COEXISTENCE IN THE GERRIDAE

by

GLEN STEWART JAMIESON

B.Sc. (Agr.), McGill University, 1967
M.Sc., University of British Columbia, 1970

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Department of Zoology

The University of British Columbia
Vancouver 8, Canada

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ABSTRACT

A comparative analysis has been made of the biologies of five species of the waterstrider Gerris, G. incurvatus, G. buenoi, G. notabilis, G. incognitus and G. remigis, which occur together in southwestern British Columbia. The aim of this study was to investigate how coexistence is achieved, and through the construction of a computer model, to simulate the interactions arising from this coexistence. The thesis is divided into six main sections: field biology, temperature preferences on a gradient, food consumption, reactive distance and movement, gerrids as predator and prey, and the model.

Field studies in 1971 and 1972 indicated that the five species of Gerris studied are not ecological homologues. Both spatial and temporal differences were detected, although considerable overlap does occur. The spatial separation results from the fact that G. remigis prefers a stream habitat, G. incognitus prefers a littered water surface habitat, and although G. buenoi, G. notabilis and G. incurvatus all prefer an open water habitat, the distances from shore preferred by each species are respectively greater. Temporal separation of the species results from differences between the species in their response to temperature. The optimum temperature for growth in G. remigis and G. buenoi is 22°C. and in G. incurvatus, G. incognitus and G. notabilis 26°C. The threshold temperatures below which growth ceases are 9.3°C. for G. incognitus, 10.3°C. for G. notabilis, and 12.6°C. for G. buenoi, G. remigis and G. incurvatus.
Temperatures voluntarily selected by each species on a water gradient differed. *G. remigis* selected a temperature of about 20°C, *G. incognitus* temperatures between 14-30°C, and *G. incurvatus*, *G. buenci* and *G. notabilis* temperatures from 25-30°C. The significance of these temperature preferences in the context of those temperatures encountered by each species in the field situation was discussed.

Food consumption in a quantitative manner was described for the larvae and adults of the five species. The following parameters being determined: satiation time, the mean length of feeding and non-feeding periods in the presence of excess food, the effect of food deprivation on amount consumed, maximum gut capacity, the effect of temperature on food consumption, and the effect of developmental state on food consumption. A significant difference in digestive rate between larval and adult gerrids was found, with the time required by an adult gerrid to achieve maximum hunger being about twice that required by a larva. There were no significant differences among the larvae or among the adults. Temperatures affected food consumption, and within the temperature range tested, 5-32°C, the amount consumed increased with increasing temperature for every species except *G. remigis*. In this latter species, food consumption peaked at 20°C. Within any one instar, food consumption was found to peak about 40% of the way through the stadium, following a rapid rise from the previous ecdysis. After peaking, feeding declined gradually until the occurrence of the next ecdysis.
The two parameters which determine the rate at which prey are encountered by the instars of the five species studied, namely the distance at which they respond to prey items and their rate of movement, were measured. These parameters allowed calculation of the swath the predator covered as it moved across the water surface.

Results suggest that Gerris species prefer to attack live prey in front of them, and tend to ignore prey if the attack requires a turn of more than 100°. The state of hunger was found to affect the visual angle required to elicit an attack by G. remigis, and regardless of species, smaller gerrids required the prey to be closer before an attack was initiated.

The rate of movement in Gerris was measured as a function of stride length and the number of strides made per unit time. Stride length varied according to the length of the mesothoracic leg, and the frequency of movement was observed to be species specific. G. remigis, a stream species, moved 4 to 6 times as often as the four other species studied, all of which are characteristically found on non-moving water surfaces. The propensity to move in G. remigis was significantly influenced by hunger, with a maximally starved gerrid moving only one sixth as much as a satiated gerrid. Within a species, gerrid size had no significant effect on the frequency of movement, although there was a tendency for smaller gerrids to move less. The significance of the different propensities to move is discussed for the five species studied.
Predation studies demonstrated that no significant differences existed among the species in the efficiency with which they killed prey. However, they did show that differences existed among the species in their propensity to attack, and that these differences resulted in significantly different numbers of prey killed by the species. *G. remigis* in particular, both as a larva and as an adult, killed more prey than any of the other four species. The ability of each instar to prey upon gerrids its own size or smaller was also investigated to permit assessment of the extent of cannibalism. Preference studies where the larger gerrids were presented simultaneously with all the prey size classes they could capture efficiently, demonstrated that the prey gerrids most preferred were those most efficiently handled. The effect of different "habitats" on kill success was also investigated. These studies indicated that the ease with which certain gerrids are captured approaches that with which terrestrial insects trapped on the water surface are captured, suggesting that cannibalism may be an important mechanism in population regulation and perhaps in the ability of different species to coexist.

The results of this study were incorporated into a mechanistic computer model based on an experimental components analysis type of approach (Holling, 1966), which was expanded to include a number of species and to simulate an entire season under field conditions. Predictions by the model, which was based on laboratory-derived data, were compared to field observations, and were found to agree favourably. Cannibalism
was predicted to be an important phenomenon in all the situations studied, and mean hunger level of the gerrids affected only slightly the predicted number of progeny produced at the end of the summer.

The model when run with only single species present showed that each species completed its life cycle with the observed number of generations each year and with the temporal spacing of these generations much as observed in the field. When all five species were simulated to coexist in the same habitat, *G. incognitus* was found to virtually eliminate all of the other species present. This prediction is suggested to be the reason little overlap in field distribution occurs between this species and the other pond species.

The open water pond species, *G. incurvatus*, *G. buenoi* and *G. notabilis*, were all predicted capable of coexisting in the same habitat. The spatial separation among these species in the field may thus be concerned with long term coexistence rather than the short term problem of occupying the same habitat.
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GENERAL INTRODUCTION

The competitive displacement principle states that "different species having identical ecological niches, ie. ecological homologues, cannot coexist for long in the same habitat" (DeBach, 1966). Implicit in this concept, and in its corollary, the coexistence principle, is the understanding that all species differ biologically no matter how closely they are related and how similar they may appear or act. One species will always be favoured in any particular situation owing to certain unique aspects of its biology, and a greater number of this species will survive to reproduce. Hence, given enough time, the favoured species will eliminate the other.

There are two main problems which must be considered in any study of coexisting species: (a) are the sympatric species actually in fact ecological homologues, and if so, (b) is coexistence of these ecological homologues in the same habitat real, or is it only suggestive and superficial. Does it seemingly occur only because of modifying circumstances such as immigration or cryptic utilization of different resources. Numerous studies of coexisting species have been reported in the literature, and in each study, coexistence of ecological homologues was either disproven or could not be conclusively proven (DeBach, 1966).

Cases of actual or apparent competitive displacement between ecological homologues, however, are too numerous to permit discussion at this point. Character displacement, the
evidence of such competition, is more easily discernable, as the result is not the elimination of one of the species but adaptive changes between the species. Field studies of competitive displacement are of two types: studies of the process in action, and more commonly, the presumable result after its completion. An example of the former is Istock's (1965, 1967) studies of sympatric species of the whirligig beetle *Dineutes*, whereas an example of a study of competitive displacement after its completion is Mitchell's (1969) study of two species of sympatric water mites of the genus *Arrenurus* which parasitize damselflies.

The aim of this study was to investigate the apparent coexistence of five species of the waterstrider *Gerris* in southern British Columbia. *G. buenoi* Kirk., *G. incognitus* L. & H., *G. incurvatus* D. & H., *G. notabilis* D. & H. and *G. remigis* Say occur in southwestern British Columbia. It is futile to think that consideration of a single trait can explain how coexistence is achieved, so a large set of traits were investigated and an assessment made of the combinations of interactions that arise from these. This necessitated the construction of a computer model incorporating all these traits. *Gerrids* are well-suited for modelling, as being restricted to a two-dimensional environment, the water surface, movement is greatly simplified.

The basic organization of this thesis is six sections. Section 1 describes a field study of the five species, with the intent here being (a) to determine if the species are ecological
homologues and (b) to describe the basic biologies of the species for the incorporation of realism into the model. Section 2 describes the voluntary temperature preferences of the different species on a gradient to again help define the niches occupied by the five species. Sections 3, 4 and 5 describe food consumption, reactive distance and rate of movement, and predatory capabilities respectively for the species. The parameters in Sections 3 and 4 were required as an experimental components analysis type of approach (Holling, 1966) was used in the construction of a computer model, described in Section 6, wherein the possible situations for coexistence and exclusion are investigated.
SECTION 1. FIELD BIOLOGY GROWTH AND FECUNDITY

INTRODUCTION

Studies on gerrids to date have largely been devoted to rather general descriptions of their biology and behaviour (Essenberg, 1915; Bueno, 1917; Riley, 1921, 1922; Poisson, 1924; Rensing, 1962; Kaufmann, 1971) and have provided useful background on species, or they have been concerned with the basis and significance of alary polymorphism, which is particularly prevalent in this group (Guthrie, 1959; Brinkhurst, 1959, 1960, 1961, 1963; Vepsalainen, 1971a, 1971b, 1971c). The latter have helped determine how morphology is related to microhabitat, but they have not provided data as to what forms are capable of coexisting in the same habitat. Population studies attempted to date (Brinkhurst, 1965, 1966; Vepsalainen, 1971c) have only investigated single species and provide little information on how different species interact.

It has been claimed that gerrids occupy identical habitats and yet coexist in almost equal numbers (Maynard, 1969), but this has not been studied in detail.

To be considered in this section are the microhabitats of the species, the temporal features of the life cycles and the responses of the species to different temperatures. The main aim of this part of the study was to detect potential differences between the species. A secondary aim was the
acquisition of data required for later modelling of the species in a coexisting situation.

MATERIALS AND METHODS

1. SPECIES DISTRIBUTIONS

Data on the distributions of the species of *Gerris* found in British Columbia was compiled from my own collections plus Drake and Harris (1934), Moore (1950), Kuitert (1942), Brooks and Kelton (1967), Scudder (1971) and Ashlock (pers. comm.).

2. THE STUDY AREA

The main study areas were on Marion Lake, a small muddy bottomed lake ca. 10 ha in area located in the University of British Columbia Research Forest, 10 km north of Haney, B.C. (latitude 49°90'N; longitude, 122°33'W). In 1971 six areas (Fig. 1) on the lake were studied commencing May 1 so as to determine the effect of microhabitat variation on the distribution of the different species on one body of water. Sampling in Area 6 commenced at the beginning of August, as prior to this date, the *Potamogeton natans* (L.) had not reached the water surface and hence no cover was available.

On the basis of the data acquired in 1971, other areas
Figure 1. Marion Lake showing the pattern of vegetation. The six areas sampled in 1971 are illustrated. Area 3 was the only area sampled in 1972.
throughout the Research Forest were selected and studied in 1972. At these latter areas, different combinations of the species were present and it was hoped that this might allow (a) a more precise delimitation of the preferred habitat of each species, and (b) an assessment of the effects of certain interspecific interactions. Figure 2 illustrates the areas that were sampled in 1972 and Table 1 lists their main characteristics.

3. ENVIRONMENTAL TEMPERATURE MEASUREMENTS

Field temperatures in each of the areas sampled, excluding Reservoir 1, Dorothy* and Placid*, were recorded continuously with Ryan Model D-30 submersible temperature recorders (Ryan Instruments, Inc., Seattle). These were suspended from floats and hung 15 cm below the water surface. Temperatures in the other areas were recorded with a thermometer on each sampling date.

4. GRID SAMPLING

Field sampling was on a weekly basis between mid-April and the end of September. Initially, occurrence of adults in each of the study areas was recorded. These adults, after identification in the field according to Scudder (1971), were released as it was felt that their removal, particularly in the spring when they were relatively few in number, might affect
Figure 2. The mid and south sections of the U.B.C. Research Forest and the areas in it that were sampled in 1972, showing their elevations in feet. A = Dorothy Pond; B = Reservoir 1; C = Jacobs Creek and Jacobs Pond; D = O Inlet; E = Gate Pond.
Table 1. The characteristics of the areas sampled in 1972.

A. The eleven areas sampled in the U.B.C. Research Forest in 1972 and their characteristics. Breeding means that at least three larval instars were collected during the season. * = heavy rain runoff can create a strong current; ** = yes near shore; () = less than three larval instars were collected during the season; WSV = water surface velocity; WSL = water surface litter.

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<td>Gate Pd.</td>
<td>Sunny, man-made pond</td>
<td>0</td>
<td>no**</td>
<td>x</td>
</tr>
<tr>
<td>Dorothy+</td>
<td>Sunny, small stream (1 m wide)</td>
<td>0</td>
<td>yes</td>
<td>(x) (x) x</td>
</tr>
<tr>
<td>Dorothy Pond</td>
<td>Sunny, man-made pond; widening of a creek</td>
<td>slow*</td>
<td>no</td>
<td>x x x x x</td>
</tr>
<tr>
<td>Placid+</td>
<td>Shaded, small stream</td>
<td>0</td>
<td>yes</td>
<td>x</td>
</tr>
<tr>
<td>Placid L.</td>
<td>Non-draining lake</td>
<td>0</td>
<td>no**</td>
<td>x</td>
</tr>
<tr>
<td>Reservoir 1</td>
<td>Shaded man-made pond; widening of a small stream</td>
<td>0</td>
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<td>x</td>
</tr>
<tr>
<td>Marion L.</td>
<td>Draining lake</td>
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<td>no**</td>
<td>x</td>
</tr>
<tr>
<td>O Inlet</td>
<td>Widening of a small stream</td>
<td>slow**</td>
<td>x x x (x) x</td>
<td></td>
</tr>
<tr>
<td>Jacobs Ck.</td>
<td>Creek (3-4 m wide)</td>
<td>fast</td>
<td>no</td>
<td>x</td>
</tr>
<tr>
<td>Jacobs Pd.</td>
<td>Stream-bank pool</td>
<td>0</td>
<td>no</td>
<td>x x x (x) x</td>
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</table>
Table 1. B. (i) the water temperature differences (°C.) between the below areas and Marion L. at the times given for different dates during the season. The mean temperature difference (± 1 SE) indicates the relative temperatures of the different areas to Marion L. * = not included in the calculation of the mean. (ii) The water temperatures (°C.) of the below areas at 12:01 pm for different dates during the season and their mean (± 1 SE).

B. (i)

<table>
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<tr>
<th>Date</th>
<th>Area</th>
<th>Gate Pd.</th>
<th>Dor. +</th>
<th>Placid+</th>
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<th>C Inlet</th>
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<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
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<td>8.6*</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>-3.5</td>
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<tr>
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<td>-2.6 ± 1.0</td>
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<td>-2.1 ± 0.7</td>
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(ii)

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<td>11.2 ± 2.3</td>
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</table>
later population levels. Commencing with the appearance of the first larval stages, a set number of square-meter samples were taken from each study area on each sampling date. All the larval gerrids were preserved either in 70% ethanol or brought back to the laboratory for further study. Larval identification was according to Scudder and Jamieson (1972).

Sampling equipment consisted of a square-meter aluminium frame 48 cm deep, with plastic screening on each of the four sides. Buoyancy in deep water was achieved by floats on each corner. Sampling consisted of tossing the frame onto the water surface from a distance of ca. 3-4 m and collecting all the enclosed gerrids. The same locations were sampled on each sampling day. As the object of the sampling was not to determine the mean gerrid density over the whole body of water, but rather to ascertain what species instars were present at any given time and place and their densities in these locations, the sampling locations chosen were those where gerrids were known to be present. However, fluctuating water levels did necessitate a change in sampling location in some areas. Generally, gerrids tend to be found around the perimeter of the lake and hence the locations sampled tended to be near the water-edge. As the water-edge varied with fluctuating water levels, especially in the shallow areas, the sampling locations also varied. Nevertheless, it was felt that the sampling procedure did allow realistic determination of the gerrids present at any given time.

In 1971 all the adult gerrids collected in the sample areas
on Marion L. from May 17 to July 30 inclusive were marked on the pronotum with a spot of Liquitex acrylic polymer emulsion (Permanent Pigments, Inc., Cincinnati). A different colour was used in each sample area, and capture of these marked gerrids at later dates was recorded, allowing a measure of the movement of the gerrids between the study areas. Preliminary observations of laboratory gerrids marked in a similar manner suggested that marking did not increase gerrid mortality.

During late April and early May of 1972, a few female gerrids of each of the five species were collected from Gate Pd., Marion L., and the vicinity of Placid L. These were preserved in 70% ethanol for later dissection. This allowed the date of commencement of ovariole egg production in each of the species to be determined. Since the first-generation gerrids of G. buenoi, G. incurvatus and G. incognitus vary in the extent of their wing development, female morphs of these species were collected and preserved on July 20 to determine if alary polymorphism affected commencement of ovariole maturation.

5. LABORATORY STUDIES
A. Effect of temperature on instar duration

Eggs or larvae of each of the five species were placed individually in open plastic containers 9.5 cm in diameter and 7 cm deep and maintained at 26° C. in a controlled environmental cabinet (Controlled Environments Inc., Winnipeg): lighting was 16 hr light: 8 hr dark. Eggs were taken on the first day following deposition and the number of days to hatching was recorded. Similarly, with larvae, the number of days between successive ecdyses were recorded. Feeding with frozen adult *Drosophila* and monitoring of development was daily.

To ascertain the effect of different temperatures on development, the above procedure was repeated with larvae at 15°, 18.5°, 22° and 35° C.

B. Fecundity

Adults collected early in the spring before they were sexually mature, were brought back to the laboratory and used to obtain a measure of fecundity. Pairs of *G. notabilis* and of *G. remigis* were separately placed in rectangular containers 30 cm by 43 cm with a water depth of 5 cm. The water surface was kept clean by use of an airstone and each container had a 13 cm², 1 cm thick plywood block for an oviposition site. Because of their smaller size, pairs of the other three species were maintained in plastic containers 26 cm in diameter and 9 cm deep, each of which had a number of 3 cm² cork slices for oviposition. The water in these latter containers was changed
weekly to keep the water surface clean.

All species were fed frozen adult *Drosophila* once daily and room temperature was recorded continuously. First instar emergence rather than eggs laid was determined daily, as it was virtually impossible to detect all eggs laid in the various crevices of the blocks provided.

Since *G. buenoi*, *G. incognitus* and *G. incurvatus* are often bivoltine, the same procedure was repeated with adults of the first summer generation. These latter adults were easily detected in the field from the overwintered ones, because the latter had a "weathered" appearance, while the former were "fresh".

It was felt preferable to use field caught gerrids for this study as larval nutrition, especially in the later larvae, can influence adult fecundity (Drooz, 1970). Larval emergence rather than eggs laid is also probably a better measure of fecundity, since at times eggs failed to hatch. Kaufmann (1971) reported that in *Gerris rufoscutellatus* there is, on the average, only an 88.1% egg viability. Eggs failing to hatch and showing no embryonic development were noted.
RESULTS

1. FIELD SAMPLING

A. Environmental temperature

Figure 3 describes the water temperatures of the different areas sampled in 1971 and in 1972. Both mean daily temperatures and accumulated degree-days on Marion Lake in 1971 and 1972 above the minimum temperatures required for growth for each of the species (see below) are presented in Fig. 3. Since the minimum temperatures of G. buenoi, G. remigis and G. incurvatus are all about the same (see below), ca. 12.6°C., a mean temperature value was used for these three species. It can be seen that the total number of degree-days accumulated was much greater in 1971 that in 1972. The consequences of this difference are described below.

B. General biology of the gerrids

The continental and British Columbia distributions of the five species of Gerris studied and two other species of Gerris found in British Columbia, namely G. pingreensis and G. comatus (Scudder, 1971), are shown in Fig. 4. G. remigis has been collected both east and west of the Rocky Mountains, but has only been recorded from southern British Columbia. G. incognitus and G. incurvatus have both been collected primarily
Figure 3. The mean daily temperatures of the water in Area 3 on Marion L. 15 cm below the surface of the water, and the accumulative number of degree-days above the three temperature thresholds of the species derived from the data. A. 1971; B. 1972.
Figure 4. The continental and British Columbia distributions of the five species of *Gerris* studied, and of two other species found in British Columbia.
west of the Rocky Mountains, although records exist for both species in southern Texas. In British Columbia, they are found only in the southern regions and along the coast. G. buenoi, like G. remigis, has been collected across continental North America but unlike G. remigis, this species has not been collected below the 40 parallel. It is found throughout southern and central British Columbia, but has only been collected along the coast in the south-west. G. notabilis has been primarily found in the western half of North America, although two records (questionable) exist for this species in the east. This species has been collected from New Mexico to northern British Columbia. G. comatus and G. pingreensis have both been collected across North America, but few records exist for either species south of Kamloops and west of the Rockies. Both species are virtually identical to G. incurvatus and G. incognitus respectively morphologically, and can be distinguished from these species only by means of a microscope. It is interesting to note that the distributions of G. comatus and G. pingreensis evidently do not overlap with those of G. incurvatus and G. incognitus.

All five species of Gerris in the study area overwintered as adults, and G. remigis and G. incognitus typically emerged earliest in the spring. By early May, adults of all five species were collected and commencing in late May, larvae began to appear. Oviposition sites in all the species were beneath the water surface, with the edges of the undersides of floating aquatic vegetation (eg. Potamogeton, Nuphar) preferred by G.
notabilis, G. incurvatus and G. buenoi. G. incognitus preferred floating wood and other more solid objects, perhaps a result of its preferred habitat being closer to shore (see below) where such debris accumulates. G. remigis was often observed to crawl beneath the water surface to a depth of several centimeters in order to reach an oviposition site. Rocks, relatively large pieces of floating wood and roots were chosen as oviposition locations.

Eggs of all the species were found to be basically similar in shape, being cylindrical and ca. 3 times as long as wide (ca. 1.3 by 0.4 mm). The eggs of G. notabilis are unique in that they are individually surrounded by a ca. 1 mm thick gelatinous sheath; eggs of the other species are without this sheath. The eggs of G. notabilis, G. incurvatus, G. incognitus and G. buenoi were laid in rows of about 10-15 eggs along leaf borders, whereas the eggs of G. remigis were laid separately.

