A COMPARATIVE STUDY OF TWO SEED BUGS,
GEOCORIS BULLATUS (SAY) AND G. DISCOPTERUS STÅL
(HEMIPTERA: LYGAEIDAE) IN THE YUKON.

By

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B.Sc. Trent University, 1980

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DEPARTMENT OF ZOOLOGY

We accept this thesis as conforming
to the required standard

June, 1985

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Abstract

Geocoris bullatus (Say 1831), (Hemiptera: Lygaeidae) has been collected and studied across North America but the present work is the first detailed study of western North American G. discopterus Stål 1874. In fact, it has been claimed that G. discopterus is solely a species of the east. As the two species are taxonomically difficult to separate, when they were apparently discovered together at several localities in the southwestern Yukon, a detailed investigation of their systematics and distribution seemed necessary. Species status of Yukon G. bullatus and G. discopterus was established morphologically using standard taxonomic characters. Biological species status was confirmed through breeding experiments. The life cycles of Yukon G. bullatus and G. discopterus were studied and significant differences were discovered in the generation time and phenology. G. discopterus is univoltine and usually overwinters in the adult stage, while G. bullatus is bivoltine and overwinters in the egg stage. Fat body dissections revealed adult G. discopterus fat body size increased toward the end of summer. No such trend was recognized in adult G. bullatus. Total fatty acid levels were assayed for each species, and adult G. discopterus were found to contain higher quantities than G. bullatus, perhaps correlating with the overwintering strategy in G. discopterus. An investigation of the habitats occupied by each species was performed through an in depth vegetation analysis. G. discopterus was found to prefer xeric sites situated on south-facing slopes and outwash plains while G. bullatus occupied disturbed mesic roadsides and wastelands. Habitat preference differences coupled with phenological differences may account for the apparent sympatry of these two Geocoris species at some
Yukon localities. Comparison of the xeric habitat of *G. discopterus* to known glacial relict sites in the interiors of Alaska, Yukon and Siberia reveal striking similarities. Late Pleistocene pollen cores also compare favorably with these *G. discopterus* habitats. In view of this and the disjunct North American distribution of *G. discopterus*, this species is hypothesized to be a relict species from the late Pleistocene ice age.
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CHAPTER I: General Introduction

The subfamily Geocorinae is an unusual taxon in the seed-bug family Lygaeidae as all of its known members are predaceous. The common name of this subfamily is the "big-eyed bugs", a name derived from their prominent eyes, a characteristic of predaceous insects.

The genus Geocoris Fallen is worldwide in distribution and contains over 124 described species (Slater 1964). Geocoris bullatus (Say 1831) and Geocoris discopterus Stål 1874 occur in North America, and Readio and Sweet (1982) suggest that these two species fall into a group of geocorines that is completely Holarctic. Within this group they propose that Geocoris bullatus, Geocoris discopterus, Geocoris floridanus Blatchley 1926, Geocoris frisoni Barber 1926 and Geocoris pallens Stål 1854 form a closely related morphological subgroup. All species in this bullatus-pallens complex have northern ranges and are distinguished by two pale vittae or stripes on the scutellum.

Geocoris species are hemimetabolous and the nymphs live in the same habitat and feed on the same food as the adults. The insects are also cannibalistic, with larger instars and adults feeding on the smaller nymphs. Geocoris species locate their prey by vision and impale it on their outstretched rostrum or beak. In the field Geocoris individuals have been observed feeding on arthropods from the Orders Diptera, Coleoptera, Lepidoptera, Hemiptera, Collembola and Acarina (Dunbar and Bacon 1972; Tamaki and Weeks 1972; Dunbar 1971a; Stoner 1970; Van den Bosch et al. 1969; Oatman and McMurtry 1966; Smith 1923). Geocoris bullatus is a significant predator of the chinch bug, Blissus leucopterus hirtus Mont. (Dunbar 1971a), the lygus bug, Lygus pratensis (L.) (Tamaki and Weeks 1972), the green peach aphid Myzus persicae (Sulzer) (Tamaki and Weeks 1972), and the clover
aphid Roepkea [= Nearctaphis] bakeri (Cowen) (Smith 1923). Thus Dunbar (1971 a) and Tamaki and Weeks (1972) think that this species has potential as a biological control agent.

According to Readio and Sweet (1982) both G. bullatus and G. discopterus characteristically occur in open sandy areas in the eastern United States. These authors find that G. bullatus is abundant in disturbed areas and along roadsides, while G. discopterus occurs primarily in the pine barrens of the east coast. G. bullatus is widely distributed throughout Canada and the northern United States, but Readio and Sweet (1982) consider G. discopterus to be a typical eastern species.

Readio and Sweet (1982) state that, "Records of G. discopterus from the western United States and Canada determined by Barber, Van Duzee and others, evidently refer instead to other brachypterous species of the western bullatus-pallens complex.". They state further that, "Geocoris discopterus was never present in the same habitat with any other species of geocorines, even though the populations may be contiguous. This clearly seems to be a case of habitat exclusion which warrants more careful study."

The discovery of what appears to be G. bullatus and G. discopterus in the Yukon, living in sympatry, contrasts with the situation described by Readio and Sweet (1982) and provides a unique opportunity to study these closely related species in a different geographic area. Not only does the Yukon situation pose interesting zoogeographic questions, but it allows for an in depth study of apparent coexistence. It would appear that the circumstances in the Yukon are not the same as those in the eastern United States.
The following flow chart summarizes the sequence of chapters and thus serves as an outline of the thesis.

Morphospecies Identity

↓

Biological Species Distinction

↓

Distribution

↓

Phenology → Fat Body Reserves

↓

Food Habits

↓

Habitat

↓

Species Comparison

↓

Zoogeography
CHAPTER 2: Identity of Yukon Species

Introduction

Geocoris bullatus was described by Say (1831) and has been considered a valid species since. G. discopterus however, was described as a separate species by Stål (1874) but was considered a subspecies of bullatus by McAtee (1914) and Parshley (1916). McAtee (1914) reported that discopterus had fewer punctures on the disc of the pronotum and intergraded with bullatus. Blatchley (1926) however, noted that if form of body, and texture and sculpture of elytra count for anything in taxonomy, then discopterus is a distinct species. He separated discopterus from bullatus in the eastern United States by the following couplet:

"Corium sparsely punctate, the punctures in evident rows; femora usually in great part or wholly piceous; macropterous form only known..........................bullatus
Corium thickly irregularly punctate; femora wholly pale or faintly dotted with fuscous; both wholly macropterous and brachypterous forms known..................discopterus"

Readio and Sweet (1982) have recently reconsidered the taxonomy of Geocoris in eastern North America, and have likewise considered bullatus and discopterus to be good species. They have redescribed them and separated them on the basis of size, coloration of the corium and pronotum, as well as by structure of the spermatheca and left parameres. Identification however, is not an easy task.

While G. bullatus is a common species throughout Canada and the northern United States, Readio and Sweet (1982) claim that G. discopterus
is a strictly eastern species: western United States and Canada material is not considered to be conspecific. Hence, it was necessary to first determine the identity of the Yukon material. Since general body color and size are quite variable, a thorough systematic analysis was necessary.

**Materials and Methods**

Authentic adult specimens of both *G. bullatus* and *G. discopterus* were obtained from the eastern United States for reference. Yukon specimens of adults and nymphs were collected weekly between May 7 and Sept. 7, 1983 in the Kluane Lake and Haines Junction regions of the southwestern Yukon. Animals were collected with an aspirator; the adults were card pointed and the nymphs were preserved in 70% ETOH for morphological study. Morphological characters were examined using a Wild M 8 zoom-lens microscope at a magnification of 9X and measurements were made with an ocular micrometer. Standard measurements included: total body length (T.L.) (from apex of head to tip of abdomen); head width (H.W.) (at widest part across eyes); and pronotum width (P.W.) (at posterior (widest) angle). Wing status was also noted and recorded as macropterous (full length wings), sub-macropterous (wings not reaching genital segments) or brachypterous (short, non-functional wings).

An in depth study was also performed on 10 adults of each sex and species recording; (i) colour, (ii) cuticular architecture and (iii) the following morphological measurements, the letter in parentheses indicates the structure on Figure 1: (A) head length, from tip of tylus to posterior of head; (B) interocular distance between the compound eyes; (C) length of
Figure 1  Diagram indicating the Geocoris morphological features measured. See text for explanation.
individual antennal segments; (D) length of individual rostral segments; 
(E) pronotal length; (F) scutellar width, at the anterior (widest) angle; 
(G) scutellar length; (H) abdominal width, at the widest segment; and (I) 
abdominal length. Wet weights were also recorded with a Mettler Micro 
Gram-Atic Balance (Model # 1-912).

Ten specimens of each nymphal instar of both species were also 
measured for head width and individual antennal segment length. I and II 
instars were checked against laboratory bred insects to be sure of their 
identity. Head width and antennal segment length were chosen in particular 
as they tend to be constant between individuals within an instar. The 
other characters used for adult comparison are highly variable in the 
instars (Scudder, pers. comm.).

Results

_G. bullatus_ and _G. discopterus_ can be distinguished on the basis of 
size and punctation of the corium. The T.L., H.W. and P.W. of _G. bullatus_ 
are significantly larger than _G. discopterus_ (Student's t-test, p<0.01) 
(see Table 1). Other body measurements also indicate that _G. bullatus_ is 
the larger of the two (see Appendix I).

Body coloration is variable in both species although _G. discopterus_ 
usually has yellow spots on the calli while _G. bullatus_ may or may not have 
brownish spots. _G. discopterus_ is without an impunctate line between the 
calli along the midline of the pronotum, while this line is present in 
_G. bullatus_. _G. discopterus_ is characterized by uniform punctation on the 
corium whereas there are impunctate areas in _G. bullatus_. Wing status also
Table 1  Comparison of adult *Geocoris* total body length, head width and pronotum width.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>X (mm) + S.E.</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>G. bullatus</td>
<td>G. discopterus</td>
<td>G. bullatus</td>
</tr>
<tr>
<td></td>
<td>N=77</td>
<td>N=96</td>
<td>N=88</td>
</tr>
<tr>
<td>Total length</td>
<td>3.67 + 0.02</td>
<td>2.75 + 0.01 *</td>
<td>4.17 + 0.02</td>
</tr>
<tr>
<td>Head width</td>
<td>1.39 + 0.01</td>
<td>1.13 + 0.01 *</td>
<td>1.49 + 0.00</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>1.33 + 0.01</td>
<td>1.00 + 0.00 *</td>
<td>1.52 + 0.01</td>
</tr>
</tbody>
</table>

* indicates significant difference (t-test, p<0.01)
appears to distinguish these two species, but because it is such a variable
coloration. The wing buds in the 5th instar extend
to the end of the second abdominal segment in G. discopterus and to the end
of the third in G. bullatus.

The T.L. of Yukon G. bullatus and G. discopterus do not differ
significantly from their eastern counterparts (t-tests, \( p < 0.05 \),
respectively) (see Table 2 a & b). Comparison of Yukon G. discopterus T.L.
to other species of the bullatus-pallens complex however, shows G. pallens,
eastern G. bullatus and male G. floridanus to be significantly different
(t-test, \( p < 0.05 \); see Table 3). Female G. floridanus and both sexes of
G. frisoni do not differ from Yukon G. discopterus in T.L.

G. floridanus however, is macropterous to submacropterous, pale in
colour and has an irregularly punctate corium; all characteristics quite
different from G. discopterus. According to Readio and Sweet (1982),
G. frisoni is different from G. discopterus as they describe it as having
the hemelytra meeting in a midline, the scutellum longer than wide and the
Table 2 a & b  Comparison of Yukon and eastern \textit{Geocoris} total body length, head width and pronotum width.

a)  

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>( \bar{x} ) (mm) ± S.E.</th>
<th>( \bar{x} ) (mm) ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male \textit{G. bullatus}</td>
<td>Female \textit{G. bullatus}</td>
</tr>
<tr>
<td></td>
<td>Yukon (N=77)</td>
<td>Eastern (N=10)</td>
</tr>
<tr>
<td></td>
<td>Yukon (N=88)</td>
<td>Eastern (N=9)</td>
</tr>
<tr>
<td>Total length</td>
<td>3.67 ± 0.02</td>
<td>3.49 ± 0.04</td>
</tr>
<tr>
<td>Head width</td>
<td>1.39 ± 0.01</td>
<td>1.38 ± 0.01</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>1.33 ± 0.01</td>
<td>1.25 ± 0.00</td>
</tr>
</tbody>
</table>

b)  

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>( \bar{x} ) (mm) ± S.E.</th>
<th>( \bar{x} ) (mm) ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male \textit{G. discopterus}</td>
<td>Female \textit{G. discopterus}</td>
</tr>
<tr>
<td></td>
<td>Yukon (N=96)</td>
<td>Eastern (N=9)</td>
</tr>
<tr>
<td></td>
<td>Yukon (N=51)</td>
<td>Eastern (N=11)</td>
</tr>
<tr>
<td>Total length</td>
<td>2.75 ± 0.01</td>
<td>2.99 ± 0.03</td>
</tr>
<tr>
<td>Head width</td>
<td>1.13 ± 0.01</td>
<td>1.27 ± 0.01 *</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>1.00 ± 0.00</td>
<td>1.09 ± 0.01</td>
</tr>
</tbody>
</table>

* indicates significant difference (t-test, \( p<0.05 \), variances not equal).

