George Lake, Alta. (Site #7, Figure 2.1)	Jun. 15, 1989
13	Glenn's Slough, Alta. (Site #8, Figure 2.1)	Apr. 30, 1989 and Sept. 15, 1989
14	Hastings Lake, Alta. (Site #12, Figure 2.1)	Jun. 13, 1989
15	Medway Creek, Ont. (Site #2, Figure 2.2)	Oct. 1, 1989
16	Lake Erie, Ont. (Site #3, Figure 2.2)	Jun.1, 1989
17	Sugarloaf Pond, Nfld. (Site # 1, Figure 2.2)	Sept. 30, 1989

Table 4.2 Non-staining and uninterpretable enzyme systems

Enzyme	Enzyme Code	Non-staining	uninterpretable (# putative loci)
aspartate amino transferase	AAT	X	
acid phosphatase	ACPH	X	
adenosine deaminase	ADA	X	
adenylate kinase	AK		X (1)
aldolase	ALD	X	
alkaline phosphatase	ALPH	X	
esterase	EST		X (4)
glutamate dehydrogenase	GDH	X	
glucose dehygrogenase	GLUO	X	
glycerine dehydrogenase	GlyDH	X	
glutamate-oxaloacetate transaminase	GOT	X	
alpha-glycerophosphate dehygrogenase	GPDH		X (2)
beta-hydroxybutyrate dehydrogenase	HBDH	X	
isocitrate dehydrogenase	IDH		X (1)
leucine napthylamidase	LAT	X	
lacate dehydrogenase	LDH		X (1)
malate dehydrogenase	MDH		X (2)
malic enzyme	ME	X	
6-phosphogluconate dehydrogenase	6-PGD		X (1)
phosphomannose isomerase	PMI	X	
superoxide dismutase	SOD	X	
sorbitol dehydrogenase	SoDH	X	
succinate dehydrogenase	SuDH	X	
xanthine oxidase	XO	X	

Table 4.3 Allele frequencies at 7 loci in 17 populations of the *S. pallipes* complex and related species. Population names as in Table 4.1.

Locus and Allele	Population 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
ADH																	
n*	13	117	12	12	3	8	8	2	9	16	8	8	1	1	15	4	4
0.180	-	-	1.000	-	-	-	-	-	-	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
0.197	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.204	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.211	-	-	-	1.000	1.000	1.000	1.000	1.000	1.000	-	-	-	-	-	-	-	-
0.227	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.232	-	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AO																	
n*	22	127	42	36	22	12	12	19	39	20▲	20	23	22	9▲	20	9	5▲
0.220	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.239	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.300
0.254	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.175	-	0.700
0.260	-	-	-	-	-	-	-	-	-	-	-	-	-	0.500	-	-	-
0.267	-	-	0.107	-	-	-	-	-	-	0.550	0.275	0.130	0.250	0.389	-	-	-
0.273	-	-	-	-	-	-	-	-	-	-	0.275	0.674	0.250	0.111	0.600	0.278	-
0.280	-	-	0.589	-	-	-	-	-	-	0.450	0.275	0.196	0.432	-	0.225	0.722	-
0.286	-	-	-	-	-	-	-	-	-	-	0.175	-	0.068	-	-	-	-
0.298	-	-	-	0.171	-	0.417	0.292	0.053	0.128	-	-	-	-	-	-	-	-
0.306	-	-	-	0.400	0.455	0.250	0.542	0.316	0.397	-	-	-	-	-	-	-	-
0.318	-	-	-	0.257	0.318	0.250	0.083	0.237	0.231	-	-	-	-	-	-	-	-
0.324	-	0.791	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.330	-	-	-	0.171	0.227	0.083	0.083	0.395	0.244	-	-	-	-	-	-	-	-
0.345	-	0.209	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
APK																	
n*	22	177	25	36	22	12	12	19▲	40▲	23	21▲	36	17	13	21▲	16	5
0.541	-	-	-	1.000	1.000	1.000	1.000	0.976	0.987	1.000	0.976	1.000	1.000	1.000	0.976	1.000	1.000
0.544	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.565	-	-	-	-	-	-	-	0.024	0.013	-	0.024	-	-	-	-	-	-
0.583	-	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.583	-	-	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.590	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.024	-	-
G6PDH																	
n*	13▲	99	29	19	13	8	8	12	29	21	15	31	23	13	21	4	8
0.146	-	-	0.034	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.158	-	-	0.862	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.164	-	-	0.069	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.171	-	1.000	0.034	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.182	-	-	-	0.053	-	-	-	-	-	-	-	-	-	-	-	-	-
0.221	-	-	-	0.421	0.154	-	0.500	0.500	0.431	-	-	-	-	0.077	-	-	-
0.228	-	-	-	0.526	0.846	1.000	0.500	0.500	0.534	-	-	-	-	0.077	-	-	-
0.237	0.077	-	-	-	-	-	-	-	0.034	1.000	1.000	1.000	1.000	0.846	1.000	1.000	1.000
0.304	0.923	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 4.3 continued.