There are considerable size differences between the five species of Gerris studied, with adult G. remigis and G. notabilis weighing ca. 3 to 6 fold more than the other species. Figure 5 presents the relation between leg length and wet weight for all the species' instars and from this it can be seen that the adults of each species are distinct in relative size and leg length: G. buenoi is smallest with medium length legs, G. incurvatus is next heaviest and possesses relatively long legs for its weight, G. incognitus is the heaviest of the three small species and has relatively short legs, G. notabilis possesses extremely long legs relative to G. remigis, although their
Figure 5. The relation of leg length to wet weight for all the instars of the five species studied (± 1 SE). • = larva; □ = adult female; ○ = adult male; N = G. notabilis; R = G. remigis; IG = G. incognitus; IV = G. incurvatus; B = G. buenoi.
average weights are about the same. The females are heavier than males and possess the longest legs in all the species except G. notabilis. In G. notabilis the male is heavier and has longer legs than the female.

G. notabilis and G. remigis were univoltine, while the other three species were usually bivoltine. Their success in having two generations per year varied and depended on the weather conditions. Larvae of the bivoltine species were often collected as late as mid-September. Adult G. notabilis and G. incurvatus entered overwintering diapause relatively soon after they reached the adult stage, since they disappeared in late August or early September. G. buenoi, G. incognitus and G. remigis remained active longer, although the former two usually left the water surface by late September. G. remigis persisted in large aggregations until the water froze over, usually in late October.

Winged adult G. buenoi, G. incurvatus and G. incognitus flew in late summer, but did not show the same tendency in the spring or early summer. Fall would thus seem the time of major flight dispersal in these species although some dispersal may occur in early spring. G. notabilis, on the other hand, seemed to primarily disperse in the spring. In late May in 1972, every pond being studied had G. notabilis on it, often in large numbers. None had been observed the week before and within a few weeks, the adult G. notabilis disappeared off those ponds which later in the season had no breeding G. notabilis populations. Data on dispersal in G. remigis were not obtained.
but since there was a very low frequency of winged morphs (ca. 5%), flight would not seem to be the main dispersal method for this species in the study area.

Alary polymorphism occurred in the gerrids. Table 2 presents the ratios of the morphs of \textit{G. incognitus}, \textit{G. buenoi}, and \textit{G. incurvatus} which were collected in 1972. \textit{G. notabilis} always possessed wings extending the full length of the abdomen (macropters), and although a few \textit{G. remigis} in British Columbia are macropterous (Scudder, 1971), not enough adults were collected in the course of sampling to permit inclusion of this species in Table 2. It can be seen that in \textit{G. buenoi} and \textit{G. incurvatus} the macropterous morph was the dominant form in the spring and fall, whereas apterous and shortwinged forms were dominant in the summer or first generations. In both the species there were two generations, with most of the first generation adults apterous or shortwinged.

C. Spatial distribution and microhabitats

The spatial distribution of the five species of gerrids collected on Marion L. in 1971 is shown in Fig. 6. \textit{G. notabilis} and \textit{G. incurvatus} were each collected in approximately equal numbers in Areas 1-5. \textit{G. buenoi} and \textit{G. incognitus}, although also collected in all five areas, were most abundant in Areas 3 and 4. In Area 6, an offshore \textit{Potamogeton} bed, only \textit{G. incurvatus} was abundant. As shown in Fig. 1, Area 1 is in a very shallow region of the lake. Grasses were present at the water-edge only in the early spring when the lake level was
Table 2. The proportions of the various adult morphs of the different species observed in the U.B.C. Research Forest during 1972. *G. notabilis* had only one form, a fully-winged one, whereas *G. remigis* was always apterous. \( W \) = macropterous; \( 1/2w \) = brachypterous; \( 1/4w \) = micropterous; \( nw \) = apterous.

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</table>
Figure 6. The numbers of the instars of each of the species summed which were collected on Marion L. in 1971. The areas shaded represent those numbers of each of the species collected at a distance greater than 3 m from shore.
high; in mid-summer, the lake level dropped, exposing a large area of lake bottom (mud) which possessed little vegetation. *G. buenoi* and *G. incognitus* were only collected from this area in the early spring. The same applied, although to a lesser extent, to Areas 2 and 5. Areas 3 and 4, however, had extensive grass and weed beds, and the water depths there were such that the water extended into these beds at all times of the year. Extensive cover was thus always available. It will be noticed that excluding the immediate vicinity of the inlet and outlet streams, *G. remigis* was only collected in Area 5. In the specific microhabitat in Area 5 where this species was collected, water from a cold spring flowed into the lake, and it was only at this one location where the maximum water temperature was ca. 20°C. that *G. remigis* occurred.

Since it was noticed that the preferred distance from the shore seemed to vary with the species, Figure 6 also shows the number of the different species in each sampled area collected at a distance greater than 3 m from the water edge. Over 50% of the *G. incurvatus* collected were obtained at a distance greater than 3 m, whereas *G. notabilis* and *G. buenoi* tended to be found closer to shore. *G. incognitus* remained closest to shore.

Figure 7 and Table 1 present the spatial distributions of the species in the areas sampled in 1972. Gate Pd. and Marion L. both contained four species (lacking only *G. remigis*), with one of the five species dominating in each of the other areas. Placid L. was somewhat unique among the areas studied in that the individual species present there were to a large extent
Figure 7. The numbers of the instars of each of the five species summed which were collected in each of the six main sampling areas in 1972.
spatially separate. *G. notabilis* was only collected on the small pools in the *Sphagnun* shelf which surrounded the lake, *G. buenoi* was only collected on the edge of the *Sphagnun* shelf where it abutted the open water of the lake, and *G. incognitus* was only collected in the smallest, algae-covered pools closest to the actual lake shore. Neither *G. incurvatus* nor *G. remigis* were collected on this lake.

Table 1 identifies the sample sites on the basis of their physical characteristics and from this, it is evident that each species seems to have a preferred microhabitat. *G. remigis* is unique in that it was usually only observed on fast flowing streams, although aggregates did occur on the more sheltered areas on the streams. Nevertheless, individuals of this species are capable of maintaining their position in the current if necessary and show an ability to direct their movements against the water flow.

*G. incognitus* was found in areas where the water surface velocity was zero or slight, and where floating material such as algae abounded. These areas were typically quite shallow, being near the shore, on large bodies of water and were not much more than surface pools if the water bodies were small. Ground seepage often produced enough water in the form of small puddles for this species.

*G. incurvatus* was only observed on large bodies of water where the offshore regions were interspersed open water and floating vegetation. The water was thus usually not very deep,
the vegetation (eg. *Nuphar* and *Potamogeton*) being well rooted. *G. incurvatus* was not found on Placid L. perhaps owing to the water being too deep to permit the development of the required offshore weeds.

*G. buenoii* was found typically in inshore areas where the water surface was not too cluttered with floating vegetation, while *G. notabilis* was found on similar water but not as far offshore as *G. incurvatus* and yet further offshore than *G. buenoii*.

It should be emphasized that these microhabitat preferences are not strictly adhered to and thus a great deal of overlap exists between the species. Thus on slow moving streams and pools such as 0 Inlet, all the species were collected, and likewise all except *G. remigis* occur together on Marion L. Further, at different times of the day, the degree of overlap can vary. Thus at mid-day on Marion L., the wind was often noted to blow north, that is from one end of the lake to the other. The effect was to force all the gerrids at the north end of the lake to the weed beds where cover was available. Here they were forced into close contact. In the early morning and evening, when the wind died down, the spatial separation once again became evident.

To obtain some measure of the movements of gerrids between different habitats, adults on Marion L. in 1971 were marked between May 17 and July 30 and then released in the area of capture. Later sampling gave recapture data from which it was
possible to determine the amount of movement. A total of 381 gerrids were marked, with 20 recaptures; 92.3% of these recaptures were in the same area that the gerrid was marked (Table 3). One recapture was in an adjacent area, and one was in an area the next beyond an adjacent area. This suggests that although some movement of gerrids around the lake occurred, they tended to remain in one area of the lake through most of the season. It will be noted that a greater percentage of the G. buenoi marked were recaptured than in the other species. This probably reflects the greater propensity of individuals of this species to move less and to remain close to shore. Since the locations within an area sampled tended to be those where gerrids were known to be present, cover was usually available, and hence the sample locations were usually relatively close to shore. Recapture of individual G. buenoi would thus be more likely than recapture of G. incurvatus, which prefers an offshore microhabitat. It would thus seem that although movement of gerrids occurred between adjacent sampled areas, the number which actually moved was quite small.

D. Temporal occurrence and voltinism

Table 4 shows the temporal occurrence of female gerrids carrying chorionated eggs for each of the five species in 1972. Three sample areas are represented, Gate Pd. at an elevation of 470', Marion L. at an elevation of 1002', and Placid L.-Dorothy Pd. at an elevation of 1650'. G. incognitus and G. remigis emerged from overwintering earliest, and chorionated eggs were
Table 3. The numbers of gerrids marked and the subsequent recaptures in the different areas sampled on Marion L. in 1971. Marking terminated on July 30.

<table>
<thead>
<tr>
<th>Date</th>
<th>Number marked</th>
<th>Number recaptures</th>
<th>Same Adj</th>
<th>2nd Adj</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IV N IG R B</td>
<td>IV N IG R B</td>
<td>Area</td>
<td>area</td>
</tr>
<tr>
<td>May 17</td>
<td>19 1 3 32</td>
<td>1 2 3</td>
<td>1(B)</td>
<td></td>
</tr>
<tr>
<td>May 21</td>
<td>36 3 32 1</td>
<td>1 2 3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 24</td>
<td>24 2 22 1</td>
<td>1 3 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 28</td>
<td>14 1 2 15</td>
<td>1 1 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 4</td>
<td>6 1 3 20</td>
<td>1 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 11</td>
<td>19 2 6 28</td>
<td>4 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 18</td>
<td>9 5 23</td>
<td>7 7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 2</td>
<td>13 1 3 6</td>
<td>1 2 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 16</td>
<td>1 3 9</td>
<td>1 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 23</td>
<td>3 2 1 3</td>
<td>1 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>July 30</td>
<td>1 2 1 4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aug 6</td>
<td>--</td>
<td>--</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>145 10 32 0</td>
<td>3 0 1 0 22 24</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Percentage recaptured</td>
<td>2.1 3.1 11.3 92.3 3.8 3.8</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4. Occurrence of female gerrids with chorionated eggs. The numbers outside the parentheses indicate the number of gerrids with chorionated eggs and the numbers in parantheses indicate the sample size. A. Overwintered adults. B. Summer adults. N = G. notabilis; IV = G. incurvatus; B = G. buenoi; IG = G. incognitus; R = G. remigis; w = winged; nw = no wings; 1/2w = brachypterous; x = female gerrids observed but not collected.

<table>
<thead>
<tr>
<th>Date</th>
<th>Area</th>
<th>Gate Pd.</th>
<th>Marion L. vic.</th>
<th>Placid L. vic.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>N IV B</td>
<td>N IV B   IG R</td>
<td>N IV E   IG R</td>
</tr>
<tr>
<td>A.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apr 16</td>
<td></td>
<td>1</td>
<td>0 x</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1)</td>
<td></td>
<td>(3)</td>
</tr>
<tr>
<td>Apr 27</td>
<td></td>
<td>x x x</td>
<td>0 0 x 0 3</td>
<td>x 0 0 0 x</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2) (5)</td>
<td>(1) (3)</td>
<td>(3) (3)</td>
</tr>
<tr>
<td>May 5</td>
<td></td>
<td>x x x</td>
<td>x 0 0 x x</td>
<td>x x 0 x</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(3) (2)</td>
<td></td>
<td>(2)</td>
</tr>
<tr>
<td>May 18</td>
<td></td>
<td>x 1 1 1</td>
<td>1 2 2 2 x</td>
<td>3 3 x x</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1) (1)</td>
<td>(1) (4) (2) (2)</td>
<td>(4) (4)</td>
</tr>
<tr>
<td>B.</td>
<td>Marion L.</td>
<td>IG nw</td>
<td>IG w  IV w IV 1w</td>
<td>B w  B nw</td>
</tr>
<tr>
<td>July 20</td>
<td></td>
<td>6 (2)</td>
<td>1 (2) 15 (17)</td>
<td>2 (3) 2 (2) 1 (1)</td>
</tr>
</tbody>
</table>
present in these species in late April, before the other three species had emerged. Chorionated eggs were observed in *G. incognitus* on Gate Pd. on April 16, but they were not found in individuals on Marion L. and Placid L. until May 18. It should be noted that Placid L. was still covered with ice on April 16, and the only gerrids observed at this elevation were *G. remigis* on Dorothy Pd., which was free of ice owing to the swift currents of Gwendoline Ck. Nevertheless, chorionated eggs were present in one *G. remigis* collected at this time at this elevation. *G. notabilis*, *G. buenoi* and *G. incurvatus* all emerged at about the same time at the three elevations since all except *G. incurvatus* were present on April 27 at the highest elevation (*G. incurvatus* was not collected on any of the water bodies studied at the highest elevation at any time during the season). Chorionated eggs were not present in these species until mid-May. There are thus temporal differences between the five species in attainment of sexual maturity in the spring.

The temporal occurrence of the various instars of the four main species of *Gerris* on Marion L. in 1971, established by quadrate sampling, is shown in Fig. 8. Adults of all four species first appeared on the lake in late April. The first larvae appeared on May 24 and larvae of *G. buenoi* were still present on the lake when collecting terminated on September 15.

The temperature until mid-July was unusually low in 1971, with water temperatures averaging ca. 13°C. (Fig. 3a). Although adults of all four species were present on Marion L. from May 7, *G. incognitus* may have deposited eggs before the
Figure 8. The temporal occurrence and numbers of first instar larvae of the four pond species collected on Marion L. in 1971. *ow* = overwintered adults; *roman numbers* = instars; *integer numbers* = summer generation adults.
other three species. However, a distinct sequence of occurrence of first instar larvae was found on Marion L. *G. incognitus* and *G. buenoi* appeared first, followed by *G. incurvatus* and still later *G. notabilis*. This temporal difference was evident throughout the year in all instars and can be seen in the time of appearance of the first summer generation adults.

In addition to the temporal differences in the occurrence of the instars of the four species, there were pronounced differences between the times of peak population numbers in the larval instars. This is best illustrated in the population curves obtained for the first instar larvae. *G. incognitus* and *G. buenoi* showed an early peak in numbers, but it was only when the temperatures increased in mid-July that the numbers of first instar larvae of *G. incurvatus* and *G. notabilis* peaked (Figs. 3a and 8). Coincident at this time was a decrease in first instar larva numbers of *G. buenoi* and *G. incognitus*, with the latter disappearing off the lake completely. When the temperature declined in the fall, the numbers of *G. notabilis* and *G. incurvatus* declined, and then the second generation numbers of *G. buenoi* increased.

It is possible that the late peaking of numbers of *G. incurvatus* may not have been entirely due to the direct dependence of the species on higher temperatures. Instead, the delay may have been caused by the late emergence of the vegetation in the deeper water. The vegetation finally reached the water surface in late July and then provided cover away from the water-edge. As has been noted earlier, *G. incurvatus*
appears to prefer a microhabitat offshore, and it is possible that the lack of offshore Potamogeton and Nuphar beds early in the year significantly reduced the numbers of this species.

The temporal occurrence of the instars of the four main species on the inshore Area 3 of Marion L. in 1972 is shown in Fig. 9. The weather this year (Fig. 3b) was very different from that of 1971, the temperatures being quite high in early June, low in late June, and then generally remaining moderate until early in September, except for one noticeable cold spell in mid-July.

The temporal sequence in 1972 was not as evident as in 1971 with the first instars of G. incognitus and G. buenoi were present earliest, but all species showed a somewhat earlier development, no doubt because of the higher temperatures present in early June. The numbers of first instar G. incognitus and G. buenoi peaked in June. However, G. buenoi did not show a pronounced second generation in the fall as in 1971, although G. incognitus, in contrast to 1971, did produce a second generation on Marion L.

Generally the numbers of G. incurvatus in 1972 were much greater than in 1971, with the numbers in Area 3 in 1972 being greater than the total number in all the areas in 1971. The first instar numbers of G. incurvatus declined in Area 3 on Marion L. in late July, as in 1971. However, at this time the offshore Potamogeton beds developed and G. incurvatus moved to these. Hence the disappearance of this species in late July
Figure 9. The temporal occurrence and numbers of first instar larvae of the four pond species collected on Marion L. in 1972. (see Fig. 8 for legend).
from Area 3 was not a lake-wide phenomenon.

All the adults, except apterous *G. incognitus* collected on Marion L. on July 20, 1972 contained chorionated eggs. The two female *G. incognitus* collected at this time were quite teneral and sexually immature. Whether they matured later was not determined. However, since the three *G. incognitus* which did produce young in the fecundity experiments in the laboratory were all apterous, this morph can at times breed the same year it matures.

Fig. 10 presents the temporal occurrence of the various instars of the four pond species on Gate Pd. in 1972. Owing to the lower altitude and sunny exposure, temperatures here averaged considerably higher during the early spring than on Marion L. This resulted in the development being more advanced than on Marion L. Comparison of *G. bueno* in the two localities clearly demonstrated that the instars on Gate Pd. were two weeks ahead of those on Marion L.

The peaks of the first instar larvae on Gate Pd. also differed from those on Marion L. Large numbers of *G. bueno* and *G. incurvatus* larvae were collected in late July and early August on Gate Pd., whereas on Marion L. the larger peaks occurred in June. Thus the size of the two generations differed markedly in these two localities.

From the study of Marion L. in 1971 and 1972, and Gate Pd. in 1972, it is clear that *G. notabilis*, like *G. remigis* on Jacobs Ck., Jacobs Ck. Pd., Dorothy Pd. and Reservoir 1 in
Figure 10. The temporal occurrence and numbers of first instar larvae of the four species collected on Gate Pd. in 1972. (see Fig. 8 for legend).
GATE POND

\[ \text{ow} \quad \text{I} \quad \text{ii} \quad \text{iii} \quad \text{iv} \quad \text{v} \]

\text{G. incurvatus}

\[ \text{ow} \quad \text{I} \quad \text{ii} \quad \text{iii} \quad \text{iv} \quad \text{v} \]

\text{G. buenoi}

\[ \text{ow} \quad \text{I} \quad \text{ii} \quad \text{iii} \quad \text{iv} \quad \text{v} \]

\text{G. incognitus}

75
50
25
0

Scale

MY \quad JN \quad JU \quad AU \quad SE

1972

1
2
3
1972, was univoltine (Fig. 11). *G. incognitus*, *G. buenoi* and *G. incurvatus* on the other hand were either univoltine or bivoltine.

Since the peaks of abundance of the first instars of the pond species that occurred together seemed to be temporally spaced, it is possible that interspecific interactions might influence the temporal occurrence of the instars, their abundance and hence the number of generations. Observations of the species in localities where only one species was dominant (Fig. 10) suggests that interspecific interactions do not greatly affect the temporal occurrence of the instars and do not affect the number of generations. However, interspecific interactions may have some influence on the timing of instar peaks of abundance. Thus the dominant species on Placid L. was *G. notabilis*, and here the numbers of first instar larvae peaked in early June (Fig. 11), although they were also collected until mid-August. In contrast, in other localities where this species occurred at lower population levels with other pond species, the peaks occurred in late June, July or August.

On O Inlet, *G. incognitus* was dominant and here the numbers of first instar larvae peaked in late May-early June (Fig. 11). Young were collected until early August following this peak production, but in greatly reduced numbers. The absence of a second generation or fall peak in first instar numbers of this species at this locality would thus not seem to be the result of interaction with other species.
Figure 11. The temporal occurrence and numbers of first instar larvae of the dominant species collected on Jacobs Ck., Placid L. and O Inlet. (see Fig. 8 for legend).
It would thus seem that whether or not *G. incurvatus*, *G. incognitus* and *G. buenoi* are univoltine or bivoltine does not depend on interspecific interactions. Instead, it evidently depends on the weather that particular year. As shown in Figs. 3a and 3b, the total accumulated number of degree-days on Marion L. in 1972 was only two-thirds that of 1971, and it would seem that this difference was sufficient to prevent a significant second generation in the bivoltine species in 1972. Gate Pd., however, at a lower elevation and less enclosed by mountains and with less cloud, had enough degree-days to allow two generations. The univoltine species, like *G. notabilis*, will breed in the spring if the temperatures are high enough, but may be delayed until early summer if cooler conditions prevail, as in 1971.

The above field results suggest that for breeding to commence in *G. notabilis*, either a critical temperature threshold must be exceeded, or a set number of degree-days must be accumulated. The other four species produced young in both 1971 and in 1972 soon after the adults emerged from overwintering, whereas with *G. notabilis*, particularly in 1971 when early June was unusually cool, the appearance of first instar larvae of this species was delayed and appeared to coincide with the onset of warmer weather. As the temperature threshold below which growth of *G. notabilis* ceases is known (see below), the calculation of the accumulated degree-days for both 1971 and 1972 is feasible and hence it is possible to determine which of the above two mechanisms is likely to be in
operation in this species. It can be seen (Figs. 3a and 3b) that accumulated degree-days seems to have little effect on the time of initiation of the main breeding period in this species. In 1971, breeding commenced after ca. 300 degree-days had accumulated, whereas in 1972 at the initiation of breeding, only ca. 125 degree-days had been accumulated. In both years, however, breeding seemed to commence after periods of a few days' duration where the temperatures averaged ca. 15°C. (Figs. 3a and 3b). Thus there seems to be a critical temperature threshold for development in G. notabilis. Later drops of the average temperature below this "threshold" did not result in the cessation of breeding, but rather resulted simply in a decrease in the number of young produced.