1 eastern measurements from Readio and Sweet (1982).
Table 3  Comparison of total body length of Yukon *G. discopterus* with those of eastern *G. bullatus*, *G. floridanus*, *G. frisoni* and *G. pallens* as recorded by Readio and Sweet (1982).

<table>
<thead>
<tr>
<th>Species</th>
<th>R (mm) + S.E. Male</th>
<th>X (mm) + S.E. Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R and S G. discopterus</td>
<td>R and S G. discopterus</td>
</tr>
<tr>
<td></td>
<td>N=10</td>
<td>N=77</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>3.49 ± 0.04</td>
<td>2.75 ± 0.01 *</td>
</tr>
<tr>
<td><em>G. floridanus</em></td>
<td>3.20 ± 0.03</td>
<td>2.75 ± 0.01 *</td>
</tr>
<tr>
<td><em>G. frisoni</em></td>
<td>2.96 ± 0.05</td>
<td>2.75 ± 0.01</td>
</tr>
<tr>
<td><em>G. pallens</em></td>
<td>3.32 ± 0.03</td>
<td>2.75 ± 0.01 *</td>
</tr>
</tbody>
</table>

* indicates significant difference (t-test, p<0.05, variances not equal)
corium being unicolorous. Alternately, \textit{G. discopterus} has hemelytra that barely touch, the scutellum is wider than long and the corium is bicolored.

\textbf{Discussion}

The adult \textit{G. bullatus} collected in the Yukon match the descriptions given by Readio and Sweet (1982) for eastern specimens in terms of general morphology and coloration. Yukon \textit{G. bullatus} however, are 61\% macropterous while the eastern specimens sustain only 18\% macroptery. While \textit{G. bullatus} from the Yukon are not significantly larger than the eastern specimens, the mean T.L. of Yukon \textit{G. bullatus} does fall between that of eastern American \textit{G. b. bullatus} and \textit{G. bullatus borealis} Dallas 1852, a subspecies reported from northern Canada and Alaska (Readio and Sweet 1982). \textit{G. bullatus borealis} is said to have highly variable corium coloration and a mean T.L. of 3.82 mm and 4.59 mm for males and females, respectively (Readio and Sweet 1982). The fact that the Yukon specimens of \textit{G. bullatus} have little variation in corium colour and do not differ in size from the eastern specimens provides evidence that there is no distinct north-south size gradient in this species. \textit{G. bullatus borealis} can be thus considered synonomous with \textit{G. b. bullatus} (Readio and Sweet 1982).

The Yukon specimens of \textit{G. discopterus} do not differ significantly in size from the eastern specimens. The brachyptery of the Yukon and eastern specimens is very similar, 99\% and 92\% respectively, as is their coloration. The evidence clearly points to Yukon and eastern \textit{G. discopterus} specimens being conspecific.

Readio and Sweet (1982) consider \textit{G. discopterus} as part of a subgroup
including *G. bullatus*, *G. floridanus*, *G. frisoni* and *G. pallens*. In all cases the coloration of *G. discopterus* distinguishes it from these other species. The T.L. of the other *Geocoris* species in the *bullatus-pallens* complex is also quite different from *G. discopterus*.

Hence, the claim by Readio and Sweet (1982) that *G. discopterus* only occurs in the eastern United States and that specimens from western U.S.A. and Canada (collected by Barber, Van Duzee and others; Readio and Sweet 1982) were not *G. discopterus*, but a brachypterous species of the western *bullatus-pallens* complex is not correct. The Yukon *G. discopterus* and *G. bullatus* are conspecific with those described from the east by Readio and Sweet (1982). The Yukon *G. discopterus* can not be confused with other brachypterous species from the *bullatus-pallens* complex. *G. bullatus* and *G. discopterus* are good morphospecies but whether they are good biological species needs to be determined.
CHAPTER 3: Breeding of Morphospecies

Introduction

While G. bullatus and G. discopterus appear to be good morphospecies, their identity as good biological species has not been established. The definition of a biological species according to Mayr (1969) is, "...a group of interbreeding natural populations that are reproductively isolated from other such groups.". To establish that G. bullatus and G. discopterus are good biological species, it is necessary to show that they do not interbreed. Hence, breeding experiments were performed on field caught adults.

Materials and Methods

Breeding experiments were conducted between May 13 and Sept. 17, 1983. Adults were collected from the field during the period of sexual maturity and were maintained in a controlled environment chamber (Hotpack # 555211) at approximately 25°C with a 14 hr L:10 hr D cycle. Pairs were kept separate in 25 ml plastic vials with a central hole cut in the lid for air circulation: the hole was covered with fine nylon mesh. Water was supplied by a damp paper towel and 2 sunflower seeds (Helianthus annuus L.) were placed on the bottom of each vial for food: food and water were replaced as required. The vials were checked 4 times daily, and matings were recorded. Since individual pairs of Geocoris sp. remain in copulation from 2 to 11 hr (pers. obs.), 4 checks per day were assumed adequate to ensure that the majority of matings were recorded.
The following crosses were tested; the number in parentheses indicate the number of replicates:

a) $\sigma^G$ G. bullatus x $\Omega^G$ G. bullatus (21)
b) $\sigma^G$ G. discopterus x $\Omega^G$ G. discopterus (24)
c) $\sigma^G$ G. bullatus x $\Omega^G$ G. discopterus (15)
d) $\sigma^G$ G. discopterus x $\Omega^G$ G. bullatus (15)

The breeding experiments were carried out at times of the year when mating was observed in the wild (see Fig. 2). The G. bullatus x G. discopterus experiment was undertaken between July 16 and Sept. 17, when the period of reproduction in the two species naturally overlaps in the field. G. bullatus pairs were tested between June 14 and Aug. 29 while G. discopterus pairs were tested between May 13 and June 29 (Group I) and between July 29 and Sept. 17 (Group II).

Results

Mating was recorded in 13 of the 21 G. bullatus pairings: a total of 47 copulations were observed in the experimental period (see Table 4). In G. discopterus pairs, mating occurred in all 8 replicates for a total of 18 copulations in the period of May 13 to June 29 (Group I), and in 5 of the 16 pairs (31.25 %) studied between July 29 and Sept. 17 (Group II). In the first group, copulation took place throughout the experimental period, but in the second group mating took place in the latter half of the experimental period only (see Fig. 3). A combined total of 26 copulations occurred in G. discopterus.

In both species these intraspecific crosses resulted in fertilized egg production. Females laid approximately 1-2 eggs per day throughout the
Figure 2  The number of Geocoris copulations recorded on the Yukon study sites.
Table 4  Interbreeding of the morphospecies *G. bullatus* and *G. discopterus*.

<table>
<thead>
<tr>
<th># Of</th>
<th>Insect</th>
<th>Male</th>
<th>Female</th>
<th>Experimental Dates</th>
<th># Pairs</th>
<th># Of Mating</th>
<th>% Pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>21</td>
<td><em>G. bullatus</em></td>
<td><em>G. bullatus</em></td>
<td>06/14 - 08/29</td>
<td>13</td>
<td>47</td>
<td>61.90</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td><em>G. discopterus</em></td>
<td><em>G. discopterus</em></td>
<td>05/13 - 06/29</td>
<td>8</td>
<td>18</td>
<td>100.00</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td><em>G. discopterus</em></td>
<td><em>G. discopterus</em></td>
<td>07/29 - 09/17</td>
<td>5</td>
<td>8</td>
<td>31.25</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td><em>G. bullatus</em></td>
<td><em>G. discopterus</em></td>
<td>07/16 - 09/17</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td><em>G. discopterus</em></td>
<td><em>G. bullatus</em></td>
<td>07/16 - 09/17</td>
<td>0</td>
<td>0</td>
<td>0.00</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3  The number of *Geocoris* copulations recorded in captivity.
experimental session with some eggs of both species hatching in the mating vials.

No mating or even attempts at copulation were recorded in any of the 30 G. bullatus x G. discopterus pairings, although the experiment took place while active mating occurred between intraspecific pairs (see Table 4). No eggs were deposited in any of these mating vials.

Discussion

As successful mating was recorded in both G. bullatus and G. discopterus, it can be assumed that the experimental conditions were conducive to mating in both species.

The decline in pair mating percentage in the second group of G. discopterus as compared with the first, is probably because the major portion of this species' mating period occurs in May and June while only a small proportion of the population mates in August and September (see Chapter 5).

Since no mating or attempts at copulation were recorded in G. bullatus x G. discopterus pairings, it can be assumed that these two species are reproductively isolated. The isolating mechanism is presumed to be a premating mechanism, but this was not investigated. Both the G. bullatus and G. discopterus morphospecies in the southwestern Yukon, thus also behave as good biological species.
Chapter 4: Distribution

Introduction

While Readio and Sweet (1982) never found *G. discopterus* present in the same habitat with other geocorines, this is not the case in the southwestern Yukon. Hence, it was important to obtain a clear picture of the range and general distribution of *G. bullatus* and *G. discopterus* in this northern area.

Materials and Methods

The distribution of the Lygaeidae in the Yukon has been under study since 1974 (Scudder unpublished). Distributional data of *G. bullatus* and *G. discopterus* in particular, were obtained from specimens in the Spencer Entomology Museum (UBC) and the Canadian National Collection (Ottawa), and plotted to obtain information on range and general distribution.

Results and Discussion

Figures 4 and 5 show the distribution of *G. bullatus* and *G. discopterus* in the Yukon. *G. bullatus* has a wider range than *G. discopterus*, which is confined to the southern half of the Territory, with the exception of one location near Old Crow in the Porcupine River valley.

In general, *G. discopterus* was found in xeric sites on south-facing slopes and outwash plains. *G. bullatus*, on the other hand, was collected
in damper, weedy roadsides and disturbed habitats.

While in most cases the two species were clearly allopatric, they occurred sympatrically at Haines Junction and Tatchun Creek. These were disturbed roadsides and campground sites, respectively.
Figure 4 Distribution of *G. bullatus* in the Yukon.
Figure 5  Distribution of *G. discopterus* in the Yukon.
Chapter 5: Phenology

Introduction

The phenology of *G. bullatus* has been studied in several localities (Readio and Sweet 1982; Tamaki and Weeks 1972; Dunbar 1971 a & b) and it is evident that this species exhibits considerable variation in its life cycle details. To date, the life cycle of *G. discopterus* has not been studied in detail. A comparative study of the phenology of these two species in the southwestern Yukon was therefore undertaken. The numerical abundance of different stages were studied throughout the summer of 1983. Reproductive state was also assessed.

Readio and Sweet (1982) report that *G. discopterus* never occurs in sympatry with other species in this genus. However, *G. discopterus* has been found with *G. bullatus* in certain Yukon localities (G.G.E. Scudder, S.G. Cannings, J.J. Robinson). This apparent case of coexistence thus warranted investigation.

Materials and Methods

Eight replicate study sites, measuring 15 m x 15 m (225 m sq) were set up within 80 km of the Kluane Lake Research Station at the south end of Kluane Lake (see Figure 6). The sites were chosen according to the occurrence of the two species and were divided into two groups. The first, the Kluane Lake group, contained sites where just *G. discopterus* was present and consisted of dry south-facing slopes and outwash plains. The second group contained sites where both *G. discopterus* and *G. bullatus* were present and consisted of disturbed roadsides (see Chapter 8 for further
Figure 6  Location of study sites and weather stations in the Yukon.
site description). Included in the first group were Cultus Bay (C.B.), Duke Meadows (D.M.), Institute (Inst.) and Silver City (S.C.). Sites in the second group were Park's Farm I (P.F.I), Park's Farm II (P.F.II), Park's Field (P.Fd.) and Mountainview (M.V.). Each plot was marked with numbered flags at 1 m intervals on all sides.

Sampling with both transects and quadrats was tested and confidence limits expressed as a percentage of the mean number of animals counted on each transect/quadrat were calculated. As there was less variance among transect samples than among quadrat samples and the total number of animals counted was greater when using transects, sampling with transects was implemented. These calculations also provided the necessary information to determine the optimal number of transects needed per site per week.

The insects occurring in ten transects, each 10 cm x 15 m (15 sq m) were counted weekly at each site. Sites were sampled for 17 weeks between May 14 and Sept. 06, 1983. Thus, theoretically, each site was sampled in its entirety by the end of the season.

A random number table was used to generate the co-ordinates for the weekly transects. Two groups of 5 transects each were established at right angles to each other. The boundaries of a transect were defined by two strings stretched across the site. Animals within the transect were collected with an aspirator. The "edge effect" of such a transect was minimal as the insects were so small it was easy to tell if an individual was "in" or "out".

To aid in detection of insects, the ground within a transect was disturbed by quickly moving my hand across the top layer of soil as I proceeded down the site on hands and knees. Once collected, an insect was counted but not released until all 10 transects were completed, at which
time all insects were released at the centre point of the plot. This ensured individuals were not recounted during sampling. Immigration and emigration from sites were assumed equal.

The transect counts on a particular site were taken over a three hour period during the warmest part of the day. Heavily overcast and rainy days were not sampled as insect activity generally decreases in inclement weather.