Locus and Allele	Population 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
GPI																	
n*	18	78	36	32	18	12▲	11	15▲	31	21	16▲	23	22	10	21	5▲	5
0.315	0.889	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.524	0.111	0.924	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.536	-	0.063	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.540	-	-	0.028	0.172	0.031	0.458	0.045	0.367	0.242	-	-	-	-	-	-	-	-
0.548	-	-	0.083	0.406	0.313	0.375	0.500	0.233	0.323	0.214	0.156	-	0.068	0.350	0.048	0.200	-
0.553	-	-	-	-	-	-	-	-	-	0.024	-	-	-	-	-	0.200	-
0.560	-	-	0.028	0.313	0.406	0.083	0.364	0.400	0.436	0.381	0.344	0.065	0.091	0.550	0.952	0.400	1.000
0.570	-	-	0.861	0.109	0.186	0.033	0.091	-	-	0.381	0.500	0.935	0.841	0.100	-	0.200	-
HK																	
n*	12	49	18	24	16	8	8▲	15▲	32▲	23	21	28	22	11	21	9	5▲
0.181	-	0.867	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.187	-	-	0.667	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.191	-	-	0.333	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.196	-	-	-	-	-	0.500	-	0.133	0.063	0.674	0.214	-	-	0.045	-	-	-
0.208	-	0.020	-	0.875	0.875	0.500	0.938	0.867	0.938	0.087	-	-	-	0.409	0.905	0.889	0.100
0.213	-	-	-	0.125	0.125	-	0.063	-	-	-	-	-	-	-	-	0.111	-
0.217	-	0.092	-	-	-	-	-	-	-	-	0.548	1.000	-	-	-	-	-
0.221	-	-	-	-	-	-	-	-	-	0.239	0.238	-	0.523	0.545	0.095	-	0.900
0.226	-	-	-	-	-	-	-	-	-	-	-	-	0.477	-	-	-	-
0.231	1.000	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PGM																	
n*	20	80	20	32	18	12	12▲	15	31	18▲	18	19▲	20	9	21▲	6	5▲
0.389	-	-	-	-	-	-	-	-	-	0.031	-	-	-	-	0.667	-	0.100
0.411	-	-	-	-	-	-	-	-	-	-	0.063	0.053	0.050	-	-	-	-
0.421	-	-	0.875	-	-	-	-	-	-	0.094	-	-	-	-	-	-	-
0.451	-	-	0.225	0.125	0.167	0.083	-	0.133	0.113	0.625	0.938	0.868	0.625	0.500	0.333	0.438	0.900
0.462	-	-	-	0.547	0.500	0.917	0.917	0.867	0.742	-	0.063	0.079	0.325	0.500	-	-	-
0.473	-	-	0.100	0.297	0.333	-	0.042	0.167	0.145	0.250	0.194	-	-	-	-	0.563	-
0.484	-	-	-	0.031	-	-	0.042	0.033	-	-	-	-	-	-	-	-	-
0.517	-	0.094	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.532	0.200	0.706	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.545	-	0.200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.558	0.750	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0.586	0.050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

*n, number of individuals sampled per population

▲, population in Hardy-Weinberg equilibrium for specified locus

Table 4.4 Genetic variability of sampled saldid populations. Population names as in Table 4.1.

Population	Mean sample size per locus (SE) *	Mean # alleles per locus	Percentage of loci polymorphic (SE) **	Unbiased heterozygosity (SE)
1	17.1 (1.7)	1.6	42.9	0.11 (0.06)
2	105.4 (15.3)	2.1	57.1	0.17 (0.07)
3	26.0 (4.0)	2.4	71.4	0.24 (0.07)
4	27.1 (3.4)	2.7	71.4	0.40 (0.12)
5	15.7 (2.5)	2.3	71.4	0.35 (0.11)
6	9.9 (1.1)	2.1	57.1	0.30 (0.13)
7	10.1 (0.8)	2.4	71.4	0.30 (0.11)
8	13.9 (2.2)	2.6	71.4	0.39 (0.11)
9	30.1 (3.9)	2.6	71.4	0.36 (0.12)
10	20.0 (1.1)	2.3	57.1	0.32 (0.12)
11	17.0 (1.7)	2.6	57.4	0.37 (0.13)
12	23.7 (3.4)	1.7	42.9	0.12 (0.07)
13	19.0 (3.0)	2.1	57.1	0.29 (0.11)
14	9.4 (1.5)	2.3	71.4	0.37 (0.10)
15	20.0 (0.8)	1.9	42.9	0.19 (0.09)
16	6.9 (0.9)	1.9	57.1	0.28 (0.12)
17	4.9 (0.1)	1.4	42.9	0.12 (0.07)

* sample size equals number of sampled individuals

** locus considered polymorphic if most common allele frequency less than 0.95

Table 4.5 A matrix of Nei's (1972) genetic identity measure (I) (below diagonal) and Nei's (1972) genetic distance measure (D) (above diagonal) for 17 populations of salidids electrophoresed. Refer to Table 4.1 for population names.