2. LABORATORY STUDIES

A. Effect of temperature on instar duration

Figure 12 describes the mean stadium length of the eggs and each instar of the five species of Gerris at 26°C. In G. remigis and G. incognitus, the egg stadium is the longest, whereas in the other three species, the fifth instar larvae stadium is longest. In all five species, the second and third instar larva stadia were shortest, with increasing times between mouls required by both the larger and smaller instars. Similar observations have been reported for G. odontogaster (Vepsalainen, 1971c) and G. rufoscutellatus (Kaufmann, 1971).
Figure 12. The mean stadium length (± 1 SE) of each of the gerrid instars of the five gerrid species studied.
Figure 13 describes the effect of temperature on the mean instar stadium length. *G. notabilis*, *G. incurvatus* and *G. incognitus* show a generally linear decrease in the length of the stadium with increasing temperature. *G. remigis* and *G. buenoi*, however, only show a decrease in stadium length up to ca. 22°C, and at temperatures above this, stadium length increases in duration. The optimum temperature for minimizing generation time in these two latter species was lower than for the other species.

This temperature effect, established for the first instar larvae, also seems to apply in the other four larval instars, for in experiments with the other larval instars at 15°, 18.5° and 22°C, a similar effect of temperature was noted. The average percent deviation of such measurements, when compared to the stadium length at 26°C and the ratio exhibited by the first instar larvae at the same temperatures, was ±7% (S.E. = 6%) (with an average sample size of 8.6 gerrids). Thus, even a slight change in temperature can significantly affect the relative generation length of the different species.

If it is assumed that the effect of temperature on stadium length is linear (up to 22°C for *G. remigis* and *G. buenoi*), then it is possible to obtain an estimate of the temperature at which development functionally ceases for each of the five species. Figure 14 describes this for each of the species. In order to better illustrate the effect of temperature, the reciprocal of the stadium length (days) is plotted against
Figure 13. The mean duration in degree-days (± 1 SE) above 0°C of the first instar larval stadium at different constant temperatures.
G. buenoai

G. notabilis

G. remigis

G. incognitus

G. incurvatus

TEMPERATURE (°C)

STADIUM LENGTH (DEGREE-DAYS)
Figure 14. The reciprocals of the mean duration in days of the first instar larval stadium of each of the five species at different constant temperatures. The intercept of regressions for each species plotted through the above values with the base line, set at an arbitrary maximum stadium length of 30 days, allows determination on the X-axis of the minimum temperature at which growth occurs. ° = G. notabilis; v = G. remigis; v = G. bueno; • = G. incurvatus; • = G. incognitus.
temperature. If it is arbitrarily assumed that 30 days is the maximum stadium length that is likely to exist, then the reciprocal of this value, 0.033, can be thought of as a baseline. The intercept of the linear regression describing the effect of temperature on stadium length with the base length is then the point at which development ceases. Even if 30 days is not a realistic value, it still allows the relative temperatures at which development ceases to be determined for the five species. Table 5 describes the temperatures (X-values of the intercept) at which development ceases as derived in the above manner for the five species studied: G. incognitus and G. notabilis cease development at the lowest temperatures whereas the other three species cease development at relatively higher temperatures.

B. Fecundity

Figure 15 describes the accumulative number of first instar larvae emerging from eggs deposited by females of the five species of Gerris in the laboratory. The logistic curve developed by Pearl and Reed (1920) and improved by Davidson (1942, 1944), namely

\[
YH = \frac{AS}{1.0 + e^{(EY - ED(TD))}}
\]

was used to describe the data, where \(YH\) indicates the number of young hatched, \(AS\) represents the maximum number of eggs laid by each individual female, \(TD\) represents the accumulative number of
Figure 15. The accumulative mean number of young hatched (± 1 SE) from eggs laid by females of the five species of Gerris. The logistic curve described in the text was used in each case to describe the data, which is plotted against accumulated degree-days above each species' temperature threshold, as derived in Fig. 14.
**G. incurvatus (OVERWINTERED)**

![Graph showing the degree-days for overwintered G. incurvatus](image)

ED = 0.0299

---

**G. incurvatus (SUMMER)**

![Graph showing the degree-days for summer G. incurvatus](image)

ED = 0.0279
G. incognitus (OVERWINTERED)

G. incognitus (SUMMER)
Table 5. The temperature threshold values for each of the five species below which growth ceases.

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature (°C.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. incognitus</td>
<td>9.3</td>
</tr>
<tr>
<td>G. notabilis</td>
<td>10.3</td>
</tr>
<tr>
<td>G. remigis</td>
<td>12.4</td>
</tr>
<tr>
<td>G. incurvatus</td>
<td>12.6</td>
</tr>
<tr>
<td>G. bueno</td>
<td>12.9</td>
</tr>
</tbody>
</table>
degree-days above the threshold for that species, $EY$ indicates the relative position of the origin of the curve on the abscissa, and $ED$ determines the slope of the curve. The usefulness of this curve in quantitative biology has been demonstrated by several investigators (Davidson, 1944; Lamb, 1961; Trpis, 1972). Table 6 presents the values of the unknowns in the equation. $G. \text{remigis}$ and $G. \text{incognitus}$ have a total fecundity about half that of the other species. Whether the individuals in the bivoltine species had just emerged from overwintering or had just matured as the first generation females, affected the fecundity only slightly, although in all species, the first generation females produced on the average fewer young if those individuals which did not breed are included. There was considerable variation in the fecundity of the first generation females, as shown by the relatively large standard errors. This variability was most pronounced in $G. \text{incognitus}$ where only three of the seven females produced eggs. Thus not all of the individuals of $G. \text{incognitus}$ breed the year they emerge. Further, the fecundity of those $G. \text{incognitus}$ females that did breed was about twice that of overwintered females. Hence the net production of young by the summer population may be identical to that of the spring population. Greater numbers of young from the summer generation adults were also evident in $G. \text{buenoi}$ and $G. \text{incurvatus}$. In these two species the summer morph was apterous or shortwinged, whereas the overwintering females were macropterous.

It will be noted in Table 6 that the iterative number of
Table 6. The values of the unknowns in the equation
\[ Y_H = \frac{\text{AS}}{1.0 + e^{(E_Y - E_D (T_D))}} \]
used to describe fecundity in Fig. 19, where \( Y_H \) = the accumulative number of young hatched, \( AS \) = the maximum number of eggs a laid by a female gerrid in a season, \( TD \) = the accumulative number of degree-days above that species' minimum temperature threshold for growth, and \( E_Y \) and \( E_D \) are constants.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Equation constants</th>
<th>TD</th>
<th>Observed mean AS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>AS    EY    ED</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Over-wintered</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>females:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. notabilis</td>
<td>18</td>
<td>200.7  3.30  0.0187</td>
<td>294.8</td>
<td>203.3 ± 23.2</td>
</tr>
<tr>
<td>G. renigis</td>
<td>21</td>
<td>95.5   2.42  0.0205</td>
<td>225.5</td>
<td>98.0 ± 13.6</td>
</tr>
<tr>
<td>G. buenoi</td>
<td>21</td>
<td>152.2  2.47  0.0237</td>
<td>197.9</td>
<td>152.7 ± 10.6</td>
</tr>
<tr>
<td>G. incurvatus</td>
<td>21</td>
<td>120.7  2.41  0.0298</td>
<td>155.4</td>
<td>122.8 ± 7.0</td>
</tr>
<tr>
<td>G. incognitus</td>
<td>21</td>
<td>70.6   2.58  0.0228</td>
<td>211.4</td>
<td>72.6 ± 9.7</td>
</tr>
<tr>
<td>Summer females:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. buenoi</td>
<td>14</td>
<td>145.4  3.00  0.0182</td>
<td>285.6</td>
<td>143.1 ± 15.1</td>
</tr>
<tr>
<td>G. incurvatus</td>
<td>9</td>
<td>110.3  2.86  0.0279</td>
<td>180.3</td>
<td>112.7 ± 18.0</td>
</tr>
<tr>
<td>G. incognitus</td>
<td>7</td>
<td>48.4   1.93  0.0160</td>
<td>258.6</td>
<td>49.1 ± 30.6</td>
</tr>
</tbody>
</table>
degree-days required for the hatching of 90% of the average total number of young produced per female is greater for the first generation females than it is for the overwintered females. This may indicate that the former are acclimated to the higher temperatures that prevail in the summer.

A few first generation females raised in the laboratory provided some indication of the time required for these insects to produce young following the moult to the adult. Young hatched from eggs laid by one female *G. incurvatus* and two *G. buenoi* required on average 258.7 (S.E. = 1.3) degree-days following their moult to the adult.

**DISCUSSION**

Previous to this study, there have very few detailed published papers on gerrid species studied over the whole season. Kaufmann (1971) stated that *G. rufoscutellatus* in Alaska is univoltine, with the overwintering adults emerging in late May, and the new adults appearing in mid-July and then disappearing in late September - mid-October. Brinkhurst (1966) studied *G. najas* in Britain and observed basically a similar life cycle of this univoltine species.

To date, the most detailed study of life cycles in *Gerris* has been by Vepsalainen (1971c) on *G. odontogaster* in southern Finland. Although primarily concerned with the factors influencing wing polymorphism, he described the life cycle of
this bivoltine species in detail and showed that it is rather similar to that of *G. buenoï* studied herein. However, as *G. odontogaster* was the only gerrid typically present in the study area, interspecific interactions were not considered by Vepsäläinen (1971c). No study of gerrid life cycles to date has involved a comparative study of several species coexisting on the same body of water.

The results show that numerous differences exist among the five species of *Gerris* studied. Table 7 summarizes these differences and demonstrates clearly that they cannot be considered as ecological homologues. There are differences in almost every aspect studied.

Each species has its own microhabitat preference and although the species overlap in distribution, even to the extent that they can be all collected in the same sample, they do not always occur together. Each species was also shown to respond differently to temperature. The combination of these microhabitat differences and the temperature differences provide a clear basis for ecological separation of the species. They do not occupy the same niche and thus do not prove an exception to the Coexistence Principle.

A relation between morphology and microhabitat is suggested in the present study. *G. incurvatus*, for example, is typically found furthest offshore on open water and has relatively long legs, and this would seem an adaptation to rowing. As discussed by Brinkhurst (1960), an increase in the surface area of the
Table 7. A summary of the biologies of each of the five species of Gerris studied.
<table>
<thead>
<tr>
<th>Microhabitat</th>
<th><em>G. notabilis</em></th>
<th><em>G. remigis</em></th>
<th><em>G. incognitus</em></th>
<th><em>G. incurvatus</em></th>
<th><em>G. bueno</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ponds, lakes; inshore; clean water surface</td>
<td>Streams</td>
<td>Ponds, lakes; inshore; cluttered water surface</td>
<td>Ponds, lakes; offshore; clean water surface</td>
<td>Ponds, lakes; inshore; clean water surface</td>
</tr>
<tr>
<td>Size</td>
<td>Large</td>
<td>Large</td>
<td>Small</td>
<td>Small</td>
<td>Small</td>
</tr>
<tr>
<td>Leg length</td>
<td>Long</td>
<td>Normal</td>
<td>Short</td>
<td>Long</td>
<td>Normal</td>
</tr>
<tr>
<td>(relative to weight)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant morphs</td>
<td>Macropters</td>
<td>Apters</td>
<td>Apters</td>
<td>Spring, Fall: macropters; Summer: micropters</td>
<td>Spring, Fall: macropters; Summer: apters</td>
</tr>
<tr>
<td>Generations</td>
<td>Univoltine</td>
<td>Univoltine</td>
<td>Bivoltine</td>
<td>Bivoltine</td>
<td>Bivoltine</td>
</tr>
<tr>
<td>Average generation duration to end of egg-laying (degree-days)</td>
<td>1045</td>
<td>900</td>
<td>924</td>
<td>789</td>
<td>844</td>
</tr>
<tr>
<td>Spring emergence</td>
<td>Late April</td>
<td>February</td>
<td>March</td>
<td>Late April</td>
<td>Late April</td>
</tr>
<tr>
<td>Chorionated eggs first present</td>
<td>Mid-May</td>
<td>April</td>
<td>April</td>
<td>Mid-May</td>
<td>Mid-May</td>
</tr>
<tr>
<td>Fall disappearance</td>
<td>Early Sept.</td>
<td>Late October</td>
<td>Late Sept.</td>
<td>Early Sept.</td>
<td>Late Sept.</td>
</tr>
<tr>
<td>Average number of eggs hatched per female</td>
<td>203</td>
<td>98</td>
<td>67</td>
<td>120</td>
<td>149</td>
</tr>
<tr>
<td>Minimum temperature for growth (°C.)</td>
<td>10.3</td>
<td>12.4</td>
<td>9.3</td>
<td>12.6</td>
<td>12.9</td>
</tr>
<tr>
<td>Optimum temperature for growth (°C.)</td>
<td>26°</td>
<td>22</td>
<td>26°</td>
<td>22</td>
<td>22</td>
</tr>
<tr>
<td>Relative effect of temperature on growth (slope)</td>
<td>Moderate</td>
<td>Pronounced</td>
<td>Slight</td>
<td>Moderate</td>
<td>Pronounced</td>
</tr>
</tbody>
</table>
tarsus (the only portion of the leg to actually come in contact with the water) compensates for the increased weight of the larger species, with an increase in length of the femur and tibia having no effect. This increase will have an effect on the maximum speed with which the gerrid can move, however, as the main retractor muscle inserts on the fulcrum of the limb (the trochanter) and hence its contraction is magnified by the length of the leg. A longer stride is thus possible, thereby allowing the gerrid to move faster. This would appear to disagree with the observation of no significant difference in stride length between the small species (Section 3), but under the conditions by which stride length was measured, all the gerrids were moving slowly and it is felt that any difference would not necessarily be apparent. A noticeable difference was observed between the large and small species, with stride length directly proportional to leg length.

*G. buenoi* in contrast possesses short legs and is typically found inshore amongst the reeds and grasses. In this microhabitat, long legs would hinder movement rather than help owing to the often dense vegetation.

*G. notabilis* would appear to be the exception to the above, as it possesses relatively long legs for its size and yet often inhabits areas of dense vegetation. Here, though, it seems that selection has favoured long legs for mating behaviour. During the mating behaviour, the sexes of *G. notabilis*, like the species of *Rhagadotarsus* studied by Wilcox (1972) in Australia, communicate with surface waves (signals). The males of *G.*
notabilis in particular produce waves, apparently by vibrating their body vertically while maintaining their legs stationary, the result being scores of tiny waves which radiate outwards. Vertical movements of the forelegs also on occasion seem to be used to produce signals. Since the males typically initiate the mating behaviour, vibrating to any gerrid which approaches, and since this species is unique among those studied in that the legs of the male are longer than those of the female, it seems that the production and perhaps reception of these waves has been the main determining factor regarding leg length. The exact microhabitat which this species prefers seems to be slightly further offshore than that preferred by G. buenoi, and this may be a result of its greater leg length.

G. remigis and G. incognitus are both typically apterous and do not possess long legs for their sizes. G. remigis is a riverine species, preferring an environment with currents, whereas G. incognitus seems to prefer the extreme inshore areas and cluttered water surfaces. G. remigis has often strong currents to contend with and G. incognitus often cannot slide on the water surface owing to its cluttered nature and hence must jump, which requires the flinging of its body into the air. Brinkhurst (1960) has shown that in short-wing G. lacustris, there was a greater than normal development of the mesothoracic limb retractor muscles filling the space normally occupied by the flight muscles. In G. remigis and G. incognitus, it seems a reasonable assumption that here too loss of the flight muscles has resulted in an increase in size of the mesothoracic limb
The temperature differences noted with the five species, together with apparent species interaction result in a temporal separation of the species with respect to their population peaks. *G. incognitus* breeds in mid-spring, as temperature has relatively little effect on its rate of development. Whether or not a second generation is present seems to depend on the accumulated number of degree-days. This species has the lowest temperature threshold (9.3°C.) for development of the species studied. However, the average generation length in this species is ca. 924 degree-days, ca. 80-125 more than is required by *G. buenoi* and *G. incurvatus* respectively.

*G. buenoi* and *G. remigis* also breed in mid-spring, and this probably is a result of a low optimum temperature for growth (22°C.). Both species have a relatively high minimum temperature for growth (12.9°C. and 12.4°C. respectively), which indicates that these two species are relatively more stenothermal than the other species. This is supported in the case of *G. remigis* by data on the effect of temperature on both food consumption and preferred microhabitat. The maximum food consumption per day was observed to be at a temperature of ca. 30°C. (see Section 2) and on a water temperature gradient, a temperature of ca. 20°C. was preferred (see Section 2). *G. remigis* is univoltine, but being the only species studied which can successfully inhabit streams, it is isolated from the other species spatially. In this species there is thus little interspecific interaction and the life cycle is spread over the summer. *G. buenoi*, however,
is bivoltine and inhabiting ponds, is influenced by the other species present. Since it can tolerate low temperatures, it breeds early in the year and again later in the fall and thus avoids much interaction with the other species.

The peak breeding periods of *G. incurvatus* and *G. notabilis* are not in the spring but in early summer. In *G. notabilis* this seems to be the result of a temperature-activated switch mechanism which must be turned on before breeding can commence. Temperatures averaging >15°C. for a few days seem to be required to initiate breeding and as these weather conditions are not normally present in the study area until mid-June, breeding of this univoltine species typically peaks in late June or July. Both *G. incurvatus* and *G. notabilis* have relatively high optimum temperatures for growth (>26°C.) and this also seems to be related to when they breed. *G. incurvatus*, although it commences breeding when *G. buenoi* does, is not so tolerant to the low spring temperatures, and this appears to delay the period of peak breeding in *G. incurvatus* sufficiently to explain the difference between them.

Thus, the bivoltine pond species breed in the spring and fall and the univoltine *G. notabilis* breeds in the summer, although considerable overlap occurs between the species. Whether these differences in voltinism are a result of interactive processes or not is not clear as the evolutionary history of the species is unknown. However, it is of interest to note that such temporal differences do exist.
Both spatial and temporal separation of the five species of *Gerris* thus exist, indicating that the water surface habitat is perhaps not quite as simple as previously thought. A number of microhabitats are discernable and in this study area at least, perhaps the maximum number of species that can coexist do so.
INTRODUCTION

Poikilothermic animals such as insects by definition have body temperatures largely determined by the external environment. A few large insects such as the bumble bee Bombus vagans (Heinrich, 1972), the sphinx moth Mandusa sexta (Heinrich and Casey, 1973) and the giant silkmoth Hyalophora cecropia (Heath et al, 1971) can adjust heat production and heat loss. Gerrids, like most insects, however, cannot significantly alter their body temperatures endothermically and must rely on adjustments in location to regulate body temperatures. To maximize reproduction, a species should attempt to locate and occupy those parts of its habitat that are at an optimum temperature, since any deviation away from this could adversely influence metabolism and hence reproductive capabilities. Only through maintaining themselves in such a microhabitat can they maximize their reproductive potential.

Closely related species living sympatrically often specialize differently so as to minimize competitive interactions. This separation may be spatial, temporal, or in the manner in which they feed or reproduce. Temperature responsiveness indirectly or directly can influence all these parameters. Different optimal temperatures have been demonstrated to effectively separate closely related species. The 17-year periodical cicadas Magicicada cassini, M.
septendecium and M. septendecula (Heath et al, 1971) and the wolf spiders Pardosa sierra and P. ramulosa (Sevacherian and Lowrie, 1972) are both examples of coexisting, closely related species separated by different temperature tolerances.

Since temperature seems to affect differently the five species of Gerris studied (see Section 1), the aim here was (a) to investigate the temperature tolerances of each gerrid species, (b) see if the different species actively select different temperatures and if so, (c) to determine if temperature preferences of the species correlate with those microhabitat temperatures typically encountered by each species in the field.

MATERIALS AND METHODS

Two troughs 122 cm long, 19 cm wide and 10 cm deep made of aluminium sheeting contained water to a depth of 1 cm. Both troughs rested on partitions in a larger tank (216 cm long, 43 cm wide and 15 cm deep) filled with water to the height of the partitions. The aluminium troughs were thus in contact with the water surface of the larger tank for their entire length. One end compartment of the larger tank contained a copper heating coil carrying hot water and the other end had a similar coil carrying a refrigerant: the cold coil was connected to a Haake circulating and thermostated pump, Model K41 (Haake Inc. Ltd., Karlsruhe, West Germany) and the hot coil was connected to a hot water tap. By this arrangement a non-continous water
temperature gradient was established in the larger tank (owing to the partitions) and a continuous water temperature gradient was set up in both the aluminium troughs, which lacked partitions. Owing to water stratification, gradients could only be established in water a few centimeters deep, but this was sufficient since gerrids are surface water bugs and often occur on very shallow water.

The troughs were illuminated by two, three-foot, cool-white fluorescent tubes placed end-to-end. The whole apparatus was surrounded by black plastic sheeting (2 mil) with vents to allow air circulation. One-way mirrors allowed observation of the gerrids and prevented sudden movements by the observer from disturbing them. Room temperature was 20-22°C throughout the study.

Each trough was marked out into sections and at the commencement of each set of observations, the water temperature in each was measured with a thermister temperature recorder (Yellow Springs telethermometer, Model 44TD). At the termination of all the observations, the water temperature in each section was rechecked and the air temperature 3 mm above the water surface, the temperature at the level of the bodies of the gerrids, were measured with a microthermocouple (see below). These data allowed determination of both the air and water surface temperatures experienced by the gerrids in each section. As the temperature range which was observed in the field during the summer exceeded that which could be established at any one time in the troughs, two temperature gradients were used: a
"cold" gradient (ca. 10-25°C.) and a "hot" gradient (ca. 18-35 °C.). Adult gerrids of each of the five species for study were collected in the field in late June and individuals were taken randomly for testing. Gerrids of each species were observed twice on each gradient and twice on a control gradient which had a uniform temperature in all sections. Gerrid introductions onto the gradient were at opposite ends of the gradient in each pair of observations. Following introduction, the gerrids were left 15 minutes to acclimate. The location of each gerrid in the gradient was then recorded. Recordings were repeated every minute for six, eight-minute observation periods, with five-minute time-out periods separating each observation period. A total of 288 recordings were thus obtained for each species in each of the gradients.