The numbers recorded from the transects were used to construct a population profile for each species. The total number of individuals, for particular developmental stages, counted from each study site were combined on a weekly basis for the respective species. Each developmental stage was then expressed as a percentage of that total. Instars I-III were combined as field identification was extremely difficult.

To determine reproductive state, five adult females collected near to the study sites, were dissected weekly to determine the presence or absence of chorionated eggs in the ovaries. In addition, copulation data were recorded for each species throughout the summer of 1983.

Results

A population profile was constructed for each species. In Appendix III, Figures 1 - 12 portray the actual number of individuals in each developmental stage collected at each study site throughout the summer of 1983. As the sequence of generations of both _G. discopterus_ and _G. bullatus_ was the same on each of their respective study sites, a generalized scheme was produced for each species (see Fig. 7).

Figure 8 shows that _G. discopterus_ was reproducing from early May
Figure 7 Geocoris summer life history. Data from all sites was totaled for each species and developmental stage and is shown as a percentage of that total.
Figure 8 Mean number of chorionated eggs recorded from weekly dissections of five adult *G. bullatus* and *G. discopterus* females, respectively.
until the end of June and at the Cultus Bay site again in August. G. bullatus on the other hand, was reproductively active from mid-June until early September (see Figs. 8).

Overwintered G. discopterus adults were seen in copulation when sampling commenced in mid-May and the females contained chorionated eggs at this time (see Figs. 8 and 9). The I-III instars were present in mid-May and they peaked in the middle of June (see Figs. 7 and 10). Sequential emergence of the IV and V instars occurred throughout June and July. Adults showed a continuous rise in abundance from the end of June on, and peaked at the end of August/beginning of September. The developmental time from the peak of the I-III instars to the peak of the adult population took about 2 1/2 months to complete.

G. discopterus was found to have just one generation per year, and the majority appear to overwinter as adults (see Figs. 7 and 10). The adult overwintering strategy was confirmed by the capture of a marked adult female from the summer of 1982 at the P.F.II site in the summer of 1983. At the C.B. site a few individuals were seen in copulation at the end of August and those females contained chorionated eggs at this time. Thus, in some localities, G. discopterus may overwinter in the egg stage as well as the adult. However, the vast majority of G. discopterus individuals overwinter as unmated adults.

G. bullatus was found to have two generations per year in the southwestern Yukon (see Figs. 7 and 10). The I-III instars of the first generation emerge in early May when temperatures are warm enough to melt the snow (see Figs. 7 and 10). A peak abundance of instars I-III was found in mid-May. The IV and V instars were present during the last half of May and the first half of June. The first adults of the spring generation were
Figure 9  Schematic representation of the proportion of Yukon Geocoris recorded in copulation and containing chorionated eggs, in relation to time.
Figure 10  Schematic representation of the sequence of generations of Yukon Geocoris. O.W.=overwintered stage, E=egg, I-V=different nymphal instars, 1=first generation adult, 2=second generation adult. The egg portions were derived from the chorionated egg data in Fig. 8
seen at the beginning of June and peaked at the end of June. The adults were sexually active starting in the middle of June (see Fig. 2). The first peak in females with chorionated eggs occurred in late June (see Fig. 8).

The I-III nymphal instars of the second generation of *G. bullatus* occurred in the middle of June and peaked in the middle of July (see Fig. 7). The IV and V instar populations peaked at the end of July and mid-August respectively. There was an overlap in the first and second generation adults, and thus it is difficult to clearly separate the two generations. However, a decline in the number of adults caught from the middle of July to the beginning of August indicates that the second generation adults began emerging at the beginning of August. Second generation adults peaked in mid-August, at which time the frequency of females with chorionated eggs also peaked (see Figs. 7 and 8). All female *G. bullatus* studied at the end of August were without chorionated eggs. This suggests that all eggs have been laid by this time, and that the overwintering form is the egg. Both generations of this species took a month to complete nymphal development.

No nymphs of either species were present in late August which strongly indicates that overwintering does not occur in the nymphal stages of development in *G. bullatus* or *G. discopterus*.

Discussion

*G. bullatus* in the Yukon overwinters in the egg stage. This is similar to many other northern insects such as some mosquitoes of *Aedes* spp. (Ring and Tesar 1982), the water boatman *Trichocorixa verticalis*
interiores Sailer (Tones 1977), the water treader Mesovelia mulsanti White (Galbreath 1976), the water strider Rhagovelia obesa Uhler (Lee et al. 1974), and the backswimmer Notonecta borealis Bueno and Hussey (Rice 1954). Tamaki and Weeks (1972) have also found G. bullatus to overwinter as eggs in Washington. However, since Blatchley (1926) records this species in the east to overwinter as adults, population differences may be indicated. Readio and Sweet (1982) note that adults are cold resistant and can survive winter conditions, but believe the chief functional overwintering stage in the east is actually the egg.

The rapid development in G. bullatus enables it to complete two generations per year in the Yukon. In the west (southern Washington) this species has at least two and even three generations per year (Tamaki and Weeks 1972); the number of generations in the east is unknown. Since developmental rate is influenced by temperature (Tamaki and Weeks 1972) difference in the number of generations may be temperature dependent, but photoperiod may also be important.

G. discopterus has only one generation per year in the Yukon. The adult population peaks in August and the insects overwinter as adults in most localities. Blatchley (1926) reported adults collected in Indiana between July 12 and November 1, and Readio and Sweet (1982) report eastern G. discopterus to overwinter as adults in reproductive diapause.

G. bullatus displays some of the characteristics of an r-strategist suggested by MacArthur and Wilson (1967), such as a rapid rate of development and two generations per year. G. discopterus on the other hand, displays characteristics of a K-strategist, such as a slow developmental rate and only one generation per year.
Since some adult female *G. discopterus* from the Cultus Bay site in the Yukon, contained chorionated eggs in late August, these could have laid overwintering eggs. There may thus be a dichotomy of overwintering strategies in the Cultus Bay population. Females either reproduce in late August and die immediately thereafter, or they reproduce in late August and then overwinter in a state of reproductive diapause. Examples of both strategies occur in other Hemiptera. *G. bullatus* and *R. obesa*, as previously mentioned, display the first strategy where the adult females reproduce in the late summer and then die. Alternately, Pajunen (1970) suggests that ovipositing waterboatman (Heteroptera, Corixidae) females may undergo ovarian regression in the autumn and thus overwinter successfully by utilizing the rerouted resources.

In either case, late summer reproduction in *G. discopterus* females is a divergence from the dominant strategy of this species. The majority of Yukon females overwinter unmated. This dominant strategy appears to be more successful than deviant strategies as exemplified by other arthropods. Dingle (1974), working on the milkweed bug *Lygaeus kalmii* Stål and Elgmork (1980), studying the freshwater copepod *Cyclops strenuus strenuus* Fischer, found that a small fraction of adult females that deviated from the usual adult diapause by reproducing early, either failed to survive or were not as successful at reproducing as those animals that diapaused without prior reproduction. Elgmork (1980) suggests that adult diapause of unmated females is the dominant life history plan for *C. strenuus*, but that alternative plans may be followed often enough that genetic plasticity is not lost.

However, without knowing the fecundity of each type of *G. discopterus* female, their mortality and the mortality of their offspring, it is
impossible to determine the advantages or disadvantages of a flexible overwintering strategy in this species. We do know however, that the overwintering reproductive diapause which occurs in the majority of adult *G. discopterus*, avoids the production of nymphal offspring that cannot survive the winter. It also facilitates the synchronization of mating in the spring.

*G. discopterus* and *G. bullatus* differ in overwintering strategies. As both species belong to a subgroup that is completely northern (Readio and Sweet 1982) it is likely that the ancestral species was temperate with an established diapause stage. It appears that the dominant overwintering stage in temperate *Geocoris* species is the adult, as observed in *G. atricolor* Montandon (Dunbar 1971 a), *G. pallens* Stål, *G. punctipes* (Say), *G. uliginosus* (Say), *G. lividipennis* Stål and *G. discopterus* (Readio and Sweet 1982). It follows that overwintering in the egg stage is the derived condition in the species group. This concept is supported by the observation that the egg diapause in *G. bullatus* is relatively weak (Readio and Sweet 1982). *Geocoris* species that overwinter in the egg stage often have two or more generations per year (as in *G. bullatus* and *G. limbatus* Stål (Readio and Sweet 1982)); the eggs of the first generation do not diapause at all. The eggs of the second generation are probably triggered into diapause by photoperiod (Tauber and Tauber 1978). Diapause intensity tends to be weaker with an increase in the number of generations per season (Masaki 1978). What is more, *G. bullatus* has been reported to overwinter in both the egg and adult stages (Tamaki and Weeks 1972; Smith 1923) again indicating weak preference for diapause in a particular stage.

Life cycle differences occur in other groups of closely related
species. Alexander (1968) for example, identified seven kinds of life cycles in crickets (Orthoptera, Gryllidae). Masaki (1978) suggested closely related species maintaining differences in overwintering strategies indicate that diapause has probably evolved at different stages repeatedly in the ancestral form. Solbreck (1978) reinforced this suggestion by stating that variations in traits occurring in closely related species are an indication of real evolutionary alternatives rather than the results of a rigid ground plan unaltered by natural selection. That Yukon G. discopterus and some eastern G. bullatus (Blatchley 1926) have dual overwintering strategies indicates that a versatile genetic system has been maintained.

Developmental rates are clearly different in G. discopterus and G. bullatus. Alexander (1968) suggests the following factors can cause changes in developmental rate: a highly nutritious diet; high, even temperatures; tactile stimulation from crowding; photoperiod and breaking of diapause. However, the differential effects of such factors on the two Yukon Geocoris species has not been established. It appears that similar selection pressures are acting on a genetically plastic program, as suggested by Masaki (1978).

Although Readio and Sweet (1982) suggest that G. discopterus is never found in the same habitat with any other Geocoris species, it is found with G. bullatus at the sites near Haines Junction. Interspecific differences in phenology is one likely factor accounting for the sympatry between these two species.
Chapter 6: FAT BODY RESERVES

Introduction

Insect fat bodies serve as storage organs for metabolic energy reserves (Locke 1980; Downer and Mathews 1976; Fast 1970; Gilby 1963; Kilby 1963). While the fat body also functions in homeostatic regulation of blood levels of glucose and intermediary metabolism, its storage function was the factor of interest in the present research. Stored energy reserves are mobilized during diapause, starvation, prolonged flight activity and oogenesis. The majority of the fat body cells, or trophocytes, become distended with stores of fat, protein and glycogen in adults preparing for overwintering diapause (Brown and Chippendale 1977; Gilbert 1967). Females also show variation in the fat body correlated with oogenesis (Engelmann 1979; Pan and Wallace 1974; Hagedorn and Fallon 1973; Gilbert 1967; Martin 1969).

Reserves are largely stored as fatty acids because they are reduced and anhydrous and thus are highly concentrated metabolic energy. Gilbert and Chino (1974) estimate that about 90% of total fat body lipids are made of triacylglycerides (TGL), of which most are fatty acids. These fatty acids are stored in a saturated form because they pack together more efficiently than do unsaturated fatty acids. In many overwintering adult insects, there is an increase in the degree of fatty acid unsaturation because such unsaturated fatty acids have a lower melting point and thus are more easily mobilized in times of cold stress (Fast 1970). Species with differing overwintering strategies may thus show differences in their proportion of unsaturated fatty acids.
Fatty acids are either ingested as carbohydrates or are synthesized in the fat body from acetate. The fat body, rather than muscle, is the site of most synthesis because it is the more effective tissue at the process; muscle is only 1/5 as effective at the process (Gilbert 1967). Fatty acid synthesis begins with acetate and involves ATP, CoA, CO₂, NAD and possibly a citric acid member, -ketoglutaric acid. The most abundant saturated fatty acids are palmitic and stearic while the most common unsaturated acids are oleic and the linolenic.

In the Yukon G. discopterus adults usually overwinter, but G. bullatus adults do not. Since the life cycle of the two species differ, the pattern of fat body development and strategy of reserve storage can also be expected to differ. A comparison of interspecific and intraspecific fat body size and total body fatty acid composition was thus undertaken. Adults were studied throughout the summer of 1983. An increase in total fat body lipids toward the fall would indicated a preparation for diapause, especially in females showing ovarian arrest. Differences in the proportion of unsaturated fatty acids might also be expected in the two species of Geocoris with differing overwintering strategies.

Materials and Methods

Fat Body Dissections

Five adult animals of each sex and species were dissected weekly during the summer of 1983 to determine the relative size of the fat body. It was rated on a scale of 0-5; zero representing animals with no visible fat body. The weekly samples were averaged and plotted according to the date of collection.
Gas Liquid Chromatography Fatty Acid Identification

Ten $\sigma^+$ and 12 $\sigma^+ G.\ discopterus$ and 13 $\sigma^+$ and 13 $\sigma^+ G.\ bullatus$ were collected in the Yukon and immediately frozen in a kitchen deep freezer until they could be transferred to a $-80^\circ C$ freezer (Forma Scientific red cell Model # 8190) 4 months later. Just prior to use, the insects were lyophilized for 24 hrs to rid them of water.