	Population																
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	-	3.09	*	*	*	*	*	*	7.61	4.27	4.23	4.39	4.29	4.41	4.35	4.31	4.40
2	0.05	-	5.09	5.63	5.67	6.27	5.64	5.66	5.60	8.00	*	*	*	6.42	5.74	5.72	7.99
3	0.00	0.01	-	3.18	2.91	3.64	3.65	4.02	4.06	0.91	0.95	0.97	0.82	1.35	1.44	0.97	1.55
4	0.00	0.00	0.04	-	0.03	0.14	0.03	0.03	0.02	1.12	1.14	1.39	1.19	0.74	0.84	0.74	1.22
5	0.00	0.00	0.06	0.97	-	0.15	0.08	0.06	0.05	1.09	1.11	1.34	1.18	0.76	0.81	0.74	1.15
6	0.00	0.00	0.03	0.87	0.86	-	0.14	0.14	0.13	1.14	1.26	1.51	1.24	0.88	1.24	1.16	1.53
7	0.00	0.00	0.03	0.97	0.92	0.87	-	0.06	0.03	1.28	1.29	1.55	1.25	0.73	0.89	0.87	1.34
8	0.00	0.00	0.02	0.97	0.94	0.87	0.95	-	0.01	1.14	1.20	1.49	1.26	0.75	0.83	0.82	1.19
9	0.00	0.00	0.02	0.99	0.96	0.88	0.98	0.99	-	1.15	1.19	1.48	1.23	0.70	0.79	0.78	1.17
10	0.01	0.00	0.40	0.33	0.34	0.32	0.28	0.32	0.32	-	0.07	0.23	0.16	0.19	0.33	0.20	0.27
11	0.02	0.00	0.39	0.32	0.33	0.28	0.28	0.30	0.30	0.93	*	0.08	0.04	0.14	0.29	0.21	0.18
12	0.01	0.00	0.38	0.25	0.26	0.22	0.21	0.23	0.23	0.79	0.93	-	0.07	0.25	0.42	0.37	0.27
13	0.01	0.00	0.44	0.30	0.31	0.29	0.29	0.28	0.29	0.86	0.96	0.93	-	0.21	0.40	0.28	0.31
14	0.01	0.00	0.26	0.48	0.47	0.42	0.48	0.47	0.50	0.83	0.87	0.78	0.81	-	0.24	0.25	0.19
15	0.01	0.00	0.24	0.43	0.45	0.29	0.41	0.43	0.46	0.72	0.75	0.66	0.67	0.79	-	0.16	0.26
16	0.01	0.00	0.38	0.48	0.48	0.32	0.42	0.44	0.46	0.82	0.81	0.69	0.76	0.78	0.86	-	0.38
17	0.01	0.00	0.21	0.29	0.32	0.22	0.26	0.30	0.31	0.76	0.83	0.77	0.74	0.82	0.77	0.68	-