For measurement of body temperatures of all five species in the field, adult gerrids were taken and a copper-constantan thermocouple made from 0.0508 mm diameter wire (Esch, 1960) was inserted into the body through the anus. The thermocouple wires, attached to a stiffer wire bent at right angles to the insect, were connected to a minithermocouple potentiometer (Doran Instrument Co. Ltd. Stroud, England) for measurement of body temperatures. The stiff wire was also used to restrain the insect in one location and position it just above the water surface, the exact height being controlled by use of a micromanipulator. Measurements were taken 3 minutes after insertion of the thermocouple or movement of the gerrid to a new location.
The field data of adults was collected at Marion Lake on July 5 and July 21, 1972 between 1:00 and 2:30 p.m. Measurements were taken on insects placed both in the sun and in the shade.

RESULTS

When first introduced onto the gradient, some of the gerrids explored the gradient, moving back and forth in the trough. Within fifteen minutes, most had settled down and their behaviour consisted of remaining stationary for a few minutes followed by relatively short periods of activity. In general, *G. remigis* moved considerably more than the other species. The number of gerrids of each species in each section in each of the three gradients (control, hot and cold) is shown in Fig. 16. Observations where gerrids were introduced into opposite ends of the same temperature gradient have been summed.

Individuals of each of the species demonstrated a marked preference for the ends of the troughs as shown by their preferences in the control gradient. This fact was used as an indicator on the experimental gradients to detect what temperatures were avoided, and hence which were tolerated by each species. If the gerrids were predominantly observed in the middle regions of the gradient, this was taken to indicate avoidance of the temperatures at the ends of the gradient, and if both ends of the gradient were equally preferred, then
Figure 16. The number of gerrids of each of the species in each section on the water gradients studied. • = temperature of each section.
G. buenoii

CONTROL

HOT

COLD

NUMBER

TEMPERATURE (°C)

GRADIENT (CM.)
The diagram shows the distribution of G. remigis across different temperature gradients.

- **CONTROL**
  - The bars indicate the number of G. remigis at each gradient level.
  - The percentage decreases as the gradient increases.

- **HOT**
  - The bars and points show a linear increase in temperature from left to right.
  - The number of G. remigis decreases as the temperature increases.

- **COLD**
  - The bars and points reflect a decrease in temperature from left to right.
  - The number of G. remigis increases as the temperature decreases.

The x-axis represents the gradient (cm), and the y-axis represents the number and temperature (°C).
temperatures in the gradient were assumed to have little effect on distribution.

G. notabilis preferred the warm end of the cold gradient and on the hot gradient avoided both ends. The sections on the hot gradient with the greatest number of gerrids present had a temperature of from ca. 24°C. to 30°C. G. remigis avoided the coldest end on the cold gradient and the hottest end on the hot gradient, preferring temperatures from ca. 16°C. to 22°C. G. incognitus avoided only the hot end of the hot gradient, and so would seem to be a rather eurythermal species, tolerant of temperatures from ca. 14°C. to 29°C. G. incurvatus avoided the cold end of both the cold and hot gradients and preferred temperatures from ca. 25°C. to 31°C. Finally, G. buenoi avoided the cold end of the cold gradient and the hot end of the hot gradient, indicating a preference for temperatures between ca. 24°C. and 30°C. Thus, the different species have different temperature preferences.

The measurement of air temperatures in each section 3 mm above the water surface were found to be very similar to water temperatures (Fig. 17). Thus, if air temperature is selected by the gerrid rather than water temperature, the results will not be greatly different.

Observations in the field (Table 8) indicated that the body temperature of a gerrid is influenced by solar radiation. Measurements demonstrated that in the shade, the body temperature was virtually identical to that of the surrounding
Figure 17. The air and water temperatures of each section on the hot and cold gradients studied. Air temperatures are 3 mm above the water surface. ° = water temperature; • = air temperature.
Table 8. Field temperature measurements of gerrids on a sunny day with a microthermocouple inserted into the body. Air temperatures were 3 mm above the water surface and water temperatures were at the water surface.

<table>
<thead>
<tr>
<th>Species</th>
<th>Time (pm)</th>
<th>Air temperature (°C.)</th>
<th>Water temperature (°C.)</th>
<th>Gerrid temperature (°C.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Shade</td>
<td>Sun</td>
<td></td>
</tr>
<tr>
<td>July 5, 1972</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. incognitus</td>
<td>1:00</td>
<td>27.0</td>
<td>29.4</td>
<td>27.2</td>
</tr>
<tr>
<td>G. remigis</td>
<td></td>
<td>27.6</td>
<td>29.4</td>
<td>27.6</td>
</tr>
<tr>
<td>G. incurvatus</td>
<td></td>
<td>28.0</td>
<td>30.5</td>
<td>28.1</td>
</tr>
<tr>
<td>G. incognitus</td>
<td>2:30</td>
<td>28.3</td>
<td>31.3</td>
<td>28.4</td>
</tr>
<tr>
<td>July 20, 1972</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G. incognitus</td>
<td>2:30</td>
<td>23.2</td>
<td>26.6</td>
<td>23.5</td>
</tr>
<tr>
<td>G. remigis</td>
<td></td>
<td>24.0</td>
<td>27.7</td>
<td>24.2</td>
</tr>
<tr>
<td>G. incurvatus</td>
<td>4:00</td>
<td>22.7</td>
<td>27.2</td>
<td>22.9</td>
</tr>
</tbody>
</table>
air, i.e. the air 3 mm above the water surface. In the sun on July 5, 1972, however, body temperatures averaged 3.9°C. warmer than the air 3 mm above the water surface, and on July 20, 1972, body temperatures averaged 5°C. warmer than the air at this level.

DISCUSSION

One of the greatest problems in experiments with gradients is setting up and determining the initial distribution of animals on the gradient. The method described in this study of using the controls to determine initial distributions has been found appropriate in previous studies (Sevacherian and Lowrie, 1972; Yinon and Shulov, 1970). The selection then of areas in experimental temperature gradients other than those preferred in the controls is taken to indicate that this selection is primarily a reaction to the temperature in the gradient.

In studies on terrestrial insects in temperature gradients, relative humidity in the different sections must be considered or responses on the gradient cannot be conclusively related to temperature. Since gerrids are found on the water surface, and since the water surface was used in this study, it is assumed that there is little or no humidity variation. Humidities were assumed high in every section of the gradient.

It should be noted that the gerrids used in this study were overwintered adults acclimated to late June temperatures.
Sevacherian and Lowrie (1972) noted that species of wolf spider of differing sex and age preferred different temperatures. In both wolf spiders studied, the immatures selected lower temperatures than did the males, which in turn selected lower temperatures than did the females. Since only unsexed adult gerrids of one age class were observed in this study, the temperature preferences suggested may not necessarily be representative of all gerrid instars and breeding states. However, Sevacherian and Lowrie (1972) did observe significant differences between the two species in all the age classes studied, which suggests that the same relative differences observed here between the species may apply regardless of instar and stage of development.

That gerrids in sunlight had higher temperatures than those in shade is as expected. Body temperatures of ca. 5°C above that of the ambient air when in the sun were also reported by Edney (1953) for the woodlouse Ligia oceanica. After discussing the effects of insolation on insects in general, Edney concluded that most insects in sunlight can be expected to undergo very considerable and rapid increases in temperature, as owing to their relatively water impermeable integument, evaporative water loss would be slight. The actual temperature attained by an insect depends on many factors. Body coloration, the intensity of radiation, the temperature and humidity of the air and its velocity all determine temperature.

That each gerrid species prefers a specific temperature range is not unexpected. That the range preferred by each
species can be correlated with the temperature that each species typically encounters in the field is of greater interest. Section 1 shows that the species have slightly different microhabitats: *G. remigis* prefers streams; *G. notabilis*, *G. incurvatus* and *G. buenoii* prefer open water on lakes and ponds; and *G. incognitus* prefers algae-covered water by the edge of ponds and on slow-moving streams. Each of these three types of microhabitat has certain temperature characteristics. Water movement in streams prevents thermal stratification and as a result, surface water temperatures on streams are typically cooler than those on still water where thermal stratification can occur. That *G. remigis* preferred the coolest temperatures of all the species would thus seem an adaptation to stream existence.

The open water areas on ponds and small lakes show thermal stratification, with the surface waters often becoming quite warm. This is typically most evident in the shallow areas near the water-edge and in the areas studied, the temperatures of still surface water often approached 30°C. on a sunny day in mid-summer. The three open water pond species prefer temperatures in this range, in agreement with the temperatures encountered in their microhabitat.

Finally, the algae-covered water microhabitat is typically found close to shore in the shallows, and in pools with only a few centimeters of water. Such habitats, like the terrestrial habitat, typically experience a wide range of temperatures in clear weather, as unlike larger bodies of water, there is no
great volume of water to heat up during the day and cool off at night. Temperatures thus fluctuate greatly, making the temperature of this microhabitat the most variable of all. That *G. incognito*us seems to tolerate the widest range of temperatures is thus perhaps not surprising.

On the basis of the results obtained herein and previously (see Section 1), it is now possible to establish some of the temperature zone characteristics of the five species following the scheme in Imms (1937). Table 9 presents these comparative data.

It is obvious that the species of *Gerris* studied differ in their responses to temperature. The responses are seen to relate closely to the microhabitat preferred by each species. The temperature preference differences may be involved in microhabitat recognition and selection by the gerrids and may thus be important in their ability to coexist. A preference for cool water might explain partly why *G. remigis* avoids ponds and lakes in mid-summer, when the temperatures there are relatively high. This is supported by observations of *G. remigis* on Marion L. in 1971, where in early spring the species ranged over more of the lake. In mid-summer however, it was confined to a cold spring upwelling area where the water temperature averaged ca. 20°C.: the gerrids apparently became cut-off and isolated there as the lake water warmed during the summer to around 25°C. The fact that *G. remigis* also prefers moving water further serves to isolate this species from the others that occur in south-western British Columbia.
Table 9. The temperature zone characteristics of the five species of *Gerris* studied.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Zone of preferred temperature (°C.)</th>
<th>Threshold temperature for growth (°C.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. remigis</em></td>
<td>Stream</td>
<td>16-22</td>
<td>12.4</td>
</tr>
<tr>
<td><em>G. notabilis</em></td>
<td>Open water</td>
<td>25-36</td>
<td>10.3</td>
</tr>
<tr>
<td><em>G. incurvatus</em></td>
<td>Open water</td>
<td>25-31</td>
<td>12.6</td>
</tr>
<tr>
<td><em>G. bueno</em></td>
<td>Open water</td>
<td>24-30</td>
<td>12.9</td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>Inshore</td>
<td>14-29</td>
<td>9.3</td>
</tr>
</tbody>
</table>
Where the gerrid species inhabit the same microhabitat and the zone of preferred temperature is the same, the thresholds of development would be expected to be somewhat different. This was observed to be the case between G. notabilis and G. buenoi, two species which prefer the same temperature range and have overlapping distributions in the field situation. This may be important in their ability to coexist as in other studies such as those of Heath et al. (1971) and Sevacherian and Lowrie (1972), it was found that temperature responses differed between closely related sympatric species.
INTRODUCTION

To date, quantitative studies on the food consumption of predatory Hemiptera have been restricted to a few species with the pentatomid Podisus maculiventris perhaps being most extensively studied (Morris, 1963; Mukerji and LeRoux, 1969a, 1969b; Gallopin and Kitching, 1972). Although Podisus is an important predator of crop pests (Morris, 1963; LeRoux, 1964), no attempt has been made to incorporate laboratory data into the context of the role Podisus plays in its habitat. Instead, the relationship between food consumption and growth has been emphasized.

Similarly, prey consumption behaviour of the mantid (Holling, 1966) and the predatory mite Amblyseius largoensis (Sandness and McMurtry, 1972) have been studied, but to date no attempt has been made to incorporate these data into the context of how the animal is adapted to its environment in the field situation. Indeed, owing to the complexity of their terrestrial habitats, such a task is extremely difficult.

In an attempt to better understand the interactions between predators, and in particular perhaps the significance of cannibalism in insect population regulation, an experimental components analysis type of approach (Holling, 1966) has been adopted to investigate interactions between gerrid species in
the field. An essential set of parameters in this approach are the feeding characteristics of the animal being investigated. The results of this section, therefore, besides describing for the first time in a quantitative manner food consumption in this family, are primarily intended as a contribution to the model.

MATERIAL AND METHODS

1. GENERAL METHODS

The five gerrid species described previously which occur together on Marion Lake in the University of British Columbia Research Forest at Haney, B.C. were used in this study. Adults were determined using the key in Scudder (1971), and larvae were identified according to data in Scudder and Jamieson (1972). The various instars of the five species were either raised in the laboratory or obtained from the field. Generally, the first four larval instars were raised in the laboratory. Owing to the rather high mortality at the fourth and fifth moults, it was often necessary to collect the fifth larval instars and the adults in the field. To some extent this was an advantage in that it probably reduced any possible effects of nutritional deficiencies on body size and hence gut size.

When collected in the field, if the temperatures differed from that in the laboratory, a three day acclimation period was
provided before testing commenced. Insects were held in constant temperature cabinets or controlled environment rooms at the required temperature.

Adult vestigial winged *Drosophila melanogaster* raised on standard *Drosophila* culture media in the laboratory were used throughout this study both as an experimental food and a standard food. The experimental food consisted of flies raised under relatively uncrowded conditions so as to standardize fly size as much as possible. Size variability did exist, as the sex of the flies was not determined prior to feeding and the male flies were usually noticeably smaller than the female. However, as it was not the number of flies but rather the total biomass eaten which was measured, these differences were not considered important.

In all feeding experiments, an excess of food was provided. Testing, unless otherwise noted, took place in round plastic containers 9.5 cm in diameter and 7 cm deep. However, fifth instar and adult *G. notabilis* and *G. remigis*, owing to their large size, were tested in containers 26 cm in diameter and 9 cm deep. Regardless of container size, water depth was 1 to 3 cm and the water surface was kept clean. Temperature, again unless otherwise noted, was maintained at 26°C. and relative humidity at 20% during both starvation and testing. The photoperiod schedule was 16 hr light: 8 hr dark throughout the study.

Gerrid feeding behaviour, once the animal has captured a food item, consists of piercing the prey with its proboscis, and
then sucking up the fluids of the prey. Since feeding usually occurs on the water surface, the possibility of water entry into the prey following termination of feeding exists; simply weighing the prey to determine biomass ingested was not acceptable. In order to overcome this, the following procedure was followed.

Initial measurements on the experimental flies showed that their water content was consistently 74% (S.E. = ±0.16), the dry weight of the flies thus being 26%. This dry weight figure therefore was assumed to apply to all flies utilized, and is the theoretical value cited below. Thus, in all studies thereafter, the wet weight of CO₂-asphyxiated flies was measured, and these insects were then frozen until required.

Following presentation to the gerrid, the flies were collected and dried (24 - 48 hours) in an oven at 95°C. to a constant weight. All weighing was done on a Mettler Grammatic Balance, Model 758 (Mettler Instrument Corp., Hightstown, N.J.) accurate to ± 0.002 mg.

After drying, the flies were reweighed, and any differences between this weight and 26% of the initial wet weight of the flies (theoretical dry weight) was considered to be the amount eaten. However, it was found that this could only be applied if the flies were removed immediately after feeding. If the flies were left with the gerrid for more than a few minutes, errors arose. These errors occurred both as a result of loss of body contents into the water in the container and perhaps as a result
of breakdown of body contents into more volatile compounds as a result of decomposition processes. These would then be lost on drying.

Since the experimental procedure often involved leaving flies on the water surface for some time, it was important to obtain a measure of possible errors over known periods of time. Table 10 presents data relevant to the percentage losses over time. From these data modified theoretical dry weights were calculated and the difference between this and the final dry weight was considered as the amount eaten.

It follows then that the amount eaten was the loss in dry weight of the flies. Since it is impossible to use this measure to determine the maximum gut capacity of the gerrids, then some conversion is required. If it is assumed that functionally the fluids of the ingested fly are homologous, then knowing the water content of the fly, it is possible to use a correction coefficient. For the relative values used in this study, such a coefficient is unnecessary and is not used. Nevertheless, to permit calculation of maximum gut capacity for comparison with other studies, if it is assumed arbitrarily that 25% of the water in the fly is unavailable to the gerrid, then \(0.740 - 0.185\) = 55.5% of the total weight of the fly is ingestable water. Experiments in which 20 starved gerrids were each fed separately one weighed fly indicated that 24.5% (S.E. = ±1.81) of the theoretical dry weight of the fly may not be utilized by the gerrid. Thus, \(0.26 - 0.064\) = 19.6% of the dry weight of the fly may be ingested. The coefficient therefore is \(19.6\) +
Table 10. Theoretical dry weight coefficients of *Drosophila* wet weights following various time periods with gerrids. * = environmental cabinet (no humidity control); ** = environmental room (R.H. = 20%); C = the theoretical dry weight coefficient (it can be calculated from the linear regression, C = 25.4 - 0.11(temp.) for any temperature).

<table>
<thead>
<tr>
<th>No. flies (groups of 4 flies)</th>
<th>Temp. (°C.)</th>
<th>Time period (hr)</th>
<th>Average water content (%)</th>
<th>% difference from expected 26% dry matter</th>
<th>Theoretical dry weight coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>24</td>
<td></td>
<td>-</td>
<td>74.0 ± 0.16</td>
<td>0.26</td>
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<tr>
<td>40</td>
<td>26</td>
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<td>8.15</td>
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<tr>
<td>20</td>
<td>26</td>
<td>2</td>
<td>&quot;</td>
<td>9.4</td>
<td>0.24**</td>
</tr>
<tr>
<td>20</td>
<td>26</td>
<td>3</td>
<td>&quot;</td>
<td>7.4</td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>26</td>
<td>24</td>
<td>&quot;</td>
<td>17.2 ± 1.0</td>
<td>0.215**</td>
</tr>
<tr>
<td>20</td>
<td>10</td>
<td>24</td>
<td>&quot;</td>
<td>12.6 ± 0.6</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>20</td>
<td>24</td>
<td>&quot;</td>
<td>18.6 ± 0.5</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>32</td>
<td>24</td>
<td>&quot;</td>
<td>22.0 ± 0.6</td>
<td></td>
</tr>
</tbody>
</table>
55.5)/19.6 = 3.83; 75.1% of the original wet weight of the fly is thus potentially ingestable.

2. SATIATION TIME

A. Effect of gerrid size

To determine the effect of gerrid size on the duration of feeding, immature and adult G. remigis and G. incognitus taken one day after ecdysis were each starved 48 hr. These species were chosen since they represent all the gerrid sizes found in the study area. Forty specimens in each instar were divided into four groups of ten gerrids. Each of these four groups was allowed to feed for different periods of time within a four hour interval. Preliminary observations indicated that no matter how long a gerrid was deprived of food, satiation in the first feeding could be achieved in less than four hours (see below).

B. Effect of starvation

Similar tests on first instar, third instar and male G. remigis and on male G. incognitus were undertaken to ascertain the effect of length of food deprivation time on the duration of the feeding period. Three sizes of G. remigis were studied so as to determine the effect of size within a species. The previous test would not be applicable if, for example, digestive
rates varied with gerrid size.

Figure 18 illustrates the criterion for satiation of a third instar *G. remigis* starved for 20 hr. In this example, 80 gerrids divided into eight groups of ten were used to demonstrate the effect of feeding on amount eaten. In this case, satiation occurred after 2 hr of feeding, the nearest period to when the amount eaten leveled off. The high value after 4 hr of feeding is thought to represent another feeding bout.

In most tests, four time periods were sufficient to establish this curve for an instar at any level of starvation.

3. DIGESTIVE PAUSE

Four male and six female adult *G. remigis* were taken individually and starved for 48 hr. They were then observed continuously for 270 minutes in the presence of an excess number of live *Drosophila*. At each minute interval, it was recorded whether the gerrid had fed (impaled a *Drosophila* on its proboscis for at least 20 seconds) or simply killed the fly. No difficulty was encountered operationally in deciding whether feeding did indeed occur, as usually, feeding on any particular fly was of several minutes' duration.
Figure 18. The effect of feeding time on the amount eaten by a third instar *G. remigis* starved for 20 hours.
4. FOOD DEPRIVATION

The effect of length of food deprivation period on the amount eaten was determined for first instar and third instar *G. remigis*, and for the males of all five species. Three sizes of *G. remigis* were studied so as to determine the effect of size within a species and the adults of all the species were studied to determine if species-characteristic differences existed. Since this study was done in the spring and early summer, only males were used, as it was felt that oocyte maturation and egg laying by the female might result in feeding variability during the course of the study. Individual male gerrids were not used for longer than three weeks, as it was felt that at the non-fluctuating and relatively high temperature under which the gerrids were maintained, aging might begin to influence feeding behaviour: in the study area, these gerrids normally lived until mid-July.

Starvation in the first and third instars commenced one day following eclosion or ecdysis, and since the mean stadium length for the first and third instars was approximately five days, depending on the food deprivation period, the same gerrid could be used in two separate tests. The male gerrids were used repeatedly, but at least one complete day in the presence of excess food separated tests. Feeding periods (time in the presence of food) were determined on the basis of the starvation tests (see above). Food deprivation intervals used were: 1, 2, 4, 6, 8, 12, 16, 20, 24, 32, 40, 48 and 72 hours.
5. MAXIMUM GUT CAPACITY

On the basis of the above studies which determined the time required to satiate gerrids depending on body size and length of food deprivation period, the amount of food that gerrids would voluntarily eat following maximum starvation was measured. The gut capacity of each instar of each of the five species was measured, with a sample size of not less than 18 for each species-instar. A food deprivation interval of 24 hr for larvae and 48 hr for adults was sufficient to attain maximum amounts ingested. Owing to the morphology and behaviour of gerrids, procedures to determine satiation such as touching the mouthparts with juices of the prey and then noting the response (Holling, 1966) were found impractical. They were also not felt to simulate realistically the conditions a gerrid would encounter in the field. Larvae were deprived of food commencing one day following eclosion or ecdysis, whereas adults (having moulted the previous fall) were used as they became available.