To prepare the samples for gas-liquid chromatography (GLC) a modified Kropinski (Kropinski et al. 1982) method of fatty acid methylation was followed. The reagent consisted of a 5 ml ampule of redistilled acetyl chloride in 100 ml of Lipopure methanol (Instant Methanolic HCL Kit, Applied Science Division) with 10 mg of pentadecanoic acid (C15:0) added as a standard. One insect was added to each clean 5 ml screw cap test tube with 1 ml of the reagent. Each tube was then vortexed for a few seconds, heated at 100°C for 20 mins, sonicated (Fisher Sonic Dismembrator, Model 300) for 1 1/2 mins in 30 second bursts, and then heated at 100°C overnight.

The next day each sample was brought to a pH $\geq 7.0$ with either 0.5 N NaOH or 0.5 N HCl. The samples were spun for 10 min on a Fisher Centrific centrifuge (Model 225) at maximum speed. The supernatants were removed and spun for 3 mins in a Brinkman (Model 5412) epindorph centrifuge, and a 100 ml aliquot was taken from each and placed in a 5 ml test tube. To each tube 100 ul of chloroform, 400 ul of hexane and 3 drops of saturated NaCl solution were added: the samples were centrifuged for 10 mins in a Western Scientific Silencer (Model H-103N) at 300 rpm, and the excess chloroform was blown off with nitrogen gas. The addition of 1:4 chloroform:hexane removed the methyl esters which otherwise would have increased background noise and the NaCl was added to enhance layer separation; the desired
lipids were in the top layer while the methyl esters sank to the bottom.

Five ul alloquots of each sample were individually injected into a Varian (Model, Vista 4600) Gas liquid Chromatograph. The column consisted of a 10 m glass capillary tube packed with SP2100 DOH resin (Supelco) and its temperature was increased from 140°C to 280°C over a 40 min run. The carrier gas was helium which flowed at 20 ml/min. A printout showing the peaks, their respective retention times, and the percentage area under each peak was obtained for each sample run on Vista 401 chromatography data system (Varian, Palo Alto, Calif.).

A methylated standard sample containing pentadecenoic acid (C15:0) was first run on the GLC. (A shorthand notation will be used throughout the text in referring to fatty acids; for example C12:0 refers to a fatty acid molecule with 12 carbon atoms and no double bonds, while C18:1 refers to a molecule with 18 carbon atoms and one double bond.) The single peak of this run was used as a reference peak in order to identify the C15:0 peaks of each other run. All other carbon peaks were interpreted according to this standard. After the major peaks for each sample were identified the quantities of each fatty acid in mg/mg dry weight were calculated. From these calculations the total fatty acid content of each insect was determined.

Results

Fat Body

When plotted against time, the fat body dissection ratings revealed that females had larger fat bodies than males (see Fig. 11). Overwintering G. discopterus adults displayed a peak in fat body size in the middle of
Figure 11  Diagram comparing the mean fat body size of adult male and female Geocoris. Data recorded from weekly dissections of five animals of each sex and species.
May after which the size rapidly decreased until mid-June (see Fig. 12). Individuals collected from mid-June until the end of August showed a gradual increase in fat body size (see Figs. 11, 12 and 14). In contrast, the fat body size for *G. bullatus* adults peaked from mid to late June and decreased until mid July (see Figs. 11 and 12). Another peak occurred in late July presumably when the second generation was mating. From this point until mid-August the fat body size of *G. bullatus* individuals was small. Females of this species displayed a rise and fall in fat body size at the end of August but the males remained consistently low at this time (see Fig. 11). Generally, *G. discopterus* had larger fat bodies than *G. bullatus* (see Fig. 12).

**Gas Chromatography**

The mean total fatty acids of each species and each sex are presented in Table 5 and Figure 13. Information concerning individuals of the same sex and species was averaged. There was no seasonal trend in total fatty acids for either species, but *G. discopterus* has a higher total fatty acid level than *G. bullatus* and (see Table 5). The males of each species have a higher level of total fatty acids than the females of the same species (see Table 5).

In reviewing the individual peaks from each sample it became apparent that the same principal carbon chains were present in all individuals (see Table 6) and that several carbon chains in particular accounted for a large percentage of the total. The major saturated fatty acids were methyl laurate (C12:0), myristic (C14:0), palmitic (C16:0), C23:0 and lignoceric (C24:0), while the principle unsaturated fatty acid was oleic (C18:1). Of these fatty acids, C12:0 and C18:1 predominated (see Table 6).
Figure 12 Diagram comparing adult Geocoris mean fat body size. Data recorded as in Fig. 11
Figure 14  Schematic representation of adult *Geocoris* fat body size in relation to time.
Table 5  Total fatty acid content of Geocoris as determined by GLC. Only those fatty acids of C12:0 length and longer, and in concentrations of 1% of the total and greater were counted.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>N</th>
<th>K (µ moles/mg dry wt) ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. bullatus</td>
<td>♂</td>
<td>13</td>
<td>3.20 ± 0.54</td>
</tr>
<tr>
<td>G. discopterus</td>
<td>♂</td>
<td>12</td>
<td>6.26 ± 0.30</td>
</tr>
<tr>
<td>G. bullatus</td>
<td>♀</td>
<td>13</td>
<td>2.39 ± 0.28</td>
</tr>
<tr>
<td>G. discopterus</td>
<td>♀</td>
<td>10</td>
<td>5.48 ± 1.83</td>
</tr>
</tbody>
</table>
Figure 13  Diagrams comparing the mean total fatty acid levels over time in adult Geocoris. Numbers indicate sample size and bars indicate S.E.
Table 6 Major fatty acids of Geocoris given as mean values. All values are in μ moles/mg dry wt.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>C 12:0</th>
<th>C 14:0</th>
<th>C 16:0</th>
<th>C 18:0</th>
<th>C 18:1</th>
<th>C 23:0</th>
<th>C 24:0</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. bullatus</td>
<td>♂</td>
<td>0.63</td>
<td>0.18</td>
<td>0.18</td>
<td>0.20</td>
<td>0.29</td>
<td>0.51</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>± 0.10 (13)</td>
<td>± 0.04 (10)</td>
<td>± 0.03 (13)</td>
<td>± 0.06 (13)</td>
<td>± 0.04 (13)</td>
<td>± 0.03 (6)</td>
<td>± 0.07 (13)</td>
</tr>
<tr>
<td>G. bullatus</td>
<td>♀</td>
<td>0.41</td>
<td>0.11</td>
<td>0.15</td>
<td>0.08</td>
<td>0.70</td>
<td>0.16</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>± 0.08 (12)</td>
<td>± 0.02 (10)</td>
<td>± 0.02 (13)</td>
<td>± 0.01 (13)</td>
<td>± 0.03 (13)</td>
<td>± 0.04 (7)</td>
<td>± 0.03 (12)</td>
</tr>
<tr>
<td>G. discopterus</td>
<td>♂</td>
<td>1.82</td>
<td>0.49</td>
<td>0.38</td>
<td>0.24</td>
<td>0.57</td>
<td>0.31</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>± 0.30 (12)</td>
<td>± 0.07 (8)</td>
<td>± 0.06 (12)</td>
<td>± 0.07 (12)</td>
<td>± 0.08 (12)</td>
<td>± 0.10 (6)</td>
<td>± 0.02 (12)</td>
</tr>
<tr>
<td>G. discopterus</td>
<td>♀</td>
<td>0.56</td>
<td>0.75</td>
<td>0.34</td>
<td>0.22</td>
<td>0.57</td>
<td>0.44</td>
<td>0.31</td>
</tr>
<tr>
<td></td>
<td></td>
<td>± 0.18 (10)</td>
<td>± 0.06 (6)</td>
<td>± 0.04 (10)</td>
<td>± 0.03 (10)</td>
<td>± 0.07 (10)</td>
<td>± 0.16 (8)</td>
<td>± 0.07 (9)</td>
</tr>
</tbody>
</table>
No seasonal trend was detected in any of the individual fatty acids, nor did the level of saturation change over time. Generally, C14:0 and C16:0 appeared fairly constant in both species throughout the summer while the other fatty acid levels varied a great deal. This variability may be owing to the time of collection relative to the last feeding period as well as to the food type: C23:0 was not present in 21 of 48 specimens.

Discussion

The fat body dissections were intended to give me a rough idea of the food storage pattern and thus the overwintering strategy of the insects. As is evident from Figure 12, _G. discopterus_ adults had larger fat bodies than _G. bullatus_ and also showed a trend of increasing fat body size toward the end of the summer that was not present in _G. bullatus_. As _G. discopterus_ adults overwinter and _G. bullatus_ adults do not, these results indicate that the former species accumulates fat reserves in preparation for diapause whereas the latter species does not.

To determine if there were qualitative as well as quantitative differences in the fatty acids of these two species, a GLC analysis was undertaken. Lambremont _et al_. (1964) found the fatty acid level to increase in the boll weevil _Anthonomus grandis_ Boheman as the insects neared diapause. Similarly, Karnavor and Nair (1969) found the fat level as well as the glycogen level of diapausing khapra beetle (_Trogoderma granarium_ Everts) larvae to be much higher than in non-diapausing larvae. As _G. discopterus_ adults overwinter I expected their total fatty acid levels to increase toward the end of the summer. There was no difference however, between animals which had overwintered and those that were about
to overwinter. High lipid levels however, may only be apparent during the middle of the overwintering period as in the mosquito _Culex tarsalis_ Coquillett (Schaefer and Washino 1969). To determine if this pattern occurs in _G. discopterus_ adults, specimens collected in mid-winter must be analysed. This discrepancy in fat body size and level of total fatty acids suggests that _G. discopterus_ fat body size may increase even more in the autumn months as the animal synthesizes more fatty acids.

Alternately, high glycogen levels may account for the large fat body size and this, of course, would not have been detected in the fatty acid analysis. However, fatty acids rather than glycogen are the usual long term storage reserves in both plant and animal systems. This is demonstrated by _T. granarium_ wherein the fat content (% body wt.) of male and female diapausing larvae was 30.23 % and 27.35 %, respectively, while the glycogen content was only 0.98 % and 1.567 %, respectively (Karnavar and Nair 1969).

_G. bullatus_ adults showed no seasonal trend of increasing fatty acid levels, but because adults are not the overwintering stage this is not a surprising result. The eggs, which do overwinter, require further investigation for lipid levels. The overall fatty acid level of adult _G. discopterus_ was higher than that of adult _G. bullatus_ which may relate to the former's winter diapause.

In many diapausing insects the degree of fatty acid unsaturation increases as the temperature decreases because unsaturated fatty acids have a lower melting point and therefore may be mobilized more readily in times of cold stress (Fast 1970). Exceptions to this generality occur in the mosquitoes _Anopheles freeborni_ Aitken, and _Culex tarsalis_ (Schaefer and Washino 1969) and in the spruce budworm, _Choristoneura fumiferana_ (Fast
1970). Both *A. freeborni* and *C. fumiferana* show little change in the degree of saturation during cold periods, while *C. tarsalis* has even been reported to show an increase the level of saturated fatty acids during cold periods (Buffington and Zar 1968). Neither *Geocoris* species displayed any change in the saturation levels of the fatty acids, but again mid-winter individuals were not sampled.

In several studies of insect fatty acids, C16:0, C16:1, C18:0, C18:1, and C18:2 appear to predominate (Soliday et al. 1974; Mauldin et al. 1971; Fast 1966; Kinsella and Smyth 1966; Barlow 1964; Lambremont et al. 1964). Downer (1978) suggested that fats in the C18 series are essential in the insect diet for proper membrane function. Keith (1967) suggested that in *Drosophila melanogaster* all even-chained fatty acids from C2 to C18, but especially C12:0, may be a precursor to C18:1. This may account for the high levels of C12:0 and C18:1 in both *Geocoris* species.

As the cuticle may account for up to 50% of an insect's dry weight, cuticular lipids will account for a large percentage of insect total lipids (Downer and Matthews 1976). Cuticular hydrocarbons tend to be long chain (Soliday et al. 1974; Lockey 1976), and thus may account for the presence of C24:0 found in the two *Geocoris* species.

Oogenesis and its relation to the lipid composition in the fat body is not completely understood. However, there does appear to be a cyclic connection between the two. Recent research suggests that a certain lipoglycoprotein (LP-II) transports protein, carbohydrates and lipid to the maturing oocytes and eventually becomes deposited as a major yolk protein (Englemann 1979; Gilbert and Chino 1974; Martin 1969; Gilbert 1967). Immunochemically, no difference has been found between the LP-II in the
haemolymph and LP-II in the yolk (Pan and Wallace 1974). In view of this, and the fact that LP-II is only found in females, it is often referred to as vitellogenin.

Martin (1969) worked with ovariectomized and normal Pyrrhocoris apterus (Linn.) and discovered a pattern wherein an initial accumulation of lipids in the fat body occurs prior to the major growth of the oocytes. Then a transfer of the lipid reserves to the oocytes occurs which is related to oocyte maturation and the presence of the ovary.