* computer unable to calculate values

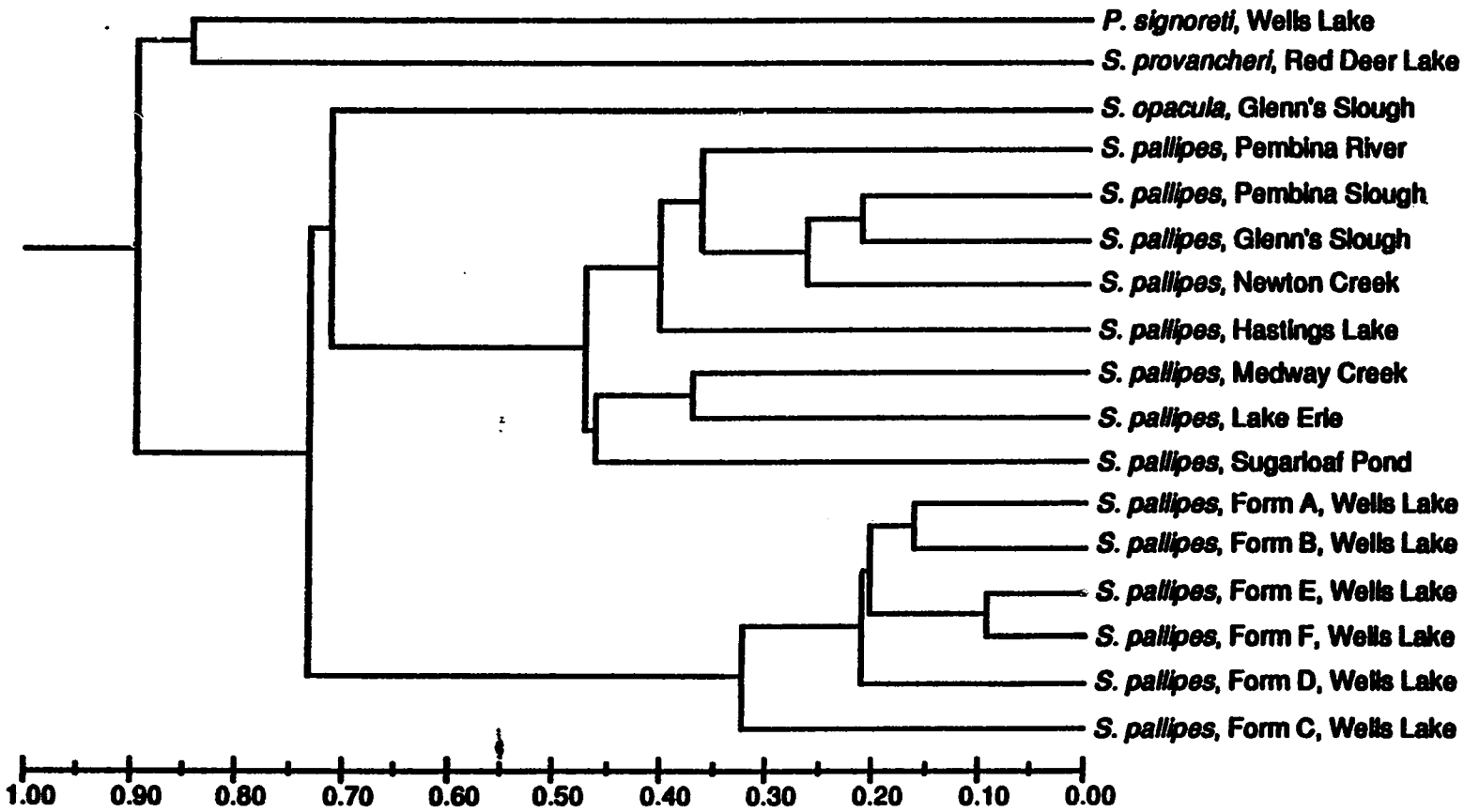


Figure 4.1 UPGMA phenogram generated from Cavalli-Sforza & Edwards (1967) chord distance matrix for all populations.