6. EFFECT OF TEMPERATURE ON FEEDING

The amount of food ingested per day by ten male gerrids of each of the five species under different temperature regimes was measured. Each gerrid was maintained in a separate container and was fed once daily. Testing took place in environmental cabinets without humidity control. Three days of acclimation followed by two consecutive days of testing were permitted at each temperature, with the temperature being changed (increased)
to the next temperature immediately following the second day of testing. Testing was undertaken at 3°C. intervals between 5°C. and 32°C., but as two environmental cabinets were available, the temperatures in each were staggered so that the temperature increase at one time for any group of insects was 6°C. G. remigis and G. incognitus were tested first starting at 5°C., as they emerge earliest from overwintering. Since the mean temperature seldom is below 8°C. in our study area when the other three species emerge, testing of those species commenced at 8°C. Regardless of species, no individual gerrid was tested at more than three temperature regimes so as to minimize aging effects which might introduce variability, especially at the higher temperatures. Thus, a complete change of animals occurred for the experimental run at 17°C. or 20°C.

7. VARIATION OF FEEDING DURING DEVELOPMENT

The amount of food ingested per day in laboratory reared gerrids was determined. Laboratory reared gerrids were used throughout so as to standardize feeding as much as possible. The five larval instars and adult of G. notabilis were studied. Feeding was once daily and regardless of gerrid size, the gerrids were maintained in the smaller plastic containers.

Owing to the relatively high mortality in the later moults and the duration of the experiment (53 days), this experiment involved a large number of gerrids. The amount eaten for each day is the mean of 10 observations. In the adult, feedings were
continued for 25 days following the final moult.

RESULTS

1. SATIATION TIME

The effect of gerrid size on the duration of the feeding period following starvation for 48 hr is shown in Fig. 19b. Since the lengths of the feeding periods were measured at half hour intervals, and the time at which satiation occurred was rounded off to the nearest half hour, the data in Fig. 19a represent the approximate values at which satiation is achieved. Nevertheless, it appears that for gerrids above about 10 mg wet weight, feeding time required to achieve satiation was between 2 and 2.5 hr. For gerrids below this weight, feeding time declined at a rate adequately described by a logarithmic function, with one hour required by the smallest gerrids tested.

Figure 19a shows the effect of food deprivation period on the duration of feeding period. Feeding periods of less than one hour duration were measured at quarter hour intervals, whereas those of longer duration were measured at half hour intervals. Logarithmic functions again seem to adequately describe the data. No noticeable difference in "best-fit" function existed between the regression for third instar G. remigis and the adult gerrids. Third instar gerrids, which have
Figure 19. The effect of (A) starvation and (B) gerrid size on the maximum duration of the feeding period. A. △ = first instar larva G. remigis; • = third instar larva G. remigis; ○ = adult male G. remigis and adult male G. incognitus. B. Starvation was for 24 hr (larva) and 48 hr (adult). • = G. incognitus; △ = G. remigis.
A

**WET WEIGHT (MG.)**

FEEDING PERIOD (HR.)

\[ y = -0.05 + 0.555 \log_e(X) \]

HOURS OF FOOD DEPRIVATION

B

**WET WEIGHT (MG.)**

FEEDING PERIOD (HR.)

\[ y = 1.58 + 0.294 \log_e(X) \]

0  12  24  36  48  60
a wet weight of 3.5 mg, respond to deprivation periods in a manner very similar to that of adult male *G. remigis*, which weigh 38.6 mg. A regression based on the pooled data can thus be used to describe the feeding characteristics. The result is basically in agreement with that observed in Fig. 19b, where it is only with the first and second instar larvae that a significant difference in feeding behaviour appears to exist.

2. DIGESTIVE PAUSE

In order to decide whether or not a significant amount of feeding did indeed occur, five consecutive minutes of either feeding or not feeding were used arbitrarily to delineate feeding bouts. Fig. 20 presents the recorded observations of *G. remigis* and Table 11 the length of consecutive feeding and non-feeding periods.

The initial feeding bout lasted on the average 147.4 minutes: this compares favourably with 2.5 hr predicted on the basis of the total amount ingested (Fig. 19b). It thus appears that, although the rate of ingestion may vary, continued ingestion occurs as long as the fly is impaled. Feeding bouts following this initial lengthy one were typically of short duration only, varying from 5 to 16.5 minutes, with a mean of 10.4 minutes. However, the periods between feeding bouts (digestive pauses) varied in length from 9 to 51.5 minutes. Whether or not this is a consequence of the experimental design, with the gerrids being completely starved before the study
Figure 20. The pattern of feeding activity over 4.5 hr as observed in ten individual *G. remigis* following starvation for 48 hr. Each vertical bar indicates that feeding occurred for at least 20 seconds in that minute period (the thick bars represent two, adjacent one-minute periods; owing to the scale, the bars may appear joined). m = male; f = female.
Table 11. Mean lengths in minutes of consecutive feeding and non-feeding periods (following 48 hr starvation) of *G. remigis* in the presence of an excess amount of food. + = time elapsed in period when observations were terminated. These values were not used in the calculation of the mean.

<table>
<thead>
<tr>
<th>Gerrid no.</th>
<th>Consecutive feeding bouts</th>
<th></th>
<th></th>
<th></th>
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<th></th>
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</tr>
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<tbody>
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<tr>
<td>2</td>
<td>92</td>
<td>11</td>
<td>21</td>
<td>18</td>
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<td>51.5</td>
<td>20.5</td>
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commenced, is uncertain. Nevertheless, under these conditions, which one might expect would maximize ingestion, the average digestive pause was 24.6 minutes.

It should be noted that in the experiments the gerrids seldom "ate" one fly completely, but rather every few minutes or so, shifted to a new fly. In contrast, when 20 starved gerrids were presented with only one fly each, the mean time of feeding from the fly was 14.8 minutes (S.E. = ±1.54 minutes). As a result, the total number of flies killed here was far in excess of that simply required to satiate the gerrid. However, field observations suggest that potential prey items in the wild are not likely ever to be as numerous and as readily available as the vestigial-winged *Drosophila* were in this study. Under normal conditions, gerrid utilization of each prey would probably be relatively complete, i.e. until either satiation of the gerrid was reached or until the prey was sucked dry.

### 3. FOOD DEPRIVATION

The effect of the duration of food deprivation (TF) on the weight of food required to satiate (or hunger) (H) for the gerrids tested is shown in Fig. 21. Table 12 summarizes the constants for the "best-fit" regression which fits the equation

\[ H = HK - BYe^{(A0(TF))} \]

where HK = the maximum amount of food the gut can hold, BY = HK
Figure 21. The effect of starvation on the amount eaten by the following gerrids; (a) first instar G. remigis; (b) third instar G. remigis; (c) adult male G. remigis; (d) adult male G. incognitus; (e) adult male G. notabilis; (f) adult male G. incurvatus; and (g) adult male G. buenoi. AD is the value of the slope, which functionally represents the rate of digestion in the equation

\[ H = HK - (BY)e^{AD(TF)} \]

which was used to describe the data. The middle regression represents the "best-fit", and the other two plus or minus one standard error of HK and AD.
A

FIRST INSTAR GERRIS REMIGIS

AMOUNT EATEN (µG)

AD = 0.169

HOURS OF FOOD DEPRIVATION

B

THIRD INSTAR GERRIS REMIGIS

AMOUNT EATEN (µG)

AD = 0.193

HOURS OF FOOD DEPRIVATION
C

MALE GERRIS REMIGIS

AMOUNT EATEN (µG)

HOURS OF FOOD DEPRIVATION

AD = 0.062

D

MALE GERRIS INCognitus

AMOUNT EATEN (µG)

HOURS OF FOOD DEPRIVATION

AD = 0.027
MALE GERRIS BUENOI

AMOUNT EATEN (μG)

HOURS OF FOOD DEPRIVATION

AD = 0.054
Table 12. Values of constants in the equation, $H = HK - (BY)e^{(AD + t)}$, used to describe the rate of digestion in *Gerris*, and the maximum gut capacities as determined by the regressions with 24 hr (larva) and 48 hr (adult) of food deprivation (mean ± SE).

<table>
<thead>
<tr>
<th>Gerrid</th>
<th>HK (ug)</th>
<th>BY (ug)</th>
<th>AD</th>
<th>Maximum gut capacity (ug)</th>
<th>Obser. Iter.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. remigis</em></td>
<td>80.5 ± 3.8</td>
<td>75.0</td>
<td>0.170 ± 0.040</td>
<td>89 ± 5</td>
<td>79</td>
</tr>
<tr>
<td>(first instar larva)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. remigis</em></td>
<td>471.6 ± 29.4</td>
<td>429.3</td>
<td>0.194 ± 0.060</td>
<td>456 ± 25</td>
<td>468</td>
</tr>
<tr>
<td>(third instar larva)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. remigis</em></td>
<td>1272.6 ± 48.8</td>
<td>959.3</td>
<td>0.063 ± 0.013</td>
<td>1335 ± 110</td>
<td>1226</td>
</tr>
<tr>
<td>(adult male)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>732.1 ± 14.9</td>
<td>579.5</td>
<td>0.029 ± 0.003</td>
<td>598 ± 20</td>
<td>588</td>
</tr>
<tr>
<td>(adult male)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td>297.5 ± 10.6</td>
<td>290.8</td>
<td>0.054 ± 0.007</td>
<td>315 ± 42</td>
<td>276</td>
</tr>
<tr>
<td>(adult male)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>440.2 ± 14.9</td>
<td>431.0</td>
<td>0.043 ± 0.006</td>
<td>422 ± 45</td>
<td>386</td>
</tr>
<tr>
<td>(adult male)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. notabilis</em></td>
<td>1892.5 ± 48.5</td>
<td>1827.2</td>
<td>0.047 ± 0.005</td>
<td>1823 ± 63</td>
<td>1701</td>
</tr>
<tr>
<td>(adult male)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
minus the Y-axis intercept, and AD = a constant, the rate of food disappearance. The centre regression in each graph represents the "best-fit" regression, with those on either side representing plus and minus one standard error of HK and AD. As the time of food deprivation increased, hunger, or the amount of food required to satiate, also increased, but as in the mantid (Holling, 1966), at a progressively decreasing rate. Thus, the same regression as used by Holling, which assumes that the rate at which hunger changes with time is directly proportional to the amount of food in the gut, was used to describe the data. The rate of change of hunger would be greater when the gut was very full than when the gut was nearly empty. As it was felt that not enough values were located on the plateau to allow averaging of these values for the determination of maximum gut capacity, this latter value was determined iteratively with a deprivation time of 24 hr for the larval instars and 48 hr for the adults. These deprivation times were chosen as it was felt that they provided reasonably realistic values (Fig. 21). In five of the seven regressions, the iterative values are within one standard error of the observed values and in the other two regressions the iterative values are within two standard errors.

It will be noted in Fig. 21 that the curves do not go through the origin but instead, intercept the Y-axis at some point above it. The values of this intercept, the difference between HK and BY in Table 12, are felt to be real and a result of the experimental design. Holling (1966), in determining the hunger curve of the mantid, used as his criterion of satiation
three consecutive refusals to eat crushed flies that were touched to the mantid's mouthparts. Besides hardly being a measure of voluntary feeding in an animal, such a procedure is impractical with Gerris, as the proboscis is held close to the body beneath the animal when it is not feeding. The only criterion for satiation used in this study was a lack of significant ingestion over a half hour time period while in the presence of excess food. Satiation in gerrids preceding food deprivation was achieved by placing them in a holding container with excess food for a time period known to allow satiation to be achieved (see above). As the "satiated" gerrids used here were not chosen for testing immediately after they had fed in the holding container, it was quite possible that voluntarily, the gerrid had not eaten for a while and was in a digestive pause following its previous feeding. The novelty of being placed in a new container coupled with the dropping in of new food could easily be enough stimulus to elicit an immediate attack. Hence, feeding would occur even in "satiated" gerrids, and the regression thus would not pass through the origin.

No significant difference in rate of digestion (the $AE$ value, or slope, in the equation) is evident between the adults of the five species, with the probability of a common slope being 69%. Similarly, for the digestive rates of the two instars studied, no significant difference is evident and the probability of a common slope is 67% (for sample sizes, see Fig. 21).
4. MAXIMUM GUT CAPACITY

Fig. 22, a and b, describe the relation between stomach capacity and wet weight when on a daily satiation ration of Drosophila. If all weights of the gerrids (expressed as weight relative to the weight of the female of their species) are plotted, the maximum stomach capacity is seen as an exponential function of the body weight, with a maximum gut capacity of 23.6% of the wet weight one day after moult for an average size first instar. It will be noticed in Fig. 22 that variability in the amount of food in a "full" stomach is much greater with the smaller than the larger gerrids. It should be noted again, however, that the value of maximum gut capacity only reflects the dry weight ingested and excludes the fluids. Thus, for comparison with other studies, if it is assumed that arbitrarily 75% of the prey's fluid are ingested, then the maximum gut capacity for an average size first instar is 90.2% of the wet weight one day after ecdysis.

Fig. 23 relates the amount eaten on a daily basis at 26°C. to maximum gut capacity for both larval instars and adult gerrids. Treating the larvae and adults separately, it is shown that the relative differences between the amount consumed on a daily basis and the maximum amount consumed at a single feeding are much greater for the larvae than for the adults. However, perhaps owing to the large standard error and small sample size for the smaller gerrids, the ratio of iterative values for the daily amount eaten over the maximum consumed at a single feeding for the smallest instars (1.20) is smaller than that for the
Figure 22. The relation between maximum stomach capacity and gerrid size. A. The relation between maximum stomach capacity, ie. stomach contents expressed as a percent of wet body weight, of each of the instars of the five species and their wet weight, expressed as relative to the wet weight of the female of their species. • = larva or adult. B. The relation between maximum stomach capacity (defined as above) of each of the instars of the five species and their wet weight. Different regressions describe this relationship depending on whether the gerrid is a larva or adult. • = larva; ▲ = adult. (It should be noted that in both (A) and (B), stomach capacity refers only to the dry weight of food ingested; to calculate total stomach capacity for comparison with other studies, if it is assumed that 75% of the prey's fluids are also ingested, multiply the values of the ordinate by 3.83.)
A

STOMACH CONTENTS - PERCENT WET BODY WEIGHT

Y = 23.0 - 3.80 \log_{e} X

RELATIVE WET WEIGHT

0 25 50 75 100 125

B

STOMACH CONTENTS - PERCENT WET BODY WEIGHT

Y = 17.8 - 3.46 \log_{e} X

WET WEIGHT (MG)

0 12 24 36 48 60

Y = 5.96 - 0.046 X
Figure 23. The relation between maximum amount consumed at a single feeding (S), expressed as a percent of wet body weight, to the average amount consumed per day (D) for larval *G. notabilis* and the males of all five species. For calculation of the actual volumes consumed for comparison with other studies (amount consumed here only refers to the dry weight of food ingested, refer to the legend of Fig. 6). • = larva; ∆ = adult.
small adults (1.63). The basic difference between the larvae and adults is in agreement with the faster digestion observed in larval gerrids over adult gerrids. Thus, an enhanced ability to consume more food is shown for the smaller gerrids over the larger gerrids, not only at a single feeding, but to a greater extent on a daily basis as well.

Owing to the overlap in species size (the fifth instars of *G. remigis* and *G. notabilis* both being larger than the adults of the three smaller species (*G. buenoi*, *G. incognitus*, *G. incurvatus*)), two regressions were required (Fig. 22b) to describe the maximum stomach capacity on the basis of body weight irrespective of species. Both fifth instars possessed stomach capacities, as a percent of body weight, larger than the adult gerrids, and this is thought to be a real phenomenon. An exponential function best describes stomach capacity among the larval instars, whereas the relationship among the adults is linear.

5. **EFFECT OF TEMPERATURE ON FEEDING**

The effects of temperature on the amount eaten in *Gerris* is shown in Fig. 24. The general trend in those species studied, excepting *G. remigis*, is for a greater amount to be eaten at higher temperatures than at lower temperatures. In *G. remigis*, however, the amount eaten increases with increasing temperature up to ca. 19°C., beyond which the amount eaten decreases with increasing temperature. In all species, the rate of change of
Figure 24. The effect of temperature on the amount consumed by males of each of the five species of *Gerris*. (a) Males of each of the five species of *Gerris*. (A). N = *G. notabilis*; R = *G. remigis*. (B). B = *G. buenoii*; IG = *G. incognitus*; IV = *G. incurvatus*. 
amount eaten can be adequately described by means of linear regressions, although with G. remigis, two regressions, one for above and one for below 19°C., are required.

6. VARIATION OF FEEDING DURING DEVELOPMENT

Figure 25b describes the relative amounts ingested per day throughout the life cycle of G. notabilis. Each stadium is characterized by an initial rapid increase in the amount of food ingested over the amount eaten in the previous stadium, followed by a gradual decrease in amount eaten. The amount eaten peaks approximately 40% of the way through the stadium irrespective of the duration of the stadium if all the values in each of the stadia are considered together (Fig. 25a). In Fig. 25a the relative position in the stadium of the relative amount eaten, expressed as a percent of the maximum amount eaten in the stadium, is plotted for all the larvae and the adults. Thus, if the stadium is of two days' duration, the relative amount eaten on the last day of the previous stadium would be at 0, the relative amount eaten on day 1 would be at 33, the relative amount eaten on day 2 would be at 67, and the relative amount eaten on day 1 of the next stadium would be at 100. The last day of the previous stadium and the first day of the following are included since ecdysis occurred somewhere between these two periods and the first and last day of the stadium being considered respectively. Assuming the period of development in the adult following the final ecdysis to be similar to that of
Figure 25. The effect of developmental state on food consumption. (A). The relative position in the stadium of the relative daily amount eaten, expressed as a percent of the maximum amount eaten in the stadium, for each day in the six stadia of *G. notabilis*. (B). The observed amounts eaten per day by the five larvae and the adult of *G. notabilis* during the course of their development. The plotted regressions for each instar are the two "best-fit" regressions derived on the basis of the data in (A).
RELATIVE AMOUNT EATEN (PERCENT OF STADIUM MAXIMUM)

\[ Y = 32.3 + 1.5X \]
\[ Y = 102.4 - 0.25X \]
the immature stages, on the basis of when amount eaten peaked, the duration of this developmental period was calculated to be in the vicinity of 8 days. Only the first 8 values of the adult "stadium" were thus incorporated into Fig. 25a. The iterative values for amounts eaten throughout the life cycle of G. notabilis were calculated on the basis of linear regressions derived from this figure which involve the stadia durations and the maximum daily amounts eaten for each stadium. These values are described in Fig. 25b. In most instances, the difference from actual amount eaten is within one standard error, which suggests that this technique of determining the amount eaten is reasonably realistic.

DISCUSSION

In all studies of feeding, the data must be considered in the context of the value of the prey as a food item. Numerous studies (eg. Hsiao and Fraenkel, 1968; Latheef and Harcourt, 1972) have shown that animals have food preferences, and so if a preferred prey item is not chosen by the experimenter, one can expect the test animal's behaviour to differ from that where the preferred food is available. Food quality may not immediately be obvious on the basis of behaviour. Thus, for example, the chrysomelid Leptinotarsa decemlineata reared on tomato, fed longer and consumed more foliage than when reared on potato, its principal host, yet it had a lower survival rate (Latheef and Harcourt, 1972). In a different manner, it was found that early
instar larvae digested tomato better, but little utilization of the food for growth resulted. Later instars, although showing lower digestibility on tomato, had a higher rate of food utilization for growth. Similar observations have been reported by Mukerji and Guppy (1970) for the larvae of *Pseudalestia unipuncta*. The above are all herbivores, however, and the same effect may not apply in carnivores, such as *Gerris*.

Gerrids are opportunistic predators that utilize whatever prey items become trapped on the surface film of the water. There is no recorded evidence that gerrids feed on plant juices. However, there is evidence that gerrids do have preferred foods (see Section 5), but this is a mechanical preference, not a nutritional one. As mentioned earlier, gerrids, like mantids, are raptorial, and this means that depending on the size of the forelegs relative to the prey, handling of the prey may or may not be efficient. Functionally, there is no upper limit with dead or motionless prey (assuming the integument is not thicker than the proboscis is long), as there is always some part of the body, such as a leg, which may be grasped. The gerrid has only to grip the prey and steady itself. However, there can be an upper limit with live prey, as the latter may be too active and may require subduing. Further, there is often a lower size limit, as very small prey, dead or alive, cannot be grasped easily. Even if small items are ultimately grasped and impaled on the proboscis, they may not provide enough nutrition to make the effort worthwhile. There is a significant difference in size between a first instar *G. buenoi* (0.109 mg.) and an adult
female *G. remigis* (50.170 mg.), and experiments with gerrids as prey and predator indicate that food items as small as *Drosophila* are not preferred by the larger gerrids. If this difference in preference does indeed result from smaller size and not behavioural differences on the part of the prey, then it may be that *Drosophila* are not the most suitable prey for the larger gerrids. However, in order to maintain nutritional constancy throughout the study, such preference differences were considered of lesser importance, as no prey other than *Drosophila* was readily available throughout the year, easy to culture, of a size acceptable to both the largest and smallest gerrids, and with an ability to float on the water surface. The prey used also had to be small so that the relatively small amounts ingested by the small gerrids would not be hidden in the normal weight variability of the prey. The results of this study should therefore be considered with these limitations in mind.

In the present study, the time to reach satiation is rather long. Long eating periods required to reach satiation are not unique to *Gerris*, as Morris (1963) reports that *Podisus* requires on the average 4.5 hours. They are perhaps characteristic of hemipterans, however, which owing to their modified mouthparts, have to suck their food. Other insects which chew, and hence eat their prey in discrete amounts, would presumably require considerably less time to achieve satiation.

Sandness and McMurtry (1972) observed in the mite *Amblyseius largoensis* during 24-hr observation periods that the
length of the digestive pause was cyclic in nature, with the longest pause generally occurring after the fourth or fifth prey was eaten, 3-9 hr after the beginning of the observation. Owing to the relatively short length of the observation period in this study, this phenomenon remains uncertain. If the existence of a digestive pause indicates, as suggested by Holling (1966), the presence of a threshold, where attack only results if the animal's hunger exceeds this threshold, then the cyclic nature of digestive pause length as reported by Sandness and McMurtry would suggest the presence of two thresholds. More confirming evidence of these cycles is required, before the exact nature and generality of their existence may be determined.