Why does the fat body accumulate lipid prior to its incorporation by the ovary? Martin (1969) suggested several reasons. Firstly, she found in P. apterus that the food ingested during the period of high oocyte growth was insufficient to support this growth. Therefore ample food must be consumed and stored in the fat body prior to vitellogenesis, otherwise reproduction would be intermitent, only occurring when food was plentiful. She also suggests that uptake and release of lipid by the fat body may provide a greater degree of regulation of lipid transport and utilization. This may very well be the case since ovarian hormones working with the fat body regulate the synthesis of vitellogenin (Hagedorn and Fallon 1973).

The G. discopterus female fat body and chorionated egg figures reveal a pattern similar to that described by Martin (1969) for P. apterus (see Figs. 11 and 8). The female fat body size peaked in mid-May and declined rapidly thereafter to a low in mid-June. The number of chorionated eggs peaked in the first week of June corresponding with the fat body low. The number of chorionated eggs remained low thereafter as G. discopterus mating pairs decreased. Meanwhile, fat body size increased, presumably as the animals approached winter diapause.
G. *bullatus* females showed an initial peak in fat body size in mid-June which continued until the end of June (see Fig. 11). It then declined to a low in mid-July and two more peaks occurred in mid to late July and August, respectively. The number of chorionated eggs present in the ovaries peaked during the initial fat body peak in mid-June and peaked again during the middle of August (see Fig. 8). The relationship between fat body size and ovary size in *G. bullatus* females is not as clear as in *G. discopterus* as this species has two overlapping generations in a season and it is impossible to know which generation the adults were from.

Male and female total fatty acid levels differed in both species and in each case the males had the higher amount. This may be explained by the fact that females would have had at least some of their lipids present in the lipoglycoprotein vitellogenin. As the extraction technique used was exclusively for non-polar fatty acids and those found in vitellogenin are polar, they would not have been detected. Karnavar and Nair (1969) also found diapausing male *T. granarium* beetle larvae to contain more fat (% body wt.) than females.

In summary, *G. discopterus* adults displayed a trend of increasing fat body size toward the end of summer that was not evident in *G. bullatus*. *G. discopterus* adults also showed higher levels of total fatty acids than adult *G. bullatus*. This is likely attributed to the fact that adults of the former species overwinter while adults of the latter species do not. In neither insect however, was there evidence of an increase in particular fatty acid levels nor in the level of unsaturation as temperatures decreased. In *G. discopterus* any rise in fatty acid levels may not occur until later on in the cold season.
Chapter 7: Plant Material As A Food Source

Introduction

Geocoris species are predominately predaceous (Readio and Sweet 1982), but there are suggestions that some species may not be obligate predators. *G. pallens* has been found to feed on cotton (Ridgeway and Jones 1968) and *G. punctipes* has been kept alive for several months on plant material and water alone (Stoner 1970; Sweet 1960). However, it has been demonstrated by Stoner (1970) that animal prey is required for proper nymphal development and fecundity in most geocorines. In the laboratory, *G. bullatus* has been shown to feed on both sunflower seeds (*Helianthus annuus* L.) and insects interchangeably (Readio and Sweet 1982), but will feed very little on plant foliage. Tamaki and Weeks (1972) also showed that the greatest survival and fecundity occurred on a mixed diet of insects and sunflower seeds. However, there have been no studies on either *G. bullatus* or *G. discopterus* using other plant food sources.

Since detailed study of the predatory habits of *G. bullatus* and *G. discopterus* was not feasible in the Yukon, it was decided to see if the insects were able to survive on plant food alone, and to determine if the species differed in this regard. Hence, survival of adult *G. bullatus* and *G. discopterus* was studied on dominant plants present in the study areas.

Materials and Methods

Five cages were set up for each species (see Fig. 15) using the following treatments: 1) no seeds; 2) shelled sunflower seeds
Figure 15 Diagram of the cages used to house *Geocoris* during feeding experiments.
(Helianthus annuus L.); 3) Polygonum aviculare L.; 4) Artemisia frigida Willd.; and 5) Potentilla pennsylvanica L.. All treatments included water and when local plants were used, all above-ground parts were included (i.e. flowers, seeds, stems and leaves). Treatments 1 and 2 served as controls; water, because it would indicate survival without food, and sunflower seeds, because this food source is known to sustain other Geocoris species in the laboratory (Stoner 1970; Sweet 1960). Food and water were changed every second day and given in sufficient amounts so as not to be limiting. Cages were kept in a controlled environmental chamber (Hotpack # 555211) at approximately 25°C. Relative humidity was not controlled, but a dish of water was kept on the floor of the chamber to prevent dessication. The above conditions are similar to those used by other authors studying Geocoris species (Crocker et al. 1975; Tamaki and Weeks 1972; Stoner 1970; Butler 1966; Champlain and Sholdt 1966; Sweet 1960).

Animals were collected from the field in the V instar and placed in the cages upon molting to adult. With this technique, the age of adults was standardized. Insects that died were not replaced, and the total number of days until the last animal died was considered to equal total survival. Mean survival and the 50% survival value were calculated for each cage.

Results

Table 7 and Figure 16 show that both Geocoris species had higher survival when fed sunflower seeds than on the other 4 treatments (significant at p<0.05, t-test). Mean survival on sunflower seeds for
Table 7  Geocoris survival on the dominant plant species from their respective habitats. All mean survivals on natural plant food are significantly less than those on *H. annuus* (t-test, p<0.05). Ten insects of each species were tested in each treatment.

<table>
<thead>
<tr>
<th>Plant Food</th>
<th>Total Survival</th>
<th>% Survival ± S.E.</th>
<th>50% Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. annuus</em></td>
<td>67</td>
<td>61</td>
<td>35.0 ± 6.8</td>
</tr>
<tr>
<td>Water</td>
<td>29</td>
<td>14</td>
<td>16.3 ± 2.1</td>
</tr>
<tr>
<td>A. frigida</td>
<td>26</td>
<td>5</td>
<td>16.1 ± 1.9</td>
</tr>
<tr>
<td>P. aviculare</td>
<td>29</td>
<td>25</td>
<td>13.9 ± 2.6</td>
</tr>
<tr>
<td>P. pennsylvanica</td>
<td>22</td>
<td>13</td>
<td>11.9 ± 1.7</td>
</tr>
</tbody>
</table>
Figure 16 Display of survival trends of adult Geocoris when fed various plant foods. A - Helianthus annuus, B - Polygonum aviculare, C - Potentilla pennsylvanica, D - Artemisia frigida, E - water.
G. bullatus and G. discopterus was 35.0 ± 6.8 and 42.1 ± 4.0 days, respectively. Maximum survival for the two species was 68 and 63 days, respectively.

G. discopterus had a significantly higher mean survival on Polygonum aviculare than on Artemisia frigida (which incurred the lowest survival rate) (t-test, p<0.05), (see Table 7). Mean survival on the remaining treatments did not differ significantly from that on P. aviculare for this species. Mean survival on A. frigida was significantly lower than on water alone (t-test, p<0.05), but mean survival on water did not differ from that on P. aviculare or P. pennsylvanica (see Table 7).

G. bullatus had a higher mean survival on water alone than on P. pennsylvanica (t-test, p<0.05) but mean survival on water did not differ from that on P. aviculare or A. frigida (see Table 7).

The general trends of survival are similar between the two insects (see Fig. 16). G. bullatus exhibited a survival rate that was fairly constant for all treatments. G. discopterus showed a constant survival rate in all treatments, except when fed A. frigida. In this case all animals were dead after 5 days.

**Discussion**

G. bullatus and G. discopterus were tested using the dominant plant species (see Chapter 8 Table 8) from their habitats to determine; a), if the species could survive on plant food, b), if the plants were used for food, and c), if there was a difference in plant food preference.

My results show little difference in survival either among the species of plants tested from the wild, or among these plants and just water. The
fact that total survival was twice as long on sunflower seeds than on habitat plant food indicates that the insects were getting little food supplement from the native habitat seeds. Stoner (1970) also found that adult *G. punctipes* reared on sunflower seeds had longer survival rates than on other plant foods.

In only one treatment for each species did survival on the local plants differ from survival on water alone. There is thus an indication that these insects may utilize the plants only as a source of water as suggested by York (1944). Stoner (1970) concluded that if prey were in short supply, *G. punctipes* might maintain itself on plant food until prey was available. As mean survival of *G. discopterus* was significantly less on *A. frigida* than on water alone, this is an indication that *A. frigida* may in fact be detrimental to the longevity of this species. Similarly, *P. pennsylvanica* may be detrimental to the longevity of *G. bullatus* as mean survival on this treatment was significantly less than on water alone.

*G. bullatus* and *G. discopterus* thus appear to show little evidence of ability to utilize plant foods for survival. This supports Stoner's (1970) claim that *Geocoris* species are obligate rather than facultative predators. Dunbar (1971b), in a study of the feeding behaviour of *G. bullatus* in Connecticut lawns, found the species to be a predator on lawn insects and at the same time found no evidence that it injured lawn grasses. *G. bullatus* has also been shown to be a major predator of the clover aphid, *Roepekea [=Nearctaphis] backeri* (Cowen), (Smith 1923), and experimentally has been shown capable of effectively controlling the green peach aphid, *Mysus persicae* (Sulzer), on sugarbeets (Tamaki and Weeks 1972).
While there have been no experimental survival studies with *G. discopterus*, the species is reported to be an energetic predator (Readio and Sweet 1982). Hence, the predaceous nature of both species seems clearly established and they are thus unlikely to be distributed on the basis of plant food.
Chapter 8: Habitat

Introduction

Readio and Sweet (1982) noted that G. bullatus is a species characteristic of open disturbed sandy areas, and occurs along roadsides and in waste lots, especially where the soil is sandy or gravelly. They reported that G. discopterus in New Jersey was generally collected in sandy open areas among blueberry and bearberry scrub along with some grass cover. They further observed that G. discopterus was never present in the same habitat with any other species of geocorines, even though the populations may be nearly contiguous. They stated, "This clearly seems to be a case of habitat exclusion which warrents more careful study."

Interspecific competition is of pervasive importance in ecological systems according to Schoener (1983). Numerous studies on trophically similar species have suggested that interspecific competition can lead to competitive exclusion (see reviews in Schoener 1982; 1983). The competitive exclusion principle (Cole 1960; DeBach 1966; Patten 1961; Hardin 1960) states that no two species can coexist indefinitely if their niches are identical, and is a somewhat controversial concept with, no doubt, some limitations (Richards 1969; Federov 1966; Savile 1961; Ross 1957). However, it provides a useful tenant for research and may well be important in understanding the distribution of G. bullatus and G. discopterus in the Yukon.

Competitive exclusion is perhaps not unexpected in closely related, omnivorous predators. Hence an analysis of the habitat, and population levels at specific sites in the southern Yukon was undertaken.
Materials and Methods

The climatic information for the general study area was acquired from the Yukon Weather Office, Whitehorse. Temperature data were obtained for stations at Burwash Landing, the south end of Kluane Lake and Haines Junction while precipitation data were collected for the Upper Sheep Creek station, about 10 km from the south end of Kluane Lake (see Fig. 6). The daily maximum and minimum temperatures for the summer of 1983 (May - August) were recorded as were the mean annual temperatures for the years 1973-1983.

A total of eight dry open grassland sites were selected for detailed study and analysis and are outlined in Chapter 5. The four sites near Kluane Lake contained only G. discopterus, while the four sites near Haines Junction contained both species of Geocoris: no sites were located where G. bullatus occurred alone.

The vegetation types of these eight study sites were determined and a principle component analysis was performed as an independent test to see if G. discopterus sites differed from G. bullatus + G. discopterus sites.

Each study site was sampled for plant species frequency and percent cover in mid-July when most of the flora was in bloom. Samples of individual plants were collected and prepared as herbarium specimens. The identity of each species was later confirmed or determined by UBC botanists. Fifty randomly chosen 1 m x 1 m quadrats were sampled, which together equalled 22% of each site. Individual quadrats were quartered and the percent cover of each species quarter was estimated. The results from the four quarters were then summed to give a quadrat total.
The information from all 50 quadrats was combined to yield frequency and mean percent cover for each species from an individual site. The mean percent cover data was used in the principle component analysis using ordination.

In this analysis the degree of site similarity was detected by transforming the species percent cover data to Euclidian distances. Eight eigenvectors resulted with each representing a set of interpoint distances reflecting all differences. As the first three vectors accounted for 92.93% of the total variance, they were displayed diagramatically. Eigenvector 1 and 3 were chosen as the final display axes as they preserved the most information in a diagramatic representation of the interpoint distances (i.e. no points overlap in this view).

Population estimates of the *Geocoris* species on each site were obtained as outlined in Chapter 5. Material was identified using the characteristics described in Chapter 2.

**Results**

**Climate**

The daily max./min. temperatures for the three climate data localities over the summer of 1983 show little difference (see Fig. 17). The end of June to the beginning of July appears to be the warmest part of the summer in all three places. Over the period from 1974 - 1982 the mean annual temperature data show that both Kluane Lake and Haines Junction are warmer than Burwash Landing. The mean annual temperatures from 1974 - 1982 are, -3.99°C (N=10), -1.78°C (N=6) and -2.64°C (N=10) for Burwash Landing, Kluane Lake and Haines Junction, respectively. However, the daily maximum
Figure 17 The daily maximum/minimum temperatures recorded from Kluane Lake, Burwash Landing and Haines Junction from May to September, 1983.
summer temperature can get close to 30°C.