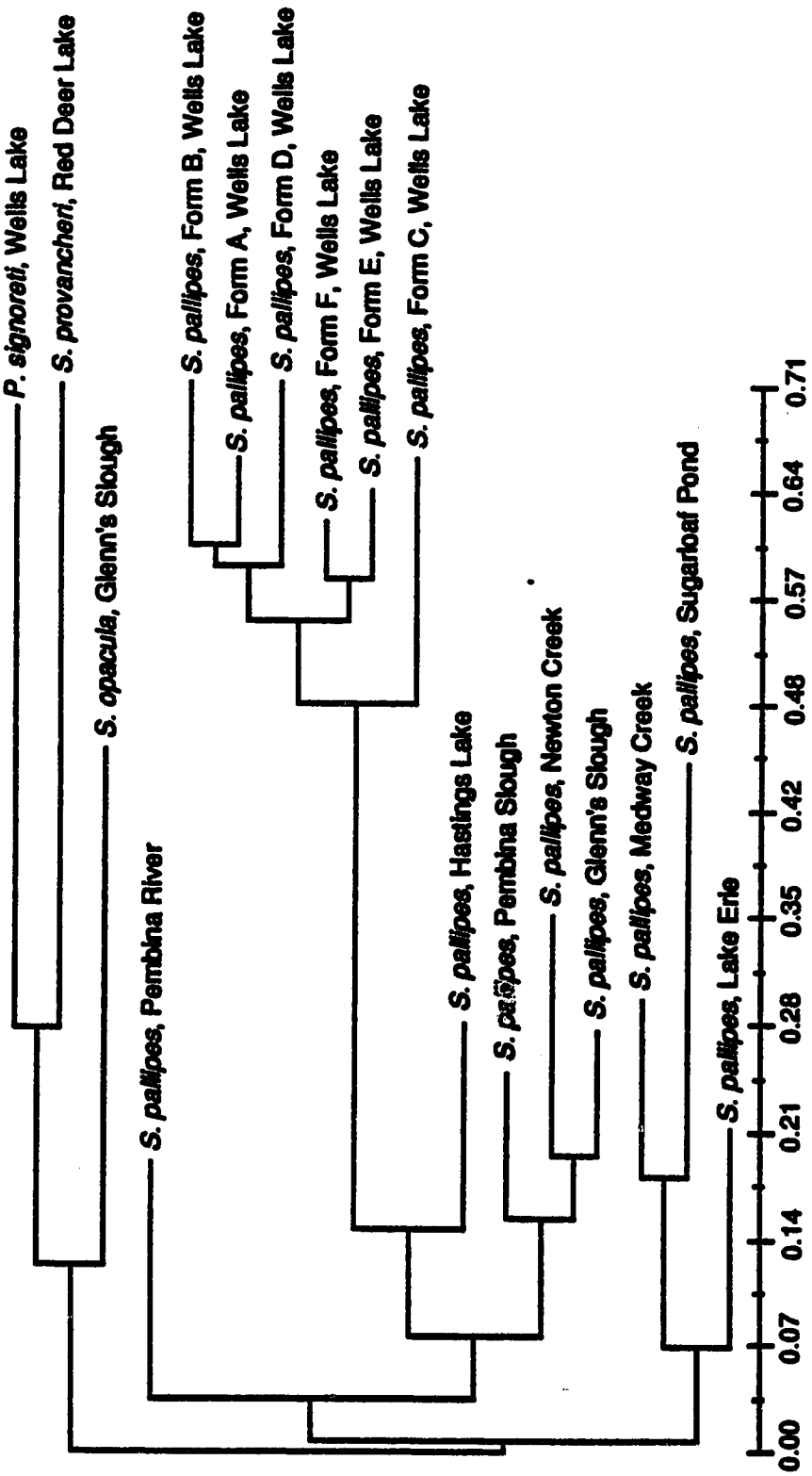


Figure 4.2 Wagner rooted tree using outgroup method generated from modified Rogers Distance (Wright 1978) matrix for all populations.

Table 4.6 Slatkin's corrected Nm values matrix for all sampled populations. Population names as in Table 4.1.

	Population																
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	****																
2	0.01	****															
3	0.03	0.02	****														
4	0.04	0.02	0.03	****													
5	0.04	0.02	0.03	0.91	****												
6	0.05	0.02	0.04	0.15	0.16	****											
7	0.06	0.02	0.04	0.95	0.50	0.46	****										
8	0.05	0.02	0.04	1.09	1.32	0.50	1.75	****									
9	0.03	0.02	0.03	1.70	0.79	0.34	2.28	7.37	****								
10	0.04	0.02	0.05	0.06	0.06	0.06	0.08	0.07	0.05	****							
11	0.05	0.02	0.06	0.07	0.07	0.07	0.09	0.07	0.05	0.79	****						
12	0.03	0.01	0.04	0.04	0.05	0.05	0.07	0.06	0.04	0.21	0.35	****					
13	0.04	0.02	0.05	0.05	0.06	0.06	0.08	0.07	0.05	0.21	0.46	0.21	****				
14	0.06	0.02	0.06	0.07	0.08	0.09	0.15	0.11	0.07	0.31	0.28	0.31	0.22	****			
15	0.03	0.01	0.04	0.06	0.06	0.06	0.10	0.08	0.05	0.10	0.13	0.08	0.10	0.18	****		
16	0.05	0.02	0.05	0.05	0.06	0.08	0.09	0.10	0.06	0.15	0.18	0.11	0.07	0.21	0.22	****	
17	0.04	0.01	0.04	0.05	0.07	0.08	0.11	0.09	0.05	0.09	0.23	0.12	0.13	0.29	0.19	0.20	****

5. Concluding comments about the *Saldula pallipes* group

5.1 The taxonomic status of the *Saldula pallipes* complex in Alberta and western Saskatchewan

Individuals of *S. pallipes* from Alberta and western Saskatchewan are either of the tan or black "variety". I believe these two "varieties" represent different species in the *S. pallipes* complex. This conclusion is based on the results from the four previous chapters. Each species can be separated by structural, habitat association, and electrophoretic characters. The tan variety is formally described in Appendix 1 as *Saldula sodanuma* Mulyk. I also recognize, with reservation, the black variety as *S. pallipes*. I agree with fellow saldid systematists that specimens of *S. pallipes* from North America are not conspecific with specimens from Europe. However, a formal systematic study is required in order to determine which, if any, of the following names applies to the North American populations of *S. pallipes*.

Saldula interstitialis (Say) 1825
S. dimidiata (Curtis) 1835
S. ocellata (Costa) 1843
S. laticollis (Reuter) 1875
S. reperta (Uhler) 1877
S. tropicalis (Champion) 1900
S. inconstans (Distant) 1909
S. chipetae Drake and Hottes 1955

Until the proposed study is completed it would be systematically incorrect to refer to the black variety as something other than *S. pallipes*.

5.2 A general discussion of the *Saldula pallipes* and *S. sodanuma* in Alberta and western Saskatchewan

The *Saldula pallipes* complex has resisted resolution for nearly 200 years. Taxonomic characters other than morphological ones must be used to resolve this complex. In this section I hope to merge the conclusions from the four previous chapters into a coherent statement regarding the status of *S. sodanuma* and *S. pallipes* in Alberta and western Saskatchewan.