The relation between hours of food deprivation and amount eaten suggests that two rates of digestion exist in Gerris, one characteristic of the immature stages with AD = 0.182 and the other characteristic of the adults irrespective of species, with AD = 0.047. Since AD indicates the slope of the regression, functionally this means that the digestive rate is faster in immature gerrids than in adult gerrids, at least in G. remigis, and as the adults are all somewhat similar, it would seem a reasonable assumption that this would apply to all immature stages irrespective of species.

In this study with Gerris, there was considerable variability in the amount of food in a "full" stomach, the variability being greater in the smaller gerrids and less in the larger gerrids. As discussed by Brett (1971), such variability can be attributed to three sources: differences resulting from
relative predator-prey sizes, and from different stomach capacities (morphological and physiological differences); reluctance of some animals to fill their stomach at every feeding (behavioural differences); and difficulties in handling the minute stomach contents of the small animals (technical difficulties). All three sources could introduce distortion which would tend to depress the mean values below the potential stomach capacity.

Being poikilothermic animals, the increase in amount eaten by the gerrids with increasing temperature presumably reflects the increased food requirements arising from an increased rate of metabolism. Since reproduction requires a relatively high rate of metabolism, ie. above that normally required for the basal metabolism of the animal, the temperature at which the amount of food eaten is maximized may represent that at which reproduction is also maximized. This assumes that no deliterious effects result from the high temperature and that the intrinsic factors maximizing reproduction have not already been optimized. Nevertheless, up to a threshold at least, higher temperatures should increase reproductive potential and so if female gerrids behave as the males of their species do, the optimal temperature for maximizing reproduction may be in the vicinity of that maximizing food intake. Hence, all the species except for G. remigis would be expected to occur in warm habitats, whereas G. remigis would be expected to occur in habitats with a temperature approximating 19°C. This was observed in the study area (see Section 1) and in the studies on
temperature preference (see Section 2).

In Fig. 24, it will be noticed that for *G. notabilis*, *G. buenoi* and *G. incurvatus*, there is a sudden increase in the amount eaten between 14°C and 17°C. No such sudden increase is as evident for *G. incognitus* and *G. remigis*. Since the data above this temperature range are linear, this sudden increase in food ingested is thought to be a real phenomenon, reflecting a change in metabolism as the temperature exceeds that required to terminate overwintering. As mentioned earlier, *G. incognitus* and *G. remigis* emerge relatively early in the spring, as soon as the snow and ice melt (late February – early March) and when temperatures are relatively low. The other three species in the study area emerge typically in late April, when higher temperatures are recorded. This suggests that in early spring, the two groups of species behave differently to rising temperatures. In the three later emerging species, since they were collected in the field and hence had already come out of overwintering, feeding is minimized from 8-14°C and is at a relatively constant level. Above 14°C these species become more active and respond to increasing temperature. The very large amounts of food eaten in the vicinity of this threshold may represent restoration of the body's stored food lost overwintering. If this restoration involved a short time period, such as only a few days, owing to the design of this experiment, it would only affect the amount eaten at the temperature just exceeding the threshold.

With respect to the effect of growth and development on
feeding, in the study area, G. notabilis is univoltine, which may explain the rapid decline in the amount eaten following the adult developmental period. Field observations suggest that the adults of this species prepare for overwintering relatively soon after their final moult; no large fall aggregations (as are found in G. remigis) were observed in G. notabilis. The decline in amount eaten by G. notabilis is at a rate similar to the decline within a stadium following peak amount eaten, as shown in Fig. 25a.

As mentioned above, the time required by a 48 hr starved, adult G. remigis to eat a measured amount of food was recorded. This allowed calculation of the maximum rate of ingestion (assuming that 75% of the prey's fluids are ingested) for this species, ca. 0.062 mg/min/individual. Over the time required to reach satiation (2.5 hr if starved for 48 hr), the average rate of ingestion was ca. 0.031 mg/min. This is less than the 0.160 mg/min calculated for adult Podisus maculiventris (from Morris, 1963) over the time required to reach satiation. Gallopin and Kitching (1972) report a feeding rate of 0.03 mg/min for Podisus, but their technique involved interruption of feeding at hourly intervals to permit weighing of the prey. Adult mantids, on the other hand, which chew rather than suck their food, eat considerably faster, with a rate of 5.6 mg/min for Mantis religiosa and 20.6 mg/min for the larger Hierodula crassa (from Holling, 1966). Since the average rate of ingestion over the 2.5 hr period required to reach satiation in G. remigis was significantly less than that when ingestion commenced, it
appears that as amount of food in the gut approaches the maximum, the rate of ingestion decreases. This is supported by data for the length of the feeding periods and digestive pauses. If the pattern of feeding bouts and digestive pauses indicated earlier is assumed to be not simply a result of the previous 48-hr starvation interval, the amount consumed per day can be calculated to be 5.425 mg at 26°C. (assuming again that 75% of the prey's fluids are ingested). This is close to the observed amount of 5.002 mg eaten per day and the iterative amount adjusting for temperature of 4.611 mg per day. With the above feeding pattern, the average rate of ingestion is 0.013 mg/min, in agreement with the lower rate of digestion expected when the gut is filled with food. However, that this may be close to, but not the real story is indicated by data which showed that with dead Drosophila as prey, 24 gerrids on a 12 hr light:12 hr dark photoperiod over three consecutive days ate on the average 3.807 mg in the dark and only 1.025 mg in the light. Why this bias towards the dark is not clear, unless being predominantly responsive to moving prey (see Section 4), they do not react proportionately to stationary prey while they can see; only in the dark do their tactile senses assume importance. The significance of this lower digestive rate is that for models operating with a short time scale, i.e. significantly less than the time required to digest a full gut, error may arise if the mean rate of consumption is simply calculated by dividing the maximum gut capacity by the time required by a starved gerrid to reach satiation. If this value is used for G. remigis, the mean daily food consumption with the observed pattern of feeding and
non-feeding bouts would be ca. 13.251 mg, greatly in excess of that observed. Similarly, since daily food consumption varies significantly through the course of a stadium, it is not accurate to simply divide the total food consumed in each stage by the number of days spent feeding in the stage to determine mean daily food consumption if a short time scale is used. This is of particular importance here, as in the overall study of coexistence in Gerris, the relatively short time scale unit of an hour is used.

With respect to feeding in Gerris, then, given the:

1. satiation time
2. length of feeding and non-feeding periods
3. effect of food deprivation on amount consumed
4. maximum gut capacity
5. effect of temperature on food consumption
6. effect of developmental state on food consumption,

it is possible to determine for any particular gerrid a value for the maximum amount of food it could eat at any time as shown in Fig. 26, if the hours of food deprivation following its previous feeding are known. The basic parameters for modelling food consumption in the five species of Gerris studied are thus available.
Figure 26. A flow diagram to illustrate how the parameters discussed in this study may be used. The total amount of food ingested over a given time period for any gerrid in the presence of excess food may be determined if the hours of food deprivation following the previous feeding are known.
SECTION 2. REACTIVE DISTANCE AND RATE OF MOVEMENT

INTRODUCTION

Gerrids are opportunistic predators which feed on insects trapped on the water surface, and are capable of capturing live prey, including other gerrids, if the need arises. Gerrids have been shown to be capable of locating their prey by responding to disturbances of the water surface through receptors on the legs (Rensing, 1961; Liche, 1936; Murphey, 1971a). Murphey (1971a) has shown that orientation in G. remigis consists of a series of discrete turning movements leading to capture of the source of the disturbance. He also analyzed (Murphey, 1971b) the system controlling orientation to prey by localizing those receptors which mediate the response through selective ablation of different parts of the legs. These experiments suggested that the system may function by determining the receptor nearest the source of the ripples, as a number of fairly accurate predictions may be made by assuming this is the case. In a closely related family, the Veliidae, Meyer (1971a, 1971b) has investigated the visual sign stimuli resulting in attack by Velia caprai Tam. and has demonstrated that this species only reacts to visual prey stimuli when they are accompanied by vibration stimuli from the same direction. Whether gerrids also require surface vibrations in association with visual stimuli before an attack is elicited has not yet been determined.

Regardless of the mechanism required to elicit an attack,
however, the number of kills made by a predator is the product of two parameters: the rate of encounter of the prey and the kill success. This section discusses the former, the parameters which determine the encounter rate. These are: the distance at which a predator will respond to a prey item, i.e., the reactive distance; and the rate of movement of the predator and the prey through the environment. Combining the two allows calculation of the swath the predator would cover as it moves across the water surface. Thus, depending on the distribution of the prey (random, contagious, etc.), the number of encounters may be determined. The distribution of the different species within the study area is discussed in Section 1 and the kill success will be considered in Section 5.

MATERIALS AND METHODS

1. REACTIVE FIELD

Recording was accomplished by videotaping on one-inch videotape the interactions of gerrids with prey (either Drosophila or other gerrids). The gerrids were placed in two arenas, and two General Electric Vidison TV cameras were used, one for each arena. As it was impossible to orient the cameras vertically above the arenas and film the interactions directly, an apparatus involving the use of a mirror set at 45° was required. The arenas, 30 by 30 cm, were opaque, white, plastic
basins 15 cm deep filled with 26°C. water to a depth of ca. 3 cm. Lighting was five, cool-white, 2-foot fluorescent tubes located beneath the basins. Back-lighting was required to avoid reflection off the water surface. Recording of only one arena at a time was possible, so the recorded action was shifted from camera to camera, depending on the arena in which the attacks were occurring at the time. Replay was on a 23" screen, and it was possible to freeze the attack at the moment it commenced - when the attacking gerrid first began to blur in its rush towards the prey. Attacks were so fast, much less than a second in duration, that at 18 frames per second, the action was blurred. Replay was of a quality such that it was just possible to discern the legs of a fruitfly - no difficulty was encountered in observing the gerrids.

The parameters measured were the distance between predator and prey, the angle of the prey relative to the anterior-posterior axis of the predator, and the angle of the prey relative to the straight line connecting predator and prey. The latter was required when gerrids were used as prey, as along with the length and width of the prey, it allowed calculation of the relative visual angle subtended by the prey to the predator. Obviously, if the prey were facing the predator, it would subtend a much smaller angle than if it were at right-angles to the predator. With Drosophila as prey, it was found that the difference between its length and width was so small as to make a correction unnecessary and so they were considered as being spherical. Whether or not the attack was successful was also
recorded, and in the case of successful attacks, the prey was removed immediately from the predator to prevent feeding.

It should be noted that the criteria for initiation of an attack was the commencement of movement by the predator gerrid. As in most instances the prey gerrid was already moving, there was no way of ascertaining the actual distance at which the predator gerrid first became aware of the prey gerrid and decided to attack. It could not be assumed that the probability of the prey gerrid moving toward the predator was the same as the probability of its moving away, as often, the prey gerrid, if initially stationary, was only moving in response to the predator gerrid's close proximity, and hence was moving away. Thus from a morphological and physiological view, this criteria will not allow determination of the exact distance at which a gerrid will respond to a prey gerrid. However, from an operational view, this approach does describe the predator's response. With prey items unable to respond to the approach of a gerrid, such as *Drosophila*, the exact distance at which a gerrid responded to a prey was described. It was for this reason and to provide a constant prey size that *Drosophila* were used as prey in the determination of the effect of gerrid size and hunger on reactive distance (see below).

To determine the overall shape of the reactive field of *Gerris*, observations of the attacks of 24 hr starved adult *G. remigis* on adult *G. incognitus* were recorded.

To assess the effect of hunger on the mean reactive
distance, observations of adult *G. remigis* at different hunger levels attacking live *Drosophila* were recorded. Four hunger levels were established (0 hr, 6 hr, 18 hr and 48 hr starved) and 20 observations were recorded at each.

The effect of gerrid size on the mean reactive distance of *Gerris* was measured by determining the distance at which ten size classes of *Gerris* attacked live *Drosophila*. Table 13 summarizes the species-instars, their size, and the state of hunger of the gerrids which were used in this study. The ten size classes used were established on the basis of leg length (mesothoracic femur + tibia plus metathoracic femur + tibia), as this is one of the few parameters to remain constant throughout the duration of an instar. Leg length was used in particular as in other related studies of predation in *Gerris* (Section 5), it was noted that leg length seemed critical in determining the success of an attack. In situations where the "predator" and "prey" gerrids were similar in size, successful attacks usually required the flipping of the "prey" gerrid onto its back. The longer its legs, irrespective of body size, the more stable it was on the surface film. These size classes are used to provide constancy in terminology in the overall study: the relation between species-instars and size class is shown in Fig. 27.

In determining the angle subtended by an animal, body size, not leg length, is the critical parameter. Thus mean body size was used to characterize the size classes used in this aspect of the study. The mean body size of each gerrid size class in Table 13 is the mean of the (width + length)/2 of randomly
Figure 27. The relation between species-instar and leg length (± 1 SE), and their grouping into ten size classes used in this study. Leg length is the sum of the femurs and tibias of the meso- and metathoracic legs. ● = larvae; △ = adult female; ▲ = adult male.
Table 13. The gerrid species-instars, the mean body size, and the state of hunger used in determining the effect of body size on mean reactive distance.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Species-instar</th>
<th>Mean body size (mm)</th>
<th>Hours starved</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>G. incurvatus</em> 1st</td>
<td>5</td>
<td>1.2</td>
</tr>
<tr>
<td>2</td>
<td><em>G. remigis</em> 1st</td>
<td>5</td>
<td>1.5</td>
</tr>
<tr>
<td>3</td>
<td><em>G. remigis</em> 2nd</td>
<td>5</td>
<td>2.1</td>
</tr>
<tr>
<td>4</td>
<td><em>G. incognitus</em> 4th</td>
<td>5</td>
<td>3.1</td>
</tr>
<tr>
<td>5</td>
<td><em>G. notabilis</em> 3rd</td>
<td>5</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td><em>G. incurvatus</em> 4th</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>6</td>
<td><em>G. incognitus</em> 5th</td>
<td>5</td>
<td>3.8</td>
</tr>
<tr>
<td></td>
<td><em>G. incurvatus</em> 5th</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>7</td>
<td><em>G. remigis</em> 4th</td>
<td>5</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td><em>G. notabilis</em> 4th</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>G. buenoi</em> adult</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>8</td>
<td><em>G. incurvatus</em> adult</td>
<td>5</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td><em>G. incognitus</em> adult</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td><em>G. remigis</em> 5th</td>
<td>5</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td><em>G. notabilis</em> 5th</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td><em>G. remigis</em> adult</td>
<td>5</td>
<td>9.6</td>
</tr>
<tr>
<td></td>
<td><em>G. notabilis</em> adult</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>
chosen insects collected in the summer from the field and preserved in 70% ethanol. As differences in leg length do not always reflect corresponding differences in body size, two size classes with only a small difference in leg length may vary such that the "larger" size class has a smaller mean body size. This is why size class 5 in Table 13 has a smaller body size than size class 4.

2. MOVEMENT

The rate of movement of the instars of the five gerrid species studied were measured as two components: the mean stride length and the number of strides per unit time. The mean stride length was measured by tracing on transparent, acrylic sheeting the distance the individual consecutive strides moved the gerrid on the videotape system described above. Measurements of this distance (= stride length) of adults of each species were made to determine species differences. Additional tracings from the larval instars representing the different size classes in Table 13 were used to assess the effect of leg length on stride length.

The number of strides per unit time were measured by observing individual gerrids for 15 consecutive minutes each. Gerrids of size classes 4 to 10 were studied in a circular tank 1.22 m in diameter and 11 cm deep, with 20 gerrids at each time being observed in the tank. Size classes 1 to 3 were studied in a plastic container 31 cm by 25 cm and 9.5 cm deep, with 10
gerrids being present. Regardless of container size, water depth was 3-4 cm and water temperature was ca. 25°C. An air stone was placed in the larger tank to keep the water surface clean. Each gerrid was satiated before testing commenced and the various activities of each insect were recorded on magnetic tape. A panel which emitted sounds at different frequencies was connected to a tape recorder, and by identifying a particular behavioural movement with a particular sound, it was possible to record as a series of "beeps" at different frequencies, the activities of the gerrids (Dawkins, 1972). Replay of the tape into a computer allowed calculation not only of the number of times each behavioural movement occurred, but the temporal sequence of the different movements and total time spent at each movement.

To determine if species differences were present, adults of each of the five species were observed as described above. Then to assess the effect of size, satiated individuals of each of the size classes 1 to 7 and 9 were observed, the larvae involved being as noted in Table 14. The effect of hunger was measured by observing individual adult G. remigis after 6, 26 or 48 hr of starvation. Finally, gerrids representing all five species were also observed in the field for 15 minutes each to determine if the data obtained in the laboratory accurately reflected that found in the field. On the day when observations were made (July 21, 1972, 10:00 a.m. To 3:00 p.m.), the weather was sunny and the ambient water temperature was 23-25°C. The state of hunger of the gerrids observed in the field is unknown.
Table 11. The species-instar representing the various size classes tested in determining the effect of size on frequency of movement, and the mean number of strides ($\pm 1 \ SE$) observed in the 15 minute test period.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Species-instar</th>
<th>n</th>
<th>Strides/15 min.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>G. incurvatus</em></td>
<td>1st</td>
<td>10</td>
</tr>
<tr>
<td>2</td>
<td><em>G. incurvatus</em></td>
<td>2nd</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td><em>G. incurvatus</em></td>
<td>3rd</td>
<td>10</td>
</tr>
<tr>
<td>4</td>
<td><em>G. buenoii</em></td>
<td>4th</td>
<td>10</td>
</tr>
<tr>
<td>5</td>
<td><em>G. incurvatus</em></td>
<td>4th</td>
<td>10</td>
</tr>
<tr>
<td>6</td>
<td><em>G. buenoii</em></td>
<td>5th</td>
<td>10</td>
</tr>
<tr>
<td>7</td>
<td><em>G. incurvatus</em></td>
<td>5th</td>
<td>10</td>
</tr>
<tr>
<td>9</td>
<td><em>G. remigis</em></td>
<td>5th</td>
<td>10</td>
</tr>
</tbody>
</table>
RESULTS

1. REACTIVE FIELD

The overall shape of the reactive field of *G. remigis* is illustrated in Fig. 28. A definite preference for moving prey (Fig. 28b) was exhibited, with only 12.9% of the 178 observed attacks being against stationary prey (Fig. 28a). Only 10.7% of the total observed attacks were directed behind the gerrid, i.e. at an angle greater than 100° when the 0-180° axis is the body axis of the gerrid and 0° the anterior end. The total number of successful attacks (9) is too small to indicate if this observed preference to attack anteriorly truly reflects the probability of making a successful attack. However, if the probability of making a successful attack at an angle of less than 100° (anterolateral region) is weighted against that at an angle greater than 100° (posterolateral region), the probability of making a successful attack (5%) is the same for both regions. That the preference for attacking in the anterolateral direction is not simply a result of the gerrid's s being unable to detect prey behind it, either visually or by surface waves, can be seen in escape responses when the gerrid is prey (Fig. 28c). Of 97 successful escapes by the prey gerrid observed, 55.6% were escapes in which the predator attacked the prey gerrid from behind, i.e. at an angle greater than 100° to the prey gerrid's body axis. Gerrids can thus respond to attacks irrespective of the angle from which they are launched.
Figure 28. The effect of prey location relative to the predator on the propensity of adult *G. remigis* to attack (A) stationary prey and (B) moving prey (prey = adult *G. incognitus*), and (C) the effect of predator location relative to the prey on the ability of the prey to successfully avoid capture, i.e. escape, from the predator. The histograms on the outer concentric circle represent the number of attacks made in the 5 degrees on either side; the numbers at the top indicate the number of attacks which were successful. The solid circles represent the mean distance ($\pm 1$ SE) in each of the 18 10-degree segments at which a 2 mm prey item would be attacked (A and B) and in (C), the mean distance for each segment at which a prey item would commence evasive action when attacked by a 2 mm predator. The inner semicircle in each figure passing through the solid circles depicts the overall mean distance (irrespective of the angular location of the stimulus) at which the gerrid will respond.
No significant difference was observed between the two regions (anterolateral and posterolateral) for the mean angle relative to the predator gerrid (Fig. 28b) which moving prey must subtend before an attack is elicited. This angle, $3.72^\circ \pm 0.22$, was considerably less than the mean angle stationary prey must subtend, $15.02^\circ \pm 2.12$. The mean angle the predator must subtend before evasive action is taken by the prey was found to be $13.15^\circ \pm 0.95$.

Hunger has a significant effect on the visual angle required to elicit an attack by G. remigis. Fig. 29 shows the effect of hours of food deprivation on visual angle. Knowing the hours of food deprivation allows calculation of the amount of food required to fill the gut (see Section 3) and hence food in the gut. Fig. 30 illustrates the relation between amount of food in the gut, expressed as a percent of the maximum gut capacity, and the visual angle required to elicit an attack. The visual angle is slightly smaller with less food in the gut, (ie. the hungrier the gerrid), with a 4.9% probability of the slope in Fig. 30 being zero.

The effect of gerrid size on the angle required to elicit an attack is shown in Fig. 31. Smaller gerrids require the prey to subtend a larger angle, while the larger gerrids require a smaller angle; the smallest gerrids require an angle of $5.71^\circ \pm 0.37$ and the largest, $3.23^\circ \pm 0.29$. Operationally, this means that for a standard size prey item, the larger the gerrid, the greater the relative distance at which it will attack the prey.
Figure 29. The effect of hours of food deprivation on the mean visual angle (± 1 SE) which must be subtended by a prey item before an attack is elicited by adult G. remigis.
Figure 30. The relation of the amount of food in the gut, expressed as a percent of that required to achieve satiation, to the mean visual angle (± 1 SE) required to elicit an attack by adult G. remigis.
29

\[ Y = 3.34 + 0.015X \]

30

\[ Y = 4.34 - 0.021X \]
Figure 31. The relation between gerrid size, expressed as the sum of the lengths of the femurs and tibias of the meso- and metathoracic legs, and the mean visual angle (± 1 SE) which a prey must subtend before an attack is elicited.
Figure 32. The relation between stride length (± 1 SE) and the mean length of the mesothoracic leg, expressed as the sum of the lengths of the femur, tibia and tarsus, for the ten size classes used in this study.
31

$Y = 5.71 - 0.044X$

VISUAL ANGLE (DEG.)