From August 1982 to September 1983, 299.7 mm of precipitation fell at Upper Sheep Creek. The study region as a whole is relatively arid, with much of the annual precipitation falling as snow.

**Vegetation**

All sites were in close proximity to mixed black spruce/trembling aspen (*Picea mariana* (Mill.) Britt., Sterns and Pogg. and *Populus tremuloides* Michx., respectively) forest and C.B., D.M. and S.C. were also close to thick cover of bearberry, *Arctostaphylos uva-ursi* (L.) Spreng (see Plates 1-4 for representative examples of sites).

A total of 50 plants were identified (see Table 8). Most were xerophilous or mesoxerophilous perennial herbs (see Table 9). Only eight plant species occurred on both the Kluane Lake and Haines Junction sites (See Table 8). Horse and cow dung were present as transitory ground covers. A characteristic of all study sites was the high percentage of bare ground (see Table 8).

Of the eight plant species common to the Kluane Lake and Haines Junction sites, five (*Phleum pratense* L., *Erysimum inconspicuum* (S. Wats.) MacM., *Oxytropis campestris* (L.) D.C., *Androsace septentrionalis* L. and *Achillea millefolium* L. ssp. borealis (Bong.) Breitung) account for no more than 4% of the total ground cover at any one site, and these are thus not of prime importance. The remaining three common species were the grasses *P. rupicola* Nash. (is included in *P. glauca* according to Hulten 1968), *Bromus inermis* Leyss. var. tweedyi (Scribn) and *Agropyron spicatum* (Pursh) Scribn and Smith (hybridizes with *A. yukonesis* according to Hulten 1968). *P. rupicola* occurred on three of the Kluane Lake sites (C.B., D.M. and
Plate 1 Typical Kluane Lake habitat. Silver City site.

Plate 2 Typical Kluane Lake habitat. Cultus Bay site.
Plate 3  Typical Haines Junction habitat. Park's Farm I and II sites.

Plate 4  Typical Haines Junction habitat. Mountainview site.
Table 8  Ground cover composition of the 8 Yukon study sites. Data given in frequency (F) and percent cover (P).

<table>
<thead>
<tr>
<th>Ground Cover</th>
<th>Kluane Lake Sites</th>
<th>Study Site</th>
<th>Haines Junction Sites</th>
<th>N.V.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dirt</td>
<td>1.00 52.48</td>
<td>0.46 3.72</td>
<td>0.94 22.08</td>
<td>0.96 43.94</td>
</tr>
<tr>
<td>Cow dung</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Horse dung</td>
<td>-</td>
<td>0.20 1.18</td>
<td>0.30 2.24</td>
<td>0.17 0.46</td>
</tr>
<tr>
<td>Lichen</td>
<td>Psora decipiens (Hedw.) Hoffm.</td>
<td>0.04 0.04</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Moss</td>
<td>Ceratodon purpureus (Hedw.) Brid.</td>
<td>-</td>
<td>1.00 38.72</td>
<td>1.00 27.58</td>
</tr>
<tr>
<td>Tortula ruralis (Hedw.)</td>
<td>-</td>
<td>-</td>
<td>0.86 15.08</td>
<td>-</td>
</tr>
<tr>
<td>Gaertn., Meyer &amp; Scherb.</td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Grass</td>
<td>Phleum pratense L.</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Calamagrostis purpurascens R. Bro.</td>
<td>-</td>
<td>0.92 9.40</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Poa trivialis L.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>*Poa rupicola Nash.</td>
<td>1.00 16.68</td>
<td>0.98 8.70</td>
<td>0.02 0.02</td>
<td>-</td>
</tr>
<tr>
<td>Poa palustris L.</td>
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<td>Oxytropis splendens Doug.</td>
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<td>Taraxacum officinale Weber</td>
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* Indicates ground cover occurs on both Kluene Lake and Haines Junction sites.
Table 9 Vegetation types of the 8 Yukon study sites.

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<th>Vegetation Type</th>
<th>Kluane Lake Sites (%)</th>
<th>Haines Junction Sites (%)</th>
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<td>Xerophilous</td>
<td>78.79</td>
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<tr>
<td>Mesoxerophilous</td>
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<td>32.00</td>
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<tr>
<td>Mesophilous</td>
<td>12.12</td>
<td>24.00</td>
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Inst.) and on one Haines Junction site (P.Fd.), while _B. inermis_ and _A. spicatum_ occurred on just two sites, Inst. and M.V.

Fig. 18 demonstrates the relatedness of sites by species percent cover as determined by principal component analysis. The eight sites are clearly divided into two groups; P.F.I, P.F.II and M.V. in one group and S.C., D.M., Inst., C.B. and P.Fd. in the other. According to this analysis, P.F.I., P.F.II. and M.V. are the most closely related while P.Fd., although found in the same locality, is less similar to this group and more similar to the Kluane Lake group. This may be explained by the following; P.Fd. contained no _P. aviculare_, but had high percent covers of _B. inermis_ (see Table 8). The former species is abundant on the other Haines Junction sites while _B. inermis_ only occurs on the Kluane Lake sites.

C.B., S.C., Inst., D.M. and P.Fd. are related on the abscissa of Fig. 16, but not on the ordinate axis. A reason for this may be that the percent cover values of species they have in common vary considerably. For example, _A. frigida_ ranges from 1.4% on D.M. to 18.3% on Inst., and bare ground ranges from 3.72% on D.M. to 52.48% on C.B.

The most dominant ground covers from those sites where _G. discopterus_ only was present, (i.e. Inst., S.C., C.B. and D.M.) were the sage _Artemesia frigida_ Willd., the grasses _Poa rupicola_ Nash and _Poa trivialis_ L. and the mosses _Tortula ruralis_ and _Ceratodon purpureus_ (Hedw) Bird. (see Table 8). The most dominant ground cover from those sites where both _Geocoris_ species were found (P.F.I, P.F.II, P.Fd. and M.V.) was _Polygonum aviculare_ L. (see Table 8). Bare ground was dominant in both _G. discopterus_ and _G. discopterus + G. bullatus_ localities.
Figure 18 Diagramatic representation of site interpoint distances resulting from principle component analysis of species percent cover by ordination.
Figure 19 Diagram comparing the *G. discopterus* populations on allopatric and sympatric sites in the Yukon.
Population Estimates

Figures 19 a and b shows clearly that the population density of G. discopterus on the Kluane Lake sites was significantly higher than that on the Haines Junction sites, where it occurred with G. bullatus. Although the P.Fd. site at Haines Junction was grouped with the Kluane Lake sites in the principle component analysis, the population level of G. discopterus on this site was lower than that on the Kluane Lake sites and was typical of the other three sites on which G. bullatus was recorded (see Appendix III, Fig. 7).

Discussion

The southwestern Yukon study area has a continental climate (Hoefs et al. 1975). It has cold winters and short warm summers. The precipitation is low, and while the region would be classified as subarctic in the classification of Trewartha (1943), the area characteristically has steppe-like vegetation and is one of the driest areas in the Yukon. Climatically it is very similar to certain areas of northeastern Siberia, which also have steppe-like vegetation (Yurtsev 1982).

Following the interpretation of Lavrenko (1940) and Yurtsev (1982, 1978), the well drained, sunny south-facing slopes and river valleys in the study area are steppe since they are dominated by xerophilous and mesoxerophilous perennial herbs. The plants are both frost and drought resistant. The climax and subclimax phytocoenoses have characteristic discontinuous above-ground vegetation with a complex root system below ground. Bare ground is clearly evident, and there is a prevelance of graminoids, especially tufted grasses.
These steppe-like areas in the Yukon are restricted to the steep, dry south-facing slopes along the Yukon and Pelly rivers on morainal, colluvial and glaciofluvial material (Oswald and Senyk 1977). As in the Kluane Lake study sites, these region have *Artemisia frigida* as a dominant or subdominant ground cover, show no permafrost above 1 m and have a soil type that is predominantly Cumulic Regosol: the soil texture is mainly gravel-sand-silt, and the drainage is good (Stanek 1980).

While all four Kluane Lake sites have *A. frigida* as a dominant or subdominant ground cover, Hoefs et al. (1975) have shown that the floristic composition of such xeric sites at lower elevations, can change appreciably with both altitude and aspect. Nevertheless, it is in these severe xerophilous steppe-like areas that *G. discopterus* occurs allopatrically in the Yukon. The plants in such areas are all indigenous, and although none were located in the study areas, it is in such xeric habitats that many of the rare endemic vascular plants are found in the Yukon and adjacent areas of Alaska (Douglas et al. 1981; Kassler 1979). Most of these endemics probably originated in the unglaciated Alaska-Yukon refugium (Douglas et al. 1981).

Only one Kluane Lake site contained an introduced species. The S.C. site contained the introduced grass, *Poa trivialis*. This contrasts with the Haines Junction sites where 7 introduced species were found: each site had at least 3 or 4 introduced species, with the dominant being *Polygonum aviculare*. The Haines Junction sites are close to an old agricultural experimental farm which could account for the high number of introduced plant species in the area.

The Haines Junction sites have a high percentage of mesoxerophilous and mesophilous plants (see Table 9). This could be related to the fact
that the area is known to have been submerged only 100 years ago (Johnson and Raup 1964). The neighbouring Alsek River has been dammed at least 5 times in neo-glacial times, owing to the advancement of the Lowell Glacier (Rampton 1981; Johnson and Raup 1964). At least 5 lakes have been formed as a result. The oldest lake had a shoreline at about 646 m, while the most recent had a shoreline at about 600 m, and did not disappear until approximately 1850 (Johnson and Raup 1964). These lakes are likely to have had an impact on the local vegetation, leading to the high percentage of mesoxerophils and mesophils.

Thus, while all of the xeric Kluane Lake sites, except the D.M. site which was inundated by the Duke River 1600-1700 years ago (Johnson and Raup 1964), have been relatively stable in neo-glacial times, the Haines Junction area has been subject to considerable change. Nearly all of the sites have been disturbed by either horse or cow grazing.

*G. bullatus* occurred with *G. discopterus* only on the disturbed mesic sites at Haines Junction, where *Polygonum aviculare* primarily dominated. The vegetation analysis shows that there were distinct differences between the sites where *G. discopterus* occurred alone, and where it occurred with *G. bullatus*. This suggests that these two species do not have identical ecological requirements. However, it is clear that these differences are unlikely to be because of any food plant association, since it is evident that both species are omnivorous predators.

The population analyses show that population levels of *G. discopterus* were highest in the xeric Kluane Lake sites where it occurred alone. When sympatric with *G. bullatus* on the Haines Junction sites, population levels were lower. Mean population densities of *G. discopterus* in allopatri ranged from 0.14-1.19 insects per sq m, while with *G. bullatus* the density
ranged from 0.01-0.45 per sq m. It is possible that the numbers of *G. discopterus* were reduced because of the interaction with *G. bullatus*. Whether this might be consumptive, preemptive or encounter competition (Schoener 1983) is not clear, but because of its larger size and less rigorous habitat requirements, *G. bullatus* is likely to be the superior competitor of the two (Schoener 1983; Grant 1970; Miller 1967).

It is also possible that the population levels of *G. bullatus* are influenced by interaction with *G. discopterus*. Tamaki and Weeks (1972) reported densities of *G. bullatus* up to 1.9-2.9 insects per sq m in peach orchards in the Yakima Valley of Washington State. However, on the Haines Junction sites with *G. discopterus*, peak population density ranged from 0.07-0.50 insects per sq m. However, control studies on allopatric populations of *G. bullatus* in the Yukon have not been undertaken.

As noted by Schoener (1983) field experiments on interspecific competition requires manipulation of the abundance of one or more hypothetically competing species. While removal and addition experiments were attempted at the Haines Junction and Kluane Lake sites, respectively, conditions did not allow for successful completion of these attempts to unravel population levels and interactions.

It should be acknowledged that in many Arctic invertebrates, population levels that are controlled by climatic factors tend to be reduced compared with those living in more optimum conditions (Miller 1967). If population numbers are influenced by climatic factors in *G. bullatus*, then low numbers at the Haines Junction sites may not be because of interspecific interaction. Certainly, Tamaki and Weeks (1972) have shown that in *G. bullatus*, developmental rates are influenced by
temperature. Hence, no conclusive statement can be made about the interspecific competition between these two predators.

However, there is some habitat overlap between the two species, and it is expected that they have considerable food resource overlap. Food resources are unlikely to be identical, because of size differences in the species. Whether food resources are limiting is another question, which could not be tackled. Certainly, no behavioural interaction was detected in mating tests. Whether competitive exclusion in this system is theoretically possible is not clear.
CHAPTER 9: COMPARISON OF G. BULLATUS AND G. DISCOPTERUS

At this point it is useful to summarize and compare what has been found with regard to the two species in question (see Table 10). Firstly, it has been demonstrated that the smaller Geocoris found in the southwestern Yukon were indeed G. discopterus and not just a morph of some other northern Geocoris, as suggested by Readio and Sweet (1982). Morphologically, G. discopterus was found to have a more uniformly punctate corium and to have a significantly smaller total body length (T.L.) than G. bullatus. The majority of G. discopterus specimens were brachypterous while the G. bullatus specimens were generally macropterous. Yukon G. discopterus specimen T.L. measurements were not statistically different from the material from the east studied by Readio and Sweet (1982). The T.L. of the Yukon specimens were however, statistically different from other closely related species in the bullatus-pallens complex as described by Readio and Sweet (1982).