Saldula sodanuma and *S. pallipes* had very apparent morphological differences once these two species were separated by the other techniques. The habitus color of each species is markedly different, black versus tan. Similar situations have occurred in blackflies where a morphospecies was differentiated cytologically into several cytotypes which were later found to have slight structural differences (Adler and Currie 1986). Further, the collection data indicated slight quantitative habitat differences between these sibling species (Adler and Currie 1986).

Quantitative habitat differences were also noted for each species of the *S. pallipes* complex. Individuals of *S. sodanuma* were collected on alkaline shores. Alkaline shores occur predominately in the *Saline Lakes Limnological Region* of the prairie provinces (*sensu* Northcote and Larkin 1966). The absence of saline habitats in the *Forest Zone of Freshwater Lakes* (*sensu* Northcote and Larkin 1966) suggests this may be the northern limit for *S. sodanuma*. Individuals of *S. pallipes* were collected on a variety of temporary and permanent freshwater habitats. These habitats occur all over the province of Alberta, but are especially predominant in the northern half (Northcote and Larkin 1966). Freshwater corridors through the *Saline Lakes Limnological Zone* are provided by rivers (Northcote and Larkin 1966) thus allowing *S. pallipes* into the *Great Plains* area (*sensu* Allen 1892). Therefore, although the two species occur in the same geographic area of central Alberta and Saskatchewan they were collected in markedly different habitats which maintain their separation.

Based on laboratory and field observations, individuals of Form A *S. sodanuma* probably use visual and olfactory clues to locate, assess, and select distant shore habitats. Further, since saldids mate in the habitat, individuals of both species must be present in the same habitat for interbreeding to occur. Yet, individuals of either species were infrequently collected in habitats where the other species was readily collected. This type of assortative mating maintains and promotes the isolation of these two species.

These two species have unique alcohol dehydrogenase and aldehyde oxidase alleles for which no hybrid individuals were observed. While it is possible that individual adults of these species could hybridize their seemingly distinct habitat preferences should minimize contact and hence interspecific mating.

The Forms of *S. sodanuma* represent different phenotypes of the same genotype and should be viewed as panmictic. The continual turnover of shoreline habitats, extremely vagile adults, multiple matings by a single individual, and multivoltism may explain the genetic similarity of *S. pallipes* across Alberta and western Saskatchewan. The highly fixed state of the saldid genome may not only allow saldids to survive ephemeral habitats but may provide accurate replicable allozyme markers for systematists to delineate species.

5.3 Future research in the Saldidae

The knowledge base of the Saldidae is quite small compared to other families of insects (e.g., Carabidae) so almost every aspect of saldid biology (e.g., systematics, natural history) has many unanswered questions. In particular, I believe that continued habitat selection studies using individuals of both species how habitat specific these species are. Comparisons of mitochondrial DNA restriction site analyses of all members of the *S. pallipes* complex may answer questions about their relationship to one another and species concepts within *Saldula*. Comparing these results with those of the rather 'life history-diverse, yet non-speciose' tribe Saldini will aid in elucidating the process(es) of speciation within the family Saldidae.

5.4 Personal Concluding Remarks

I believe that classification systems drawn from a single source of information are inherently flawed. Specialists, whether taxonomists examining genitalia, molecular biologists analyzing restriction site data, or ethologists observing wasp oviposition behavior, tend to limit their classification systems only to what they observed. By doing so, specialists ignore the wealth of information associated with every organism. Saldid classification to date was has been based on morphological characters which has left several species complexes unresolved. The *S. pallipes* group has not been resolved using a single technique, nor do I believe it will ever be resolved using a single technique. By combining several different approaches, I believe, I have made a significant contribution to the understanding of the *S. pallipes* group.

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Appendix 1. Description of *Saldula sodanuma* Mulyk

It was recommended by colleagues that I formally recognize the tan variety as an undescribed species. I therefore have described it as *Saldula sodanuma* Mulyk.

The description of the new species contained herein is the basis for a description in a separate publication (i.e., in a referred journal); under Article 8b of the International Code of Zoological Nomenclature, the author requests that neither this thesis, nor the description contained herein, be considered as published (*sensu* International Code of Zoological Nomenclature).

A1.1 Key for *Saldula pallipes, S. sodanuma, and S. opiparia* of central Alberta and western Saskatchewan

In the study area, two species are recognized (see key below), and one is described below. A third species, *Saldula opiparia* (Drake and Hottes) is similar in its features to one of the species noted above and is included here for comparative purposes.