LEGG LENGTH (MM)

32

$Y = 1.32 + 0.062X$

STRIDE LENGTH (CM)

LEGG LENGTH (CM)
Table 15 summarizes the mean distances at which the different size classes of gerrids will attack each other when maximally starved.

2. MOVEMENT

No difference appeared to exist between species of gerrid in stride length. Rather, stride length, as shown in Fig. 32, seems to be directly related to leg length (here measured as the sum of the mesothoracic femur, tibia and tarsus); the longer the legs, the larger the stride.

Significant species differences were observed, however, with respect to the number of leg strokes measured over the 15 minute observation period (Fig. 33). *G. remigis* made 4 to 6 times more strokes than any of the other four species. This was largely a result of the manner in which the different species responded to the water currents set up by the air stone in the tank. *G. remigis* tended to remain in the current, maintaining a constant position within the tank; this required constant, regular strokes. The other species, however, either drifted with the current or stationed themselves in areas of the tank with no current, making little effort to direct their movements against the current. In observations when an air stone was not present, however, *G. remigis* was still observed to move considerably more frequently than the other species.

As movement in all five larval instars of the five species,
Table 15. The mean distance (cm) at which the different size classes of gerrids will attack each other at maximum starvation.

<table>
<thead>
<tr>
<th>Predator size class</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.24</td>
<td>1.26</td>
<td>1.29</td>
<td>1.32</td>
<td>1.35</td>
<td>1.37</td>
<td>1.44</td>
<td>1.44</td>
<td>1.63</td>
<td>1.83</td>
</tr>
<tr>
<td>2</td>
<td>-</td>
<td>1.58</td>
<td>1.61</td>
<td>1.65</td>
<td>1.69</td>
<td>1.71</td>
<td>1.80</td>
<td>1.81</td>
<td>2.03</td>
<td>2.29</td>
</tr>
<tr>
<td>3</td>
<td>-</td>
<td>-</td>
<td>2.26</td>
<td>2.31</td>
<td>2.36</td>
<td>2.40</td>
<td>2.52</td>
<td>2.53</td>
<td>2.85</td>
<td>3.21</td>
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<td>3.41</td>
<td>3.49</td>
<td>3.54</td>
<td>3.72</td>
<td>3.73</td>
<td>4.20</td>
<td>4.74</td>
</tr>
<tr>
<td>5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.15</td>
<td>3.20</td>
<td>3.36</td>
<td>3.37</td>
<td>3.79</td>
<td>4.28</td>
</tr>
<tr>
<td>6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4.34</td>
<td>4.56</td>
<td>4.57</td>
<td>5.15</td>
<td>5.81</td>
</tr>
<tr>
<td>7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.64</td>
<td>5.66</td>
<td>6.37</td>
<td>7.19</td>
</tr>
<tr>
<td>8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.62</td>
<td>7.45</td>
<td>8.41</td>
</tr>
<tr>
<td>9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>9.49</td>
<td>10.70</td>
</tr>
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<td>10</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>14.68</td>
</tr>
</tbody>
</table>
Figure 33. The relation between *Gerris* species and the mean number of strides (± 1 SE) made per individual over a 15 minute time period. N = *G. notabilis*; R = *G. remigis*; IG = *G. incognitus*; IV = *G. incurvatus*; B = *G. bueno*. 
Figure 34. The relation between gerrid size, expressed as the sum of the lengths of the femurs and tibias of the meso- and metathoracic legs, and the mean number of strides (± 1 SE) made per individual over a 15 minute time period, expresses in terms of G. remigis units. (The propensity to move was assumed species-specific, regardless of gerrid size, and on the basis of the data in Fig. 33, coefficients were determined for each species to set their frequency of movement equal to that of G. remigis).
was not measured, in order to assess the effect of gerrid size on stroke frequency for each species, it was assumed that the tendency to move for the instars of each species was the same as that for the adult, since they occur together in the same microhabitat. Thus, if a correction coefficient is determined for the adults of each species in terms of G. remigis, multiplication of the number of strokes observed for any instar by the corresponding coefficient should indicate the number of strokes per unit time measured in terms of G. remigis. Fig. 34 describes the relation between gerrid size and frequency of movement, and shows that great variation was observed. There is evidently no clear effect of gerrid size on the number of strokes made (the probability of the slope being zero is 23.3%), although the "best-fit" linear regression suggests that the smaller gerrids tend to move slightly less.

The amount of food in the gut, however, did have a significant effect on the frequency of movement, as shown in Figs. 35 and 36. Again, knowing the hours of food deprivation allowed calculation of the percent of gut satiation (see Section 2). These data (Fig. 36) show that with increasing hunger, the number of strokes made by G. remigis declines significantly, with a gerrid with an empty gut moving only one-sixth as much as a gerrid with a full gut.

The only behavioural movement apart from locomotive strokes observed in the gerrids was grooming (excluding the vibratory movements made by adult male G. notabilis as they courted the females). If one second on the average is considered the time
Figure 35. The effect of hours of food deprivation on the frequency of movement by *G. remigis*, measured as the mean number of strides (± 1 SE) made per individual over a 15 minute time period.
Figure 36. The relation of the amount of food in the gut, expressed as a percent of that required to achieve satiation, to the mean number of strides (± 1 SE) over a 15 minute time period.
Figure 35

Y = 259.4 - 4.27X

Figure 36

Y = 87.2 + 2.10X
involved in making one leg stroke (the actual leg movement is much faster but unless the gerrid is responding to an external stimulus, a slight pause usually follows each stroke), the percent of the total time (15 minutes) spent by the gerrids in moving, grooming, and remaining stationary in both the laboratory and the field can be calculated (Table 16). In terms of movement, no significant difference was observed between G. buenoi, G. notabilis, G. incognitus and G. incurvatus, and so these species are treated as a group rather than individually. No significant difference in the amount of time spent grooming (2-4%) was observed between any of the species in either the laboratory or the field.

DISCUSSION

That a predator would prefer to attack prey in front of it rather than behind it is not surprising. However, the significance of why this preference in gerrids is only for angles requiring a turn of less than 100°, even though they are capable of detecting prey items irrespective of their angular location, is not apparent from this study. Murphey (1971a), however, demonstrated in G. remigis that the extent of remotion of the mesothoracic leg contralateral to the prey is relatively constant only as long as the turn produced is less than approximately 90°. Turns in excess of 90° often involve two powerstroke movements of the leg contralateral to the target, whereas a single powerstroke is characteristic when the target
Table 16. Mean percent of the total time spent by *Gerris* species either moving, grooming or remaining stationary.

<table>
<thead>
<tr>
<th>Species</th>
<th>Laboratory</th>
<th></th>
<th></th>
<th>Field</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Moving (%)</td>
<td>Stationary (%)</td>
<td>Grooming (%)</td>
<td>Moving (%)</td>
</tr>
<tr>
<td><em>G. remigis</em></td>
<td>32.7</td>
<td>65.2</td>
<td></td>
<td>35.5</td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. notabilis</em></td>
<td>7.6</td>
<td>90.3</td>
<td>2.1</td>
<td>6.4</td>
</tr>
<tr>
<td><em>G. incurvatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
deviation is less than 90°. It would thus seem that it is the "double powerstroke" which is avoided, perhaps owing to the increased time involved in initiating the attack. Regardless, however, of the reason, functionally, attacks requiring a turn in excess of ca. 100° are avoided.

The preference by gerrids for moving prey items over stationary ones is also not in itself surprising, as some discriminatory capability must be present or gerrids would attack any floating object on the water surface. This could be very time-consuming in areas where floating debris collect. Gerrids possess a well-developed visual system with relatively large eyes projecting laterally from the head. This suggests that vision as well as water surface vibration, which has already been documented as sufficient to instigate an attack (Murphey, 1971a), may be involved. Field observations of G. remigis on streams support the role of vision in prey detection. On a fast moving stream, with numerous surface ripples present, gerrids were observed to position themselves in and against the current, and to respond to every prey item that floated by regardless of its nature. Pieces of bark, bubbles, as well as insects, were all approached and grasped, and if inedible, released. Since the items approached were often floating passively with the current, making no ripples on their own, it seems unlikely that water surface vibration was the attacking stimulus, especially in lieu of all the other ripples present. Whether this is unique to stream species is uncertain, however, and on the calm water surface of a pool, ripples may indeed be
the main stimulus required. The surface water bug *Velia caprai*,
which also occurs at the edge of streams, reacts to visual prey
stimuli only when they are accompanied by vibration stimuli from
the same direction (Meyer, 1971a, 1971b). Gerrids, however,
being larger and possessing more powerful legs, can position
themselves in areas of stronger current and hence more turbulent
water, which may mean that the stimulus required is not the
same. However, here again, it is the effect rather than the
mechanism which is of prime importance. Irrespective of the
exact stimuli which make moving prey preferred, recognition that
a difference in eliciting an attack exists between moving and
stationary prey is all that is required for this study. Thus,
the concept of a visual angle determining reactive distance,
even though vision may not always be involved, is felt suitable
for use. The values used here were obtained directly from the
observations, and hence accurately describe the data. They did
not originate in theory, utilizing such parameters as ommatidia
width, the refractive index of the cornea, etc., which would
make them dependent on the validity of the role of vision in
prey detection. It should also be noted that the visual angles
presented do not indicate the distance at which the gerrid
becomes aware of a nearby gerrid, but rather the distance at
which a gerrid first responds to a nearby gerrid. Operationally, therefore, this approach is suitable in the
realistic simulation of a gerrid's reactive distance.

That the mean angle the predator gerrid must subtend to a
prey gerrid before evasive action by the prey gerrid is
commenced is slightly smaller than that which the prey must subtend to the predator before the predator will attack is also of interest. Functionally, this means that for the predator and prey gerrids used in this study (predator = *G. remigis*; prey = *G. incognitus*), the mean distance at which the prey will be attacked by the predator is 8.6 cm if the prey is moving and 2.1 cm if it is stationary. However, the prey will commence evasive action when the attacking predator's mean distance from it is 4.2 cm. If the predator is already attacking, since its line of attack will present to the prey gerrid the predator's smallest subtendable visual angle, namely its width, evasive action will commence only when the predator is relatively close. This mean distance, 1.5 cm, however, is usually just enough to allow successful escape. The fact that the prey gerrid usually does escape is a result of specific escape behaviour. The escape movement from a stationary position is often an initial movement at right angles to the predator's line of attack, followed by a quick circling around behind the predator. Since gerrids are unable to stop quickly on the water surface, such a movement rapidly places the prey gerrid in a position where it is unlikely to be again immediately attacked, i.e. behind the gerrid. If the prey gerrid is relatively large, it will often achieve the same effect by leaping straight up into the air, allowing the predator to skim by beneath it. This, often followed by a few quick strokes, is usually enough to again result in a successful escape. When attacking very small prey, which are unable to outrun or outjump the predator gerrid, escapes usually occur only as a result of miscalculation by the
predator. If too much momentum is gained, the predator may be unable to stop and may slide right over the prey. The predator usually then grasps seemingly randomly around the vicinity where it stopped, and may or may not find the prey which is beneath it. When attacking moving prey, the predator usually attacks along a line of intercept. Since the prey, like the predator, cannot maneuver sharply on the water surface once moving, its only recourse for escape is to alter its speed and hence the time of potential intercept. This can only be accomplished by accelerating, since slowing would result in almost certain capture, as the predator could then slow too and alter its line of attack. Regardless, however, of the evasive response of the prey, it is to the prey's advantage to wait as long as possible before responding to a predator gerrid's close proximity or attack. If it were initially stationary and moved too soon, it might be attacked when otherwise it would be bypassed. If the attack is already launched, premature movement would allow the predator time to adjust its line of attack, and premature jumping would cause it to land just in time to be caught. Hence, one would expect only a slight difference to exist between the angle at which a prey gerrid responds to a predator gerrid and the angle required to elicit an attack by a predator. It was observed that the prey had the advantage.

This suggests, as one might guess, that cannibalism in gerrids is not a feature which has been selected for. Larger gerrids, at least, seem to have evolved mechanisms which tend to decrease the probability of a successful capture. It should be
noted, that except for cases where only a slight difference in size exists between the predator and the prey, making the main difficulty that of subduing the prey, behavioural mechanisms only appear to prevent cannibalism. No specific morphological structures or defenses are known which make gerrids immune to attack by other gerrids. As a result, the greater the relative size difference between a prey gerrid and a predator gerrid, the greater the probability of a successful capture, and hence cannibalism. The speed and jumping ability of smaller gerrids are much less than that of larger gerrids, making some cannibalism at least seemingly unavoidable.

The effect of hunger on the size of the reactive field of G. remigis is slight, but seems to be that of an increasingly larger reactive field with increasing hunger. Whether this is a valid assumption for the other species of Gerris as well is unknown. However, that a hungry animal would respond to prey at a greater distance from it than would a satiated animal would seem reasonable, although the rate at which the reactive field increases in size may vary with the species. Thus, although the size of the reactive field is directly proportional to hunger, the size of the reactive field of a hungry animal relative to that when it is satiated is not necessarily constant.

In an effort to determine how the size of the reactive field does vary with the species-instars studied, the effect of gerrid size on this parameter was investigated. Leg length was the measurement used to determine gerrid size, both to be consistent with the above-mentioned size classes and because if
ripples were indeed the stimulus that elicited attack, the distance the legs were apart, a function of their length, might be the critical parameter allowing orientation to the prey. Predator size did affect the distance at which a standard-size prey item would be attacked, with larger gerrids attacking the prey item at a greater distance (smaller visual angle) than smaller gerrids. Whether this is a result of the smaller gerrids' being unable to detect, or at least orient to, the fainter ripples (as their legs are closer together), or the result of a complex visual mechanism involving some type of depth perception is not clear. Certainly, the concept that there is a "visual angle the prey must subtend before an attack is elicited" is an over-simplification. This study indicates that other variables are involved. Nevertheless, regardless of the mechanism, this study shows that gerrid size does influence the size of the reactive field.

The much greater activity observed by G. remigis over the other four species presumably reflects the modifications which have evolved to allow this species to use the stream habitat. However, by itself, increased activity is not sufficient to remain in position on a stream. The activity must be directed against the current: such rheotrophic activity is suggested in this study for this species. That this increased activity is not just in response to current, is indicated by the field observations of G. remigis on pools where the water surface was not moving (as opposed to the laboratory studies where the water surface was moving owing to the presence of an airstone).
Almost identical periods of time were devoted to movement under the field and laboratory conditions. Activity would thus seem to be the result of an internal drive, rather than a response to the external environment. That the latter can and does influence activity, however, is shown by the directed nature of this activity on a stream.

Since *G. remigis*, being a stream species, is somewhat unique when compared to the four pond species in our study area, whether these other species respond to increasing hunger in the same manner as does *G. remigis* is open to question. *G. remigis* shows a significant decrease in overall activity with increasing hunger, but this may simply represent conservation of energy. The maintenance of position in a fast-flowing stream would probably involve a considerable expenditure of energy. However, as the reactive distance is not significantly increased with increasing hunger, but rather remains relatively constant regardless of hunger, this may simply represent a change in hunting strategy with increasing hunger. It may change from an active satiated predator which can afford time to search for a mate, an oviposition site, or whatever, utilizing what food items it encounters on the way, to a hungry one which waits for and ambushes its prey. If the above is true, then regardless of the species of gerrid, increasing hunger could result in decreased activity as the same could apply to pond species. This is assumed to be the case for the other species discussed in this study, even if the above suggested explanation is not completely accurate: no increase in activity of the other four
species with increasing hunger seemed apparent. A similar decrease in activity with increasing hunger has been reported for the larva of the dragonfly *Aeschna cyanea* (Etienne, 1972) and for the lycosid spider, *Pardosa vancouveri* (M. Hardman, pers. comm.), which also behaves as an ambush predator. In contrast, we may note that it is with insects that are not predaceous, such as the blowfly *Phormia regina* (Green, 1964) and the gypsy moth *Porthetria dispar* (Leonard, 1970), that one sees an increased rate of locomotion with increasing hunger.

The effect of size on the propensity to move in gerrids is not clear, although the results suggest that smaller gerrids move less than larger gerrids. This agrees with the conclusions suggested on the basis of reactive distance. Small gerrids, being unable to outrun or outjump large gerrids, can most successfully avoid being cannibalized by remaining stationary as much as possible. There would thus seem to be a selective advantage for small gerrids to move less.

Combining the stride length and the frequency of movement of the different size classes of gerrids with the species-propensity to move allows calculation of the mean distance each of the species-instars would be likely to move in a given time period (Table 17). This can be expressed as a rate if it is assumed that the gerrids are always moving throughout the time period. Combining the distance moved with the reactive field width, allows determination of the mean area of the swath or "encounter path" different gerrids would cover as they moved across the water surface (Table 18).
Table 17. The mean distance (m) which each of the species-instars would be likely to move in one hour.

<table>
<thead>
<tr>
<th>Instar</th>
<th>G. notabilis</th>
<th>G. remigis</th>
<th>G. incognitus</th>
<th>G. buenoi</th>
<th>G. incurvatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larva 1</td>
<td>2.82</td>
<td>11.03</td>
<td>1.51</td>
<td>2.93</td>
<td>2.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>3.35</td>
<td>13.10</td>
<td>1.70</td>
<td>3.29</td>
<td>2.3</td>
</tr>
<tr>
<td>&quot;</td>
<td>4.37</td>
<td>16.84</td>
<td>1.93</td>
<td>3.91</td>
<td>3.0</td>
</tr>
<tr>
<td>&quot;</td>
<td>6.00</td>
<td>22.73</td>
<td>2.31</td>
<td>4.80</td>
<td>3.4</td>
</tr>
<tr>
<td>&quot;</td>
<td>9.23</td>
<td>31.49</td>
<td>2.78</td>
<td>6.23</td>
<td>3.9</td>
</tr>
<tr>
<td>Adult 6</td>
<td>14.18</td>
<td>37.84</td>
<td>3.37</td>
<td>7.63</td>
<td>4.6</td>
</tr>
</tbody>
</table>
Table 18. The mean area of the swath (m²), or "encounter path", the various species-instars would cover per hour as they moved across the water surface, assuming a prey size of 2 mm (an average size often observed in the field).

<table>
<thead>
<tr>
<th>Instar</th>
<th>G. notabilis</th>
<th>G. remigis</th>
<th>G. incognitus</th>
<th>G. incurvatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Larva 1</td>
<td>0.1190</td>
<td>0.4654</td>
<td>0.0625</td>
<td>0.1213</td>
</tr>
<tr>
<td>&quot;</td>
<td>0.1440</td>
<td>0.5633</td>
<td>0.0717</td>
<td>0.1388</td>
</tr>
<tr>
<td>&quot;</td>
<td>0.1967</td>
<td>0.7578</td>
<td>0.0830</td>
<td>0.1681</td>
</tr>
<tr>
<td>&quot;</td>
<td>0.2880</td>
<td>1.0910</td>
<td>0.1016</td>
<td>0.2160</td>
</tr>
<tr>
<td>&quot;</td>
<td>0.5003</td>
<td>1.7068</td>
<td>0.1273</td>
<td>0.2990</td>
</tr>
<tr>
<td>Adult 6</td>
<td>0.8678</td>
<td>2.3158</td>
<td>0.1624</td>
<td>0.3678</td>
</tr>
</tbody>
</table>
The basic parameters necessary for modelling the rate of prey encounter, if the prey distribution is known, are thus available for the five species of Gerris considered in this paper.
SECTION 5. GERRIDS AS PREDATORS AND PREY

INTRODUCTION

As predators, gerrids are unique in that their habitat, the water surface, is a trap for most other insects, not only for terrestrial forms landing from above but also for the aquatic ones emerging from below. Gerrids prey on whatever is available on the water surface but prefer live over dead prey and are adapted to detecting movement which they use as cues in identifying potential prey items (see Section 4). Owing to the nature of the habitat and the fact that gerrids are more or less confined to the water surface, they are forced to be dependent for food on the items occurring in the water surface trap. In certain situations, particularly in mid-summer when gerrid numbers reach a peak and when small ponds dry up or become smaller, considerable crowding can occur. Under circumstances such as this, and cannibalism may become significant.

This section is primarily concerned with the predatory capabilities of gerrids with particular emphasis on size relationships and species interactions. However, field observations of the availability of potential prey other than gerrids, field hunger levels of the gerrids, and the effectiveness of potential insect predators other than gerrids preying on gerrids are also considered.
MATERIALS AND METHODS

1. FIELD HUNGER LEVELS

The same basic procedures as were used in Section 3 in determining the amounts of food ingested by gerrids were used here. The wet weight of Drosophila was determined prior to feeding, and following feeding, the flies were dried and reweighed. Controls were used to determine the effect of experimental procedures, and on the basis of these data, an expected theoretical dry weight percentage of the initial wet weight was determined. Any deviation in dry weight following feeding from this expected theoretical dry weight was considered the amount eaten.

Experimental procedures were as follows: gerrids collected on Marion L. were immediately placed in separate containers and fed a known quantity of Drosophila. Exposure to the flies was for 2 hr, and at the end of this time, the flies were removed and immediately taken back to the laboratory where they were dried. The volume of food eaten by each gerrid species instar was then compared with the maximum amount eaten by the species instar when maximally starved (see Section 3). Field hunger levels are thus expressed in terms of the percent of the gut that is filled with food.
2. GERRIDS AS PREDATOR AND PREY

A. The size classes of gerrids

With five species of Gerris, each with adult and five larval instars, the present study involves 30 categories of gerrids altogether. In order to reduce the number of experiments in this study, ten "size classes" were established as in Section 4 based on leg length, as it was noted that this parameter often was the critical one in determining whether an attack would lead to a kill. In struggles between gerrids of similar size, kills usually require the immobilization of the prey and this can only be achieved by flipping the prey gerrid over onto its back. Longer legs in the prey provide greater stability on the water surface, hence reducing the probability of being killed. The ten size classes used in this study are thus the same as those used in Section 4.