Morphology is not the only distinguishing factor between these two species. Interspecific mating experiments were performed on Yukon G. bullatus and G. discopterus and the results indicate that the two are reproductively isolated.

There are also temporal differences in the phenologies: G. bullatus completes two generations annually while G. discopterus only completes one. This indicates that G. bullatus is an r-strategist while G. discopterus is a K-strategist. Comparison of life-cycles shows that G. discopterus usually overwinters in the adult stage, while G. bullatus overwinters as eggs. The different overwintering strategies correlate with differences in fat body development; fall adult G. discopterus have larger
<table>
<thead>
<tr>
<th>Characteristic</th>
<th>G. bullatus</th>
<th>G. discopterus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Total Length g</td>
<td>3.67 ± 0.02 mm</td>
<td>2.75 ± 0.01 mm</td>
</tr>
<tr>
<td></td>
<td>♀</td>
<td>♂</td>
</tr>
<tr>
<td>Corium</td>
<td>4.17 ± 0.02 mm</td>
<td>2.99 ± 0.02 mm</td>
</tr>
<tr>
<td>Wing Status</td>
<td>impunctate areas</td>
<td>uniformly punctate</td>
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<tr>
<td>Fall Fat Body Size</td>
<td>small</td>
<td>large</td>
</tr>
<tr>
<td>Mean Total Fatty</td>
<td></td>
<td></td>
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<tr>
<td>Acid Level</td>
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<td></td>
</tr>
<tr>
<td>in µ moles</td>
<td>3.20</td>
<td>6.26</td>
</tr>
<tr>
<td>mg dry wt</td>
<td>± 0.54</td>
<td>± 0.30</td>
</tr>
<tr>
<td></td>
<td>2.39</td>
<td>5.48</td>
</tr>
<tr>
<td></td>
<td>± 0.28</td>
<td>± 1.83</td>
</tr>
<tr>
<td>Life Cycle</td>
<td>two generations/year</td>
<td>one generation/year</td>
</tr>
<tr>
<td>Overwintering Stage</td>
<td>egg</td>
<td>adult</td>
</tr>
<tr>
<td>Life History Strategy</td>
<td>r-strategist</td>
<td>K-strategist</td>
</tr>
<tr>
<td>Location</td>
<td>Haines Jctn.</td>
<td>Kluane Lake &amp; Haines Jctn.</td>
</tr>
<tr>
<td>Habitat</td>
<td>disturbed wasteland</td>
<td>arid south-facing slopes</td>
</tr>
<tr>
<td>Range</td>
<td>continuous across W.A.</td>
<td>disjunct</td>
</tr>
<tr>
<td>Distribution in Yukon</td>
<td>generally distributed</td>
<td>restricted</td>
</tr>
<tr>
<td>Species Type</td>
<td>non-relict</td>
<td>relict</td>
</tr>
</tbody>
</table>
fat bodies than fall adult *G. bullatus*. *G. discopterus* adults also have higher total fatty acid levels than *G. bullatus* adults, which is also likely related to their respective overwintering strategies.

At the Haines Junction sites *G. discopterus* and *G. bullatus* were found together, which is an unusual situation according to Readio and Sweet (1982). Both species have been shown to be omnivorous predators. As *G. discopterus* numbers are much lower on sympatric sites than on allopatric sites, there is an indication of competitive interaction. However, habitat climatic differences may also account for the differences in *G. discopterus* population levels.

Vegetation analysis indicated that the Kluane Lake sites were populated primarily with xerophilous plant species while the Haines Junction sites were populated with mesoxerophilous and mesophilous species. *G. discopterus* clearly prefers the drier habitats.

This habitat preference may account for its very disjunct and restricted distribution. It is to be noted that *G. discopterus* has not dispersed from unglaciated areas of North America to any extent (see Fig. 20), whereas *G. bullatus* has spread throughout areas glaciated in the late Pleistocene (see Fig. 21). Indeed, *G. discopterus* is almost confined to glaciated and periglacial areas in the Yukon (see Fig. 22). The possible reasons for this are explored in the next chapter.
Figure 20  Distribution of G. discopterus in North America. Dots are placed in the middle of states or provinces in which specimens have been collected.
Figure 21 Distribution of G. bullatus in North America. Dots are placed in the middle of states or provinces in which specimens have been collected.
Figure 22  Distribution of Yukon G. discopterus in relation to ice sheet boundaries of the late Pleistocene and earlier periods of glaciation. Dark - Unglaciated; Light - Unglaciated during the late Pleistocene but previously glaciated; Plain - Glaciated
CHAPTER 10: THE ZOOGEOGRAPHY OF G. DISCOPTERUS: A POSSIBLE RELICT SPECIES

INTRODUCTION

Disjunction in distribution can occur in two ways according to Young (1982). Firstly, a barrier to the migration of a species is jumped by long distance dispersal; by wind, river or animals for example. Secondly, a previously continuous range is disrupted by some event such as a volcanic eruption or a drastic climatic change. If the species is a recent invader, its main range would be increasing, but if the species is a relict from a previously more continuous population, its present range would be stable or shrinking. A species with an expanding area tends to have a continuous boundary while a contracting area tends to have a discontinuous boundary (Seddon 1971). Species with expanding areas have not been stopped by barriers (either climatic or geographic) whereas species with contracting areas leave behind relict colonies in local situations which are unable to bridge gaps between surviving populations.

Denno et al. (1981) suggest that because of their colonizing abilities, macropterous species are more successful in unstable environments where resources fluctuate and better alternatives are available elsewhere. On the other hand, brachypterous species would be suited to stable environments and/or areas where there is no alternative nearby. *G. discopterus* appears to occupy glacial refugium and relict areas in the Yukon which are not abundant. In contrast, *G. bullatus* is common on roadsides and areas of early succession an high disturbance. In the southwestern Yukon these habitat types are abundant.
G. bullatus is a macropterous species which is able to disperse by flying. It has a continuous range across North America as its habitat requirements are not as restricted as those of G. discopterus (see Fig. 21).

As G. discopterus is largely a brachypterous species with a slow developmental rate it is a poor disperser. I suggest that this species formerly had a more widespread distribution that was severely disrupted during the late Pleistocene ice surge. As it is such a poor disperser, this insect has remained associated with relict habitats in the Yukon (see Fig. 22). G. discopterus then, appears to be an example of a relict species with a disjunct distribution similar to that described by Young (1982).

THE LATE PLEISTOCENE ICE AGE

Regions to the north of Kluane Lake are known to have been ice-free during the glacial advance of the late Pleistocene. A comparison of the vegetation present on the Kluane Lake sites with the vegetation thought to have existed in the Beringian refugium, suggests that the xeric habitats with G. discopterus may be Beringian relicts.

Glacial refugia refer to those pockets of nonglaciated land which were surrounded by ice during the glacial advance in the late Pleistocene. A relict, in this context, refers to a species which survived this ice age by occupying a refugium. Relict species are important in determining the community structure of refugia both past and present, and thus reveal much about the survival and evolution of biota. Refugia are also of interest as they provide the conditions necessary for rapid speciation, i.e
geographical barriers resulting in the isolation of populations, decrease in population size and increased environmental stress (Kavanaugh 1979).

In northern latitudes the present day distribution of flora and fauna has been greatly effected by the most recent glacial advance which took place during the late Pleistocene. This ice age began approximately 30,000 years B.P. and lasted until about 12,000 years B.P. Cold and moist conditions triggered the beginning of ice sheet formation, but once the ice had extended over much of the land mass, the climate shifted to cold dry winters and warm dry summers (Hibbert 1982). By the beginning of the Holocene (12,000 years B.P.) however, the climate had become generally warmer and more humid causing the ice sheets to melt.

As a result of the glacial surge, the prevailing sea level was lowered by about 90 - 100 m and the surrounding continental land mass increased. What is now the Bering Sea was once a continuous isthmus of land as wide as 1300 km in some places (Seddon 1971). This isthmus connected Siberia and Alaska and has come to be known as the Bering Land Bridge.

The extent of glaciation in northern Canada was nearly total with the exception of much of the Yukon and small portions of the Northwest Territories (see Fig. 23). Most of Alaska also remained ice free as did much of northern USSR. This northwestern refugium is now referred to as Beringia and was an extension of the Siberian Chukotka Platform refugia. In the southern Yukon, the surrounding ice had a surface elevation of 1860 m which left most mountain tops ice free (Rampton 1981).

Colonization of eastern Beringia (i.e. western North America) came from the west while the Bering Land Bridge existed. This migration occurred mainly across the landbridge, but there is some evidence of vascular plant migration along the Aleutian Island chain as well (Lindroth
Figure 23  Location of North American ice sheet boundaries during the late Pleistocene (Scudder 1979).
1979). Yurtsev (1982) estimates the current steppe vegetation of the northeast Yakutia area in Siberia to comprise of 142 species of which 1/4 also occur in xerophytic areas in western North America and at least as many more are represented by closely related variant species. *Chamaerhodos erecta* (L.) (Bunge) for example, is found in central Alaska and Yukon with disjunct populations over 1900 km away in Siberia (Kassler, 1979).

Argus (1977) recognized 11 major Canadian centres of botanical endemism of which the central Yukon is one. Hulten (1937) pointed out that many vascular plants survived glaciation in Beringia and that this area formed the centre of radiation for plant distribution in the north.

YUKON XERIC SITES AS POSSIBLE REFUGIA

Two schools of thought have come to the surface regarding the vegetative communities of Beringia in the late Pleistocene. Matthews (1976; 1974 a and b; 1982), Young (1982; 1976) and Yurtsev (1982) have put forth a theory utilizing evidence from pollen cores, vertebrate fossils, invertebrate and plant macrofossils, and soil stratigraphy while Ritchie (1984) and to a lesser extent Cwynar (1982) rely strictly on pollen cores for their hypotheses. The former group hypothesizes an Arctic-steppe or grassland environment throughout Beringia, while the latter two support the idea of tundra or fell-field in the north and tundra to tundra-steppe in the south. As both groups have similar interpretations of Beringian pollen cores the discussion will centre around these data. Both groups also concur that the more southerly portions of Beringia included at least some grassland or Arctic-steppe.
The Beringian pollen spectra from 18,000 - 13,000 years B.P. is characterized by a low influx rate, high proportions of Graminae (grass) and Cyperaceae (sedge) pollen and exceptionally high, but also highly variable proportions of *Artemisia* pollen (Hibbert 1982; Young 1982; Matthews 1974a). Another mark of the late Pleistocene pollen assemblage is a distinct lack of spruce and birch.

Young (1976) defines the basic criteria for Arctic-steppe relict communities. Firstly, the modern flora must be consistent with the pollen records of Arctic-steppe in both species and relative frequencies. Secondly, the distribution of analogous species today will have broad disjunctions with Asia, thus indicating a previously continuous range. Thirdly, species narrowly endemic to proposed relict sites would be expected in relics of Arctic-steppes.

The high quantities of Graminae and *Artemisia* L. presently found in interior Alaska and the Yukon are consistent with the pollen record. *A. frigida* and *A. alaskana* Rydb. are also found west of the Kolyma River in the Chukotka Platform and thus form disjunctions over 1500 km away. *Populus tremuloides* is presently abundant at the outskirts of proposed relict sites, but is not in the pollen record. However, pollen of this species is known to be difficult to identify and preserves poorly, and thus even if it were present in the late Pleistocene it would not be identified in the pollen rain (Young 1976). It is also very closely related to or even conspecific with *P. tremula* L. which is presently found in Eurasia (Young 1976; Hulten 1968). *Agropyron spicatum* (Pursh) Scribn and Smith and *Chamaerhodos erecta* both have populations on dry slopes in Alaska and the Yukon. The former species has disjunct populations 1200 km to the south in
western North America and the latter has disjunct populations 1900 km away in Siberia (Kassler 1979).

Periglacial Beringia (i.e. interior of Alaska and Yukon) contained species that do well on outwash plains such as *Epilobium latifolium* L., *Hedysarum mackenzii* Richards, *Oxytropis* L. sp., *Castilleja Mutis* sp., and *Artemisia frigida* (Young 1982). Co-dominants of *A. frigida* would have been the moss *Calamagrostis purpurascens*, the grasses *Agropyron spicatum*, *Poa glauca* M. Vahl (includes *P. rupicola* according to Hulten 1968) and some *Bromus* and *Festuca* species (Young 1982). (Festuca spicata Pursh equals *A. spicatum* according to Hulten 1968).

Yurtsev (1982) claims that a typical steppe climax situation consists of cryophytes and xerophytes living in slightly basic soil. Some present relict sites in Siberia, Alaska and the Yukon (including the sites at Kluane Lake) occur on steep south facing slopes upon which loess or basic soil is deposited from non-vegetated flood plains of glacial rivers.