1.a Hemelytral habitus leucine to fuscous; head, pronotum, and scutellum faintly rugulose; postclypeus tumid 2

1.b Hemelytra habitus black; head, pronotum, and scutellum distinctly rugulose; facial callosities; postclypeus not tumid .....*S. pallipes*

2.a Hemelytral habitus leucine; third and fourth antennomeres slender; pronotal margin straight; distal fuscous stripe on dorsal surface of forefemur; usually collected on shores of non-alkaline lacustrine and palustrine habitats .....*S. opiparia*

2.b Hemelytral habitus is testaceous to fuscous; third and fourth antennomeres tumid; pronotal margin slightly convex; fuscous stripe extending from base to near apex on dorsal surface of forefemur; usually collected on shores of alkaline lacustrine and palustrine habitats .....*S. sodanuma*

A.1.2 Description of *Saldula sodanuma* Mulyk

Saldula sodanuma, *new species*

Type material.- HOLOTYPE male, labeled: CANADA Saskatchewan, Wells Lake 2.5 km west Marsden, on dried wrack deposit, Sept 27, 1989, Dean S. Mulyk. ALLOTYPE female, labeled same as male. 63 additional PARATYPES (32 male: 31 female) labeled same as holotype.

Type locality.- Wells Lake, Saskatchewan, Canada. The precise locality where specimens were collected was the beach parallel to the highway approximately 2.5 km from the town of Marsden, on Highway 40.

Derivation of specific epithet.- This species is named after the most prominent cation (sodium) in the waters of the type locality, Wells Lake, Saskatchewan. It reflects the association between alkaline athalassic waters and the distribution of this species.

Recognition.- Adults of *S. sodanuma* are recognized by their testaceous to fuscous hemelytral habitus, a tumid postclypeus, and a pronotum which is distinctly demarcated from the posterior lobe by a sulcus; adults of *S. pallipes* have a black hemelytral habitus, non-tumid postclypeus, and their pronotums are weakly demarcated from the posterior lobe by a sulcus. Specimens of *S. sodanuma* are markedly similar to *S. opiparia*,

however adults of the latter species have a leucine hemelytral habitus, slender third and fourth antennomeres, and a straight pronotal margin.

Description.- Total length in mm: male (n = 33) range 4.82 - 5.52; female (n = 32) range 5.41 - 6.15. Greatest width in mm: male (n = 33) range 2.07 - 2.56 ; female (n = 32) range 2.28 - 2.76.

Ground color black. Dorsum with very fine recumbent golden pubescence, without long setae. Venter black. Head, pronotum, scutellum faintly rugulose, faintly shiny.

Head with postclypeus tumid. Facial callosities curved (Figure A.1 A) to broadly oval and extended down past base of tylus (Figure A.1 B). Antennal scape mostly leucine to yellow with small ventral testaceous to fuscous marking, other articles testaceous to fuscous. Scape stout, pedicel long and slender, antennomeres three and four tumid.

Pronotal margins slightly convex, distinctly demarcated from posterior lobe. Pronotum either entirely black (Figure A.1 D) or with lateral margins marked with yellow to testaceous (Figure A.1 C). Procoxal lamella margins narrowly leucine.

Hemelytra faintly shining, clavus dull; hemelytra mostly testaceous to fuscous, with leucine, yellow, and fuscous markings. Both sexes macropterous.

Legs leucine to testaceous, marked with fuscous; entire length of forefemur marked with ventral fuscous stripe.

Variation.- Saldula sodanuma has six distinctly different Forms. These Forms are separated by differences in the size and shape of the facial callosities (Figure A.1), the size and number of wingspots on the leading edge of the corium (Figure A.1), color of the lateral margins of the pronotum (Figure A.1), and overall color. The following coding system was developed to ease sorting and classifying of collected specimens.

Basic ground color: tan (T), dark tan (DT), or black (D)

Facial callosities: large (LC) or normal (NC).

Color of the pronotal margin: pale (PPM) or dark (DPM)

Wingspot(s) on the leading edge of the hemelytra: two large spots (2WS), one large spot (1WS), or concolorous margin (0WS)

Each Form was coded using the above system and then assigned an alphabetical designation (Table A.1).

Geographical distribution.-This species has been collected in the *Saline Lakes Limnological Region* of Alberta and western Saskatchewan (*sensu* Northcote and Larkin 1966). Further collecting of alkaline shore habitats within the *Saline Lakes Limnological Region* of Canada and the United States will firmly establish the geographic limits of this species.

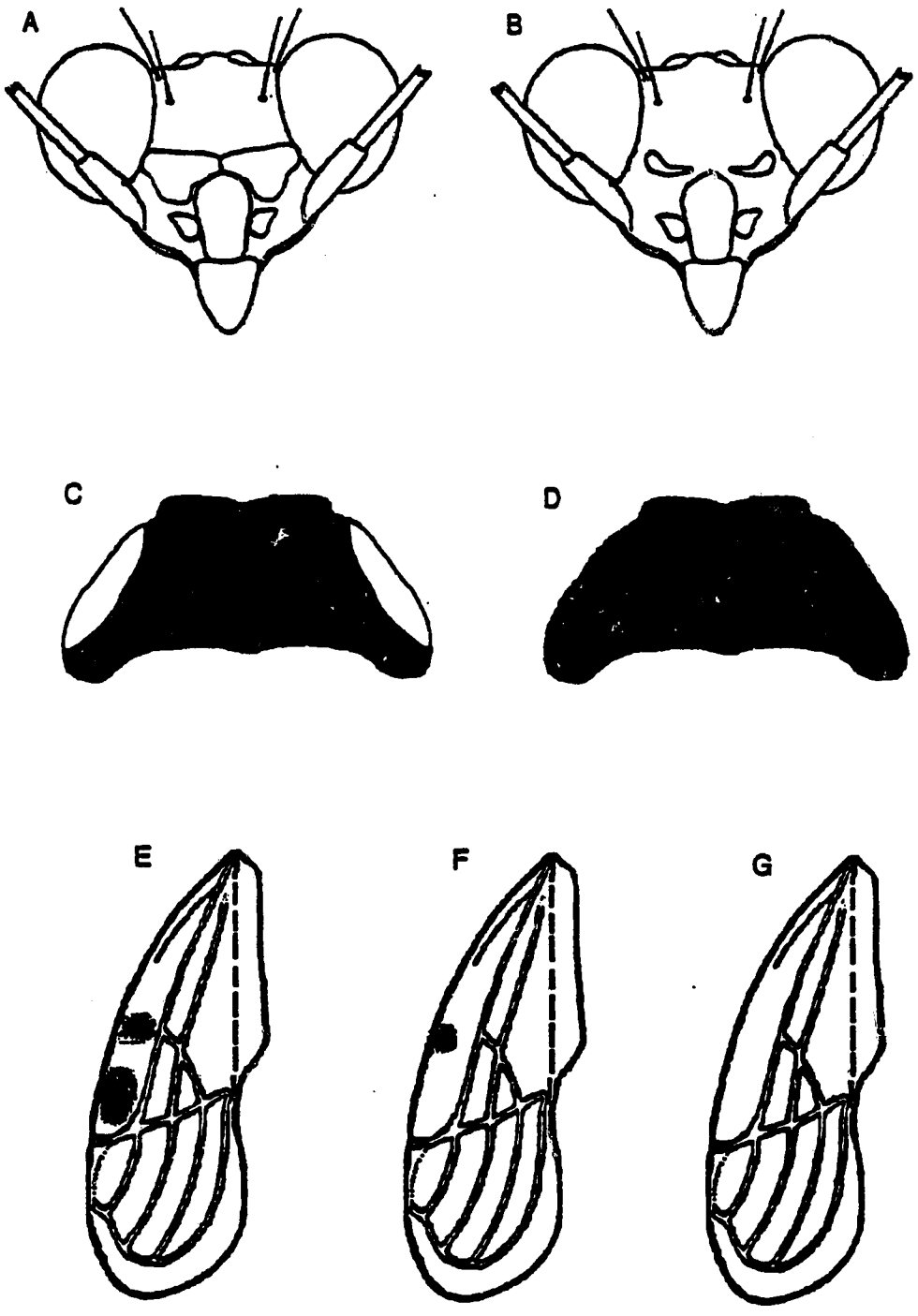

Figure A.1 Morphological characters used to separate co-occurring Forms of *Saldula sodanuma*. A. Large callosities*. B. Normal callosities*. C. Pale pronotal margin. D. Dark pronotal margin. E. Two wingspots on hemielytral leading edge**. F. One wingspot on hemielytral edge**. G. Concolorous hemielytral margin**.

* figure modifed from Figure 136 of Brooks and Kelton 1967
** note only the wingspots in question are shaded; other wing markings are not illustrated.

Table A.1 Alphabetical coding system used for co-occurring forms of *S. sodanuma*.

Form code	Ground color	Callosity size	Pronotal margin color	Number of wingspots
A	tan	large	pale	2
B	tan	large	dark	2
C	tan	large	dark	1
D	tan	small	dark	2
E	dark-tan	large	pale	0
F	dark brown	large	dark	0

Vita

I was born August 31, 1964, in Edmonton, Alberta, to Marcia Orissa Mulyk (née Ozipko) and Stefan Mulyk. I am the oldest of my parents' two children. My brother Todd is slightly less than two years my junior. While growing up in northern Edmonton I attended Kindergarden, Mee Yah Noh Elementary School, Killarney Junior High School, and finally Queen Elizabeth Composite High School. Throughout my childhood and teenage years my parents encouraged my interest in the biological sciences. During various camping trips my father would take my brother and myself on long walks (at least to a child's legs) through the woods, plains, or mountains and point out to us various "bits O'nature". I entered the University of Alberta in September 1982 and received my B.Sc., Specialization Entomology, in June 1987. I became interested in saldids and other shore insects associated with *festering mudholes* (*sensu* D. Mulyk, shortly after getting stuck in Glenn's Slough) after working for Dr. W. G. Evans during the summer between my second and third undergraduate year of University. I remember catching my first saldid on the shores of Amisk Creek near Tofield, Alberta on a warm, sunny, late-June day and realizing it was a neat bug. And so began my interest in saldids which continues' til the present day.