Today, the climate of proposed relict sites in the Alaskan and Yukon interiors is hot and dry in the summer and cold and dry in the winter. This corresponds to the continental climate of Beringia during the late Pleistocene. Species that are typical of present dry slopes are *Artemisia frigida* and *A. lacinata* Willd., *Eriogonum flavum* Nutt., *Potentilla multifida* L., *Penstemon Mitchell* sp., *Chamaerhodos erecta*, and *Rosa woodsii* Lindl (Young 1982).

Ritchie (1984) criticizes the reconstruction of Beringia as Arctic-steppe for a number of reasons. Many ground cover species, such as lichens, mosses, ericoid shrubs, Leguminous and Caryophyllaceous herbs and *Dryas* L. species which comprise up to 40% of the present day ground cover
remain silent in the pollen record. Young himself points out that many of the endemic relict species of today would be expected in Arctic-steppe zones of the past. It would be very unlikely that none of the species making up this 40% would be relicts of the past. Ritchie also points out that no present pollen samples collected have the same pollen constituents in the same frequencies as the records. He argues that we should not interpret a dry climate by the presence of Artemisia, Gramineae and Cyperaceae species as these plants grow in as diverse habitats as arid grasslands to Arctic and alpine tundra. Colinvaux (1967) also points out that important herbs belonging to Gramineae and Cyperaceae can usually only be identified to the family level.

Ritchie (1982) and Cwynar (1982) have no quarrel with the interpretation of the late Pleistocene pollen samples, but rather find problems with the conclusions drawn from them. They claim that the pollen evidence does not prove that the whole of Beringia was covered in Arctic-steppe vegetation, but rather that a mosaic of habitats were present. They see the southwestern areas of Periglacial Beringia being composed of steppe, but that the more northerly regions of Beringia were likely steppe-tundra to fell-field habitat.

Much of the work concerning refugial vegetation in the late Pleistocene has been from the northern and interior regions of Beringia. When present relict species are compared to the pollen record, the evidence strongly suggests that at least xeric loess uplands were Arctic-steppe, but that the lowlands and valleys may have ranged from Arctic-steppe to tundra-steppe to pure tundra.

As for the southwestern regions of Beringia, no studies involving
pollen cores have been completed. Until the palynology is known, modern analogues must be compared to species identified from more interior pollen cores. Hoefs et al. (1975) completed a vegetation analysis of Sheep Mountain, situated on the south end of Kluane Lake, and found *Artemisia frigida*, *A. alaskana* Rydb., *Agropyron yukonense* Scribn. and Merr. and *Calamagrostis purpurascens* to be the dominant species. The first three of these plants are analogous to those identified from pollen cores and are indicative of xeric conditions. The fourth is a moss that is found on glacial outwash plains.

The vegetation found on all of my Kluane Lake sites (see Table 8) is extremely close to that described by the above authors from relict site pollen cores from the interior portions of Beringia and for those sites on the Chukotka Platform. Common genera described from the Chukotka Platform are *Penstamen*, *Artemisia*, *Potentilla*, *Chamaerhodos* and the species *Rosa woodsii* (Yurtsev 1982) all of which occur on the Kluane Lake sites. The pollen rain of the late Pleistocene was dominated by *Artemisia* sp. and species of Gramineae and Cyperaceae. The Kluane Lake sites have an abundance of *Artemisia* sp. and all sites have high percentages of grass.

The Kluane Lake study sites also contain species that were present on outwash plains of Periglacial Beringia, i.e. *Hedysarum mackenzii*, *Oxytropis* sp., *Castillija* sp., *Artemisia* sp., *Calamagrostis purpurascens*, *Agropyron spicatum*, *Poa glauca* and *Bromis* sp. The D.M. and Inst. sites for example, each have 5 of these 8 species (see Table 8).

The Kluane Lake group of sites, although glaciated in the late Pleistocene, are extremely similar to those areas that are known or expected relict sites in the interiors of Alaska and the Yukon and on the
Chukotka Platform. The dominant plants found on the Kluane Lake sites are those that appear in high quantities in the pollen rain of the late Pleistocene and many are modern analogues of relict species. These sites were likely colonized very soon after the glaciers receded.

Thus, _G. discopterus_ is a characteristic inhabitant of these xeric _Artemisia frigida_ dominant relict sites now found on south-facing slopes along the main river valleys of the southwestern Yukon, in unglaciated and periglacial areas. As such, it can be considered a relict Beringian species, a species that has not dispersed far in the past 8000 years beyond the range probably occupied during the Pleistocene.

In conclusion then, there are two _Geocoris_ species of the _bullatus-pallens_ complex in the southwestern Yukon. The two have different external morphologies, biologies, are reproductively isolated and have different habitat preferences. Evidence that _G. discopterus_ is a relict species of late Pleistocene Beringia that has not spread much beyond unglaciated areas has also been provided.

_G. bullatus_, on the other hand, is a widespread species that has a less restricted habitat and has thus dispersed throughout North America. It has extended its range to the Yukon where it now occurs in some mesic sites with _G. discopterus_ and may interact with it. The fact that _G. discopterus_ does not occur with _G. bullatus_ in eastern North America (Readio and Sweet 1982) may be because of a longer interaction between the species that could have resulted in clear habitat exclusion or segregation in these southern areas. Alternately, the habitat preference of these species may not be the same throughout their respective ranges. Certainly, the relict steepe-like Beringian habitats now occupied by _G. discopterus_ in the Yukon, do not occur in the eastern United States.
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Appendix I: Adult *Geocoris* morphological measurements (mm ± S.E.).

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<tr>
<th>Character</th>
<th>Female Mean</th>
<th>Range</th>
<th>Male Mean</th>
<th>Range</th>
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<tr>
<td><strong>Geocoris bullatus (N=10):</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head length</td>
<td>0.57 ± 0.10</td>
<td>0.40 - 0.75</td>
<td>0.56 ± 0.07</td>
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</tr>
<tr>
<td>Intercocular distance</td>
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<td>0.55 - 0.80</td>
<td>0.73 ± 0.03</td>
<td>0.65 - 0.75</td>
</tr>
<tr>
<td>Antenna I</td>
<td>0.26 ± 0.04</td>
<td>0.20 - 0.35</td>
<td>0.26 ± 0.04</td>
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<tr>
<td>Antenna II</td>
<td>0.48 ± 0.07</td>
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<td>0.48 ± 0.05</td>
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<tr>
<td>Antenna III</td>
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<td>0.30 - 0.45</td>
<td>0.30 ± 0.04</td>
<td>0.25 - 0.35</td>
</tr>
<tr>
<td>Antenna IV</td>
<td>0.46 ± 0.07</td>
<td>0.35 - 0.55</td>
<td>0.47 ± 0.09</td>
<td>0.30 - 0.60</td>
</tr>
<tr>
<td>Rostrum I</td>
<td>0.49 ± 0.08</td>
<td>0.35 - 0.55</td>
<td>0.51 ± 0.06</td>
<td>0.45 - 0.65</td>
</tr>
<tr>
<td>Rostrum II</td>
<td>0.30 ± 0.05</td>
<td>0.25 - 0.40</td>
<td>0.29 ± 0.05</td>
<td>0.20 - 0.35</td>
</tr>
<tr>
<td>Rostrum III</td>
<td>0.48 ± 0.05</td>
<td>0.40 - 0.55</td>
<td>0.41 ± 0.05</td>
<td>0.35 - 0.50</td>
</tr>
<tr>
<td>Rostrum IV</td>
<td>0.29 ± 0.06</td>
<td>0.20 - 0.40</td>
<td>0.28 ± 0.07</td>
<td>0.15 - 0.35</td>
</tr>
<tr>
<td>Pronotum length</td>
<td>0.83 ± 0.09</td>
<td>0.65 - 0.95</td>
<td>0.79 ± 0.08</td>
<td>0.60 - 0.90</td>
</tr>
<tr>
<td>Pronotum width</td>
<td>1.25 ± 0.10</td>
<td>1.10 - 1.40</td>
<td>1.20 ± 0.06</td>
<td>1.10 - 1.25</td>
</tr>
<tr>
<td>Scutellum length</td>
<td>0.97 ± 0.24</td>
<td>0.60 - 1.35</td>
<td>0.80 ± 0.06</td>
<td>0.70 - 0.95</td>
</tr>
<tr>
<td>Scutellum width</td>
<td>0.83 ± 0.10</td>
<td>0.70 - 1.00</td>
<td>0.76 ± 0.04</td>
<td>0.70 - 0.85</td>
</tr>
<tr>
<td>Abdomen length</td>
<td>2.57 ± 0.32</td>
<td>2.00 - 3.05</td>
<td>2.39 ± 0.27</td>
<td>2.05 - 2.90</td>
</tr>
<tr>
<td>Abdomen width</td>
<td>1.69 ± 0.20</td>
<td>1.30 - 1.90</td>
<td>1.47 ± 0.06</td>
<td>1.40 - 1.55</td>
</tr>
</tbody>
</table>

| **Geocoris discopterus (N=10):** |             |         |           |         |
| Head length             | 0.45 ± 0.09 | 0.35 - 0.60 | 0.40 ± 0.05 | 0.30 - 0.45 |
| Intercocular distance   | 0.67 ± 0.23 | 0.55 - 1.30 | 0.55 ± 0.05 | 0.50 - 0.60 |
| Antenna I               | 0.25 ± 0.04 | 0.20 - 0.35 | 0.22 ± 0.03 | 0.20 - 0.25 |
| Antenna II              | 0.35 ± 0.06 | 0.30 - 0.40 | 0.32 ± 0.05 | 0.25 - 0.40 |
| Antenna III             | 0.27 ± 0.05 | 0.20 - 0.35 | 0.25 ± 0.04 | 0.20 - 0.30 |
| Antenna IV              | 0.36 ± 0.07 | 0.25 - 0.45 | 0.39 ± 0.08 | 0.30 - 0.50 |
| Rostrum I               | 0.36 ± 0.10 | 0.20 - 0.50 | 0.34 ± 0.07 | 0.20 - 0.45 |
| Rostrum II              | 0.24 ± 0.05 | 0.15 - 0.30 | 0.23 ± 0.05 | 0.15 - 0.30 |
| Rostrum III             | 0.36 ± 0.02 | 0.35 - 0.40 | 0.37 ± 0.04 | 0.30 - 0.40 |
| Rostrum IV              | 0.24 ± 0.05 | 0.20 - 0.30 | 0.29 ± 0.06 | 0.20 - 0.40 |
| Pronotum length         | 0.66 ± 0.08 | 0.60 - 0.85 | 0.61 ± 0.03 | 0.55 - 0.65 |
| Pronotum width          | 1.01 ± 0.05 | 0.90 - 1.05 | 0.93 ± 0.05 | 0.80 - 0.95 |
| Scutellum length        | 0.72 ± 0.26 | 0.60 - 1.45 | 0.58 ± 0.03 | 0.55 - 0.60 |
| Scutellum width         | 0.66 ± 0.11 | 0.55 - 0.90 | 0.60 ± 0.04 | 0.55 - 0.70 |
| Abdomen length          | 1.93 ± 0.19 | 1.65 - 2.35 | 1.76 ± 0.07 | 1.65 - 1.85 |
| Abdomen width           | 1.35 ± 0.06 | 1.25 - 1.45 | 1.20 ± 0.05 | 1.10 - 1.30 |
Appendix II. Nymphal Geocoris morphological measurements (mm ± S.E.).

<table>
<thead>
<tr>
<th>Character</th>
<th>Instar</th>
<th>Geocoris bullatus (N=10):</th>
<th></th>
<th>Geocoris discopterus (N=10):</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
<td>II</td>
<td>III</td>
<td>IV</td>
</tr>
<tr>
<td>Head Width:</td>
<td>Mean</td>
<td>0.44 ± 0.01</td>
<td>0.61 ± 0.01</td>
<td>0.79 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.40 - 0.45</td>
<td>0.60 - 0.65</td>
<td>0.75 - 0.85</td>
</tr>
<tr>
<td>Antenna I:</td>
<td>Mean</td>
<td>0.06 ± 0.00</td>
<td>0.10 ± 0.00</td>
<td>0.15 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.05 - 0.08</td>
<td>0.10 - 0.10</td>
<td>0.10 - 0.15</td>
</tr>
<tr>
<td>Antenna II:</td>
<td>Mean</td>
<td>0.11 ± 0.01</td>
<td>0.14 ± 0.01</td>
<td>0.19 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.10 - 0.20</td>
<td>0.10 - 0.15</td>
<td>0.15 - 0.20</td>
</tr>
<tr>
<td>Antenna III:</td>
<td>Mean</td>
<td>0.10 ± 0.01</td>
<td>0.10 ± 0.00</td>
<td>0.15 ± 0.00</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.05 - 0.10</td>
<td>0.10 - 0.10</td>
<td>0.10 - 0.10</td>
</tr>
<tr>
<td>Antenna IV:</td>
<td>Mean</td>
<td>0.10 ± 0.01</td>
<td>0.10 ± 0.00</td>
<td>0.28 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>Range</td>
<td>0.05 - 0.20</td>
<td>0.10 - 0.10</td>
<td>0.25 - 0.35</td>
</tr>
</tbody>
</table>
Appendix III: Figures indicating the actual number of Geocoris recorded at each Yukon study site from May to September, 1983.

Figure 1

Figure 2
Figure 7

PARK'S FIELD

Figure 8

MOUNTAINVIEW