B. Effect of species and hunger level on predation

Fifth instar larvae and adults of each of the five gerrid species were used as predators to determine if species differences in predatory behaviour exist. Only these instars were used, as preliminary experiments suggested that only the larger size instars were capable of killing efficiently more than three size classes of gerrids.

Trials consisted of placing both a predator and a prey gerrid in a partly water-filled container, and then observing
the action for a fifteen-minute period. In each trial, the number of attacks, defined here as a quick, darting movement towards the prey, was recorded, as was the time of kill if this occurred. Owing to the large number of gerrids required, the predator and prey were separated as soon as possible after it was observed that the prey gerrid was indeed caught. When no feeding occurred, predator gerrids could be used twice on a single day, although they were never used the second time with the same size class as was used in the first trial. Prey gerrids were reused repetitively until they were either crippled or killed by a predator gerrid. Container size was determined by the size of the prey gerrid: if it was of size class 3 or smaller, trials were in a clear plastic container 9.5 cm in diameter and 7 cm deep, whereas if the prey gerrid was of a larger size class, trials were in a clear plastic container 26 cm in diameter and 9 cm deep.

Various predator hunger levels were obtained by starving gerrids for known periods of time. Starvation periods of 48, 24 and 5 hr were used to attain an empty gut, a gut 1/3 filled with food, and a gut 2/3 filled with food respectively in adult gerrids. Starvation periods of 24 and 6 hr were used to attain an empty gut and a gut 1/3 filled with food respectively in fifth instar larva. These starvation periods have been shown sufficient to achieve the above hunger levels (see Section 3).

Prey gerrids were taken from size classes 1 to 7. Hunger levels of prey gerrids varied, as the same gerrid might have been used as both a prey and a predator on the same day.
Predator or prey gerrids were used as they became available or were needed. However, gerrids still pale in colour from their last moult or obviously about to moult were not used.

All observations were made with acclimated gerrids at 26°C in a controlled environment room.

C. Relative predator-prey size and kill success

Procedures used here were identical to those used above. However, in order to determine how prey size relative to predator size influenced capture success, instead of just five size classes being used as predator, gerrids from each size class were presented with gerrids from every smaller size class and with gerrids their own size. Gerrids at only one hunger level, an empty gut, were used, as for most of the species, this state maximized predatory success.

In an effort to determine how gerrids as prey compared with other prey items, the same observations as above were repeated with each of the gerrid size classes as predator and Drosophila as prey. A weighted analysis of the data was again used to correct for species differences.

D. Environmental complexity and kill success

Predator-prey size class combinations used in this part of the study were those in which the predator gerrids were able to efficiently capture and kill the prey gerrids, with efficiently being arbitrarily defined as more than five kills per 100
attacks. Thus, approximately equal numbers of trials (16) of 24 size class combinations were observed in each of four "habitats": open water, "reeds" 2.54 cm apart, "reeds" 5.08 cm apart and algae-cluttered water. All trials took place in a partly water-filled container 26 cm in diameter and 9 cm deep. Clean water was used in all the habitats except the last, where algae clumps broke the water surface. The water in this latter "habitat" was also left to stand from day to day, resulting in the formation of a slight oily film on the water surface similar to that observed in natural algae-filled pools. The "reeds" used were pipettes 14.5 cm long and 7 mm in diameter painted green with a nontoxic plastic enamel. These were placed inverted in holes bored in a plexiglass disc which was placed in the bottom of the container. The spacing of the holes thus determined the distance between the reeds, which were placed on all the intersections of either a 2.54 cm or a 5.08 cm grid pattern.

Observations consisted of placing the gerrids in the container and then recording every fifteen minutes for one hour whether or not a kill had occurred. Owing to the very large number of trials observed (1579), individual observation of each container for the whole period was not practical. As in the previous experiments, all observations were made in a controlled environmental room at 26°C under normal room lighting conditions.

In an effort to determine how the presence of light affected gerrid predation, 48 trials using the same procedures
as above were observed between size classes 10 and 2 in the "dark". Standard red photographic darkroom lamps were used to provide illumination. Normally, under white light, movement of the hand towards a gerrid resulted in an escape movement on the part of the gerrid. No such response was observed under the red light, even when the hand was only a few millimeters from the gerrid. This was felt to indicate that gerrids were unable to detect the light wavelength used. For functional purposes, then, the gerrids were in the dark.

E. Effect of predator choice of prey on predation

To determine if predator gerrids preferentially select particular prey size classes among those which the predator gerrids were found to kill efficiently, adult gerrids of all five species were presented with these size classes simultaneously. Adult gerrids only were chosen, as they kill efficiently the greatest number of prey size classes. Three prey ratios were studied, the first with only one gerrid from each prey size class present, i.e. with numbers of each prey size class equal, and the second and third with the numbers of each prey size class not equal as shown in Table 19. Adults of each species were tested separately in the first situation, but owing to a shortage of prey gerrids, in the second and third tests, the adult gerrids were lumped in their respective size classes (size class 10 comprised adult G. *notabilis* and adult G. *remigis* and size class 8 comprised adult G. *incognitus*, adult G. *incurvatus* and adult G. *buenoi*) and these were tested against
Table 19. The number of prey presented from each of the prey size classes used in determining which prey size class a predator gerrid preferred when the prey types were presented in unequal numbers. A. Prey weighted on basis of leg length. B. Prey weighted on the basis of wet weight.

<table>
<thead>
<tr>
<th>Prey size class</th>
<th>A. Prey size number</th>
<th>B. Prey size number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>small adults</td>
<td>large adults</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td>7</td>
</tr>
</tbody>
</table>
the prey. Equal numbers of each predator species within a size class were used to provide a mean size class response irrespective of species.

In the first and second tests, prey size classes 1-7 were used with adult G. notabilis and G. remigis, whereas prey size classes 1-5 were used with the other three species. In the third test, it was not practical to present all the size classes the predator gerrids were known to kill efficiently owing to the large biomass differences between the prey gerrid's weights: 54 size class 1 gerrids alone equal the weight of only one size class 7 gerrid, and for size class 10 predator gerrids, a total of 79 prey gerrids would have had to have been present. Not enough prey gerrids were available to allow this and so for size class 10 predators, only prey size classes 3-7 were presented as prey. For size class 8 predators, prey size classes 2-5 were presented as prey.

Gerrids were deprived of food for 48 hr before testing commenced and all testing was undertaken in the large clear plastic containers described above at 26°C in a controlled environment room.

3. OTHER INSECT PREDATORS OF GERRIDS

Field observations suggested that of all the predators present in the field situation, only gyrinids and notonectids would likely be major predators of gerrids. Both insects
coexist with gerrids in the field and have occasionally been observed to catch gerrids. A few gerrids have been observed caught in spider webs hung low over the water surface and one gerrid (adult _G. notabilis_ ) was observed still alive after being caught by a large odonate larva, but such predation would seem rare. Thus, the effectiveness of only gyrinids and notonectids as gerrid predators was investigated in the laboratory.

The same procedures as were used above in determining the effect of relative predator-prey size on predation were used here. Adult gyrinids, fourth instar notonectid larvae and adult notonectids were collected in the field, and all three predator types were starved for 48 hr at 26°C before testing commenced. Gyrinids, owing to their rapid movement, were tested in the large plastic containers, whereas the notonectids were tested in the small plastic containers. Testing, as above, consisted of the placing of a predator and a prey gerrid in the container, and then recording the number of attacks made in a 15-minute period and whether or not a kill was made. Each of the three predator types investigated, gyrinids, fourth instar notonectid larvae and adult notonectids, were tested with as many size classes of gerrids as was possible.
RESULTS

1. FIELD FOOD AVAILABILITY AND GERRID HUNGER LEVELS

Many of the aquatic plants support aphid populations and aphids were often observed on the water surface. In the field situation a very heavy aphid infestation (Rhopalosiphon nymphaeae (L.)) on Nuphar and Potamogeton on Marion L. in 1971 was observed, and it was hard to see how prey could be limiting for the small gerrids at least during this period. Large numbers of collembolans were also always observed on the water surface, and although very motile when alive, the turnover rate of these small insects might be quite high.

The main reasons for suggesting that food for the small gerrids at least is not limiting, however, come from the gerrids themselves. Feeding gerrids constituted less than 1% of the total number of gerrids collected on still water bodies, and hundreds were collected (see Section 1). Laboratory observations have shown that hungry gerrids are tenacious when feeding, and if the prey is small enough to be held by the forelegs, the gerrid can be handled physically without it releasing the prey. Relatively satiated gerrids, in contrast, can be easily induced to leave the prey. Thus, the low numbers of feeding gerrids collected on ponds when food was known to be present would seem to suggest that if the gerrids were not satiated, they were at least not particularly hungry, as their
prey were not retained in any number. Gerrids on streams (G. remigis) do not seem to have quite this abundance of food, however, as gerrids in this habitat were more frequently collected carrying prey items.

That hunger level of the gerrids may vary with temperature is suggested by the data in Table 20. When temperatures were low, the gerrids were satiated, but when temperatures were high (> 20°C.), they fed, indicating that the gerrids were hungry.

2. GERRIDS AS PREDATOR AND PREY

A. Effect of species and hunger on predation

Figure 37 illustrates the effect of hunger on both total percent kill (aggressiveness) and number of kills per 100 attacks (kill efficiency) for adults of each of the five species of Gerris studied. Each value for each species at each hunger level represents the weighted mean value derived from all the prey sizes which that particular size adult can kill efficiently (see below). Thus, adult G. buenoi, G. incognitus and G. incurvatus, being of size class 8, can kill efficiently prey size classes 1 to 5, and so all these size classes were used. Adult G. notabilis and G. remigis, on the other hand, being of size class 10, can kill efficiently the first seven size classes and so their mean values are calculated from seven values. Since the adults of the five species are of different sizes, it
Table 20. Gerrid hunger levels in the field situation expresses as the percent of the maximum gut capacity that was empty.

<table>
<thead>
<tr>
<th>Date</th>
<th>Location</th>
<th>n</th>
<th>% gut empty</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 14/71</td>
<td>Marion L.</td>
<td>32</td>
<td>-12.1 ± 3.1</td>
<td>9.0</td>
</tr>
<tr>
<td>May 28/71</td>
<td>Marion L.</td>
<td>22</td>
<td>24.1 ± 8.6</td>
<td>16.5</td>
</tr>
<tr>
<td>June 18/71</td>
<td>Marion L.</td>
<td>24</td>
<td>-14.0 ± 3.2</td>
<td>14.5</td>
</tr>
<tr>
<td>July 16/71</td>
<td>Marion L.</td>
<td>15</td>
<td>43.3 ± 9.5</td>
<td>20.0</td>
</tr>
<tr>
<td>July 30/72</td>
<td>Marion L.</td>
<td>12</td>
<td>73.5 ± 9.1</td>
<td>23.0</td>
</tr>
<tr>
<td>July 30/72</td>
<td>Gate Pd.</td>
<td>10</td>
<td>71.5 ± 11.7</td>
<td>24.0</td>
</tr>
</tbody>
</table>
Figure 37. The total percent kill and percent kill per attack observed for each of the five species at four hunger levels.
was felt that only through comparison of their overall performance on all their potential prey items could a realistic comparison of their predatory abilities be ascertained, since for any one size class, relative predator-prey size has a significant effect on the extent of predation.

Considering each species separately, *G. notabilis*, *G. incurvatus* and *G. incognitus* all showed significant differences in aggressiveness over the three hunger levels tested. There was no statistical difference between any of the species in number of kills per 100 attacks over the hunger levels tested (Table 21). Statistical tests on the effect of hunger did not include those values where the gerrid was satiated, as at satiation, none of the species will attack prey.

The results indicate, then, that for hungry gerrids, two basic patterns are present. Either aggressiveness declines sharply at a moderate hunger level, i.e. between when the gut is 1/3 full and when it is 2/3 full, or it declines sharply at a lower hunger level, when the gut is more than 2/3 full. *G. remigis* and *G. buenoi* seem to kill the same percent of prey presented over most states of hunger whereas the other three species do not. The situation is different, however, with respect to kill efficiency, or number of kills per 100 attacks. *G. remigis* and *G. incognitus* kill most efficiently when the gut is only 1/3 full, whereas the other species tend to kill most efficiently when maximally starved.

Table 22 and Table 23 present the results of statistical
Table 21. F-values for the effect of hunger on arcsin total percent kill and arcsin percent kill per attack for adults of each of the five species of *Gerris*. * = significant difference with 5% level of probability

<table>
<thead>
<tr>
<th>Species</th>
<th>Arcsin % kill</th>
<th>Arcsin % kill/attack</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. notabilis</em></td>
<td>12.439* (2/18)</td>
<td>2.448 (2/18)</td>
</tr>
<tr>
<td><em>G. remigis</em></td>
<td>1.708 (2/18)</td>
<td>2.204 (2/18)</td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td>0.025 (2/12)</td>
<td>0.435 (2/12)</td>
</tr>
<tr>
<td><em>G. incurvatus</em></td>
<td>5.971* (2/11)</td>
<td>0.434 (2/11)</td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>4.672* (2/11)</td>
<td>3.170 (2/11)</td>
</tr>
</tbody>
</table>
Table 22. F-values between species pairs for arcsin total percent kill by adults at each of the three hunger levels tested. * = significant difference with 5% level of probability

Arcsin % kill

48 hr starved

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>B</th>
<th>IV</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>4.037 (1/12)</td>
<td>0.046 (1/10)</td>
<td>0.922 (1/10)</td>
<td>0.154 (1/10)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td></td>
<td></td>
<td>2.684 (1/10)</td>
<td>5.785* (1/10)</td>
<td>1.519 (1/10)</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td>0.967 (1/8)</td>
<td>0.015 (1/8)</td>
</tr>
<tr>
<td>IV</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.085 (1/8)</td>
</tr>
<tr>
<td>IG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

24 hr starved

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>B</th>
<th>IV</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>11.0.9* (1/12)</td>
<td>0.030 (1/10)</td>
<td>0.095 (1/10)</td>
<td>0.426 (1/10)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td></td>
<td></td>
<td>8.437* (1/10)</td>
<td>8.144* (1/10)</td>
<td>2.553 (1/10)</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td>0.174 (1/8)</td>
<td>0.428 (1/8)</td>
</tr>
<tr>
<td>IV</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.117 (1/8)</td>
</tr>
<tr>
<td>IG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

5 hr starved

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>B</th>
<th>IV</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>27.802* (1/12)</td>
<td>5.131* (1/10)</td>
<td>0.038 (1/9)</td>
<td>0.601 (1/9)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td></td>
<td></td>
<td>0.255 (1/10)</td>
<td>29.783* (1/9)</td>
<td>29.871* (1/9)</td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td>3.104 (1/7)</td>
<td>2.375 (1/7)</td>
</tr>
<tr>
<td>IV</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.000 (1/6)</td>
</tr>
<tr>
<td>IG</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 23. F-values between species pairs for arcsin percent kill per attack by adults at each of the three hunger levels tested. * = significant difference with a 5% level of probability.

<table>
<thead>
<tr>
<th></th>
<th>Arcsin % kill/attack</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>48 hr starved</td>
</tr>
<tr>
<td>N -</td>
<td>0.311 (1/12)</td>
</tr>
<tr>
<td>R -</td>
<td>1.308 (1/10)</td>
</tr>
<tr>
<td>B -</td>
<td>0.783 (1/8)</td>
</tr>
<tr>
<td>IV -</td>
<td>0.738 (1/8)</td>
</tr>
<tr>
<td>IG -</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>24 hr starved</td>
</tr>
<tr>
<td>N -</td>
<td>1.345 (1/12)</td>
</tr>
<tr>
<td>R -</td>
<td>1.470 (1/10)</td>
</tr>
<tr>
<td>B -</td>
<td>0.094 (1/8)</td>
</tr>
<tr>
<td>IV -</td>
<td>0.774 (1/8)</td>
</tr>
<tr>
<td>IG -</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>5 hr starved</td>
</tr>
<tr>
<td>N -</td>
<td>10.066* (1/12)</td>
</tr>
<tr>
<td>R -</td>
<td>0.868 (1/10)</td>
</tr>
<tr>
<td>B -</td>
<td>0.510 (1/7)</td>
</tr>
<tr>
<td>IV -</td>
<td>2.364 (1/6)</td>
</tr>
<tr>
<td>IG -</td>
<td>-</td>
</tr>
</tbody>
</table>
tests between pairs of species for aggressiveness and kill efficiently respectively at the three hunger levels. *G. remigis* was significantly different from *G. incurvatus* at all three hunger levels with respect to aggressiveness, and with the gut only 1/3 full, was also significantly different from *G. notabilis* and *G. incognitus*. The only significant differences with respect to kill efficiency were between *G. notabilis* and both *G. remigis* and *G. incognitus* when the gut was 1/3 full.

Table 24 presents the mean values of aggressiveness and kill efficiency for the size range of prey items that fifth instar larvae of each of the species can capture. Table 25 indicates that significant heterogeneity exists between the species, with larval *G. remigis* killing about twice the number of prey items that larval *G. notabilis*, *G. incurvatus* and *G. buenoi* killed. Larval *G. incognitus* were also more aggressive than the larvae of the latter species, although not quite to the extent as were larval *G. remigis*. No significant differences in kill efficiency were noted between larvae of any of the species, although larval *G. incurvatus* and *G. incognitus* were less efficient than the larvae of the other species in capturing prey items.

The ranking of the species in terms of their aggressiveness thus depends on whether larvae or adult instars are being considered. Whether a larvae or adult, however, *G. remigis* was the most aggressive species. In the other four species, larvae generally showed a lower level of aggressiveness than did the adults, with an average of 40% fewer kills by larvae than by
Table 24. Mean values (± 1 SE) of total percent kill and percent kill per attack observed for fifth instar larvae of each of the five species of *Gerris*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Percent kill</th>
<th>Percent kill/attack</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. notabilis</em></td>
<td>25.3 ± 8.34</td>
<td>17.1 ± 8.27</td>
</tr>
<tr>
<td><em>G. remigis</em></td>
<td>62.4 ± 11.24</td>
<td>22.6 ± 7.48</td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td>17.2 ± 3.77</td>
<td>23.2 ± 8.74</td>
</tr>
<tr>
<td><em>G. incurvatus</em></td>
<td>26.2 ± 9.84</td>
<td>7.9 ± 4.00</td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>41.2 ± 4.92</td>
<td>8.9 ± 2.74</td>
</tr>
</tbody>
</table>
Table 25. F-values between species pairs for both (A) arcsin total percent kill and (B) arcsin percent kill per attack by fifth instar larvae of each of the species following starvation for 24 hr. * = significant difference with 5% probability level.

24 hr starved

A. Arcsin % kill

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>B</th>
<th>IV</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>6.374*(1/10)</td>
<td>0.015 (1/7)</td>
<td>0.004 (1/8)</td>
<td>2.043 (1/7)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>-</td>
<td>4.683 (1/7)</td>
<td>4.226 (1/8)</td>
<td>1.761 (1/7)</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>-</td>
<td>-</td>
<td>0.037 (1/5)</td>
<td>12.107*(1/4)</td>
<td></td>
</tr>
<tr>
<td>IG</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>1.731 (1/5)</td>
<td></td>
</tr>
<tr>
<td>IG</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

B. Arcsin % kill/attack

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>R</th>
<th>B</th>
<th>IV</th>
<th>IG</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>0.568 (1/10)</td>
<td>0.466 (1/7)</td>
<td>0.350 (1/8)</td>
<td>0.096 (1/7)</td>
<td></td>
</tr>
<tr>
<td>R</td>
<td>-</td>
<td>0.021 (1/7)</td>
<td>2.094 (1/8)</td>
<td>1.591 (1/7)</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>-</td>
<td>-</td>
<td>3.137 (1/5)</td>
<td>3.105 (1/4)</td>
<td></td>
</tr>
<tr>
<td>IV</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.286 (1/5)</td>
<td></td>
</tr>
<tr>
<td>IG</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
adults. In *G. remigis*, aggressiveness was virtually identical regardless of the stage of development.

An indication as to how gerrid prey items rank in comparison to other prey items in terms of catchability is provided by the data in Fig. 38. All the gerrid size classes tested (from 2 to 9) were able to capture live *Drosophila* efficiently, with the larger gerrids typically requiring only one attack to make a kill. This is quite different to when gerrids are the prey item, and suggests that as prey, gerrids might not be favoured as a food source if certain other prey items were available.

B. Relative predator-prey size and kill success

The effect of relative predator-prey size on predation is shown in Fig. 39. A species-weighted analysis of the data was used, owing to the different levels of aggressiveness shown by the different species (see above), with the results expressed in terms of *G. notabilis*. Larval *G. remigis* percent kills, larval *G. incognitus* percent kills, adult *G. remigis* percent kills and adult *G. incurvatus* percent kills were each weighted by the coefficients -0.50, -0.36, -0.20 and 1.33 respectively. No weighting of kills per unit attack was felt necessary as no significant differences were observed between the species. Relative levels of aggressiveness of each of the larval instars of the five species was assumed the same as that measured for the fifth instar larva of that species. It was also assumed that there were no species differences between how the prey
Figure 38. The total percent kill and percent kill per attack of each of the gerrid size classes when attacking *Drosophila*. • = percent kill; o = percent kill/attack; --- = 5% kill/attack threshold.
Figure 39. The (A) total percent kill and (B) percent kill/attack of each gerrid size class when attacking gerrids of its own or smaller size classes. --- = 5% kill/attack threshold.
gerrids responded, since leg length was felt to be the critical factor here and this was considered in the size class designation.

For any particular size predator, an arbitrary threshold of 5 kills per 100 attacks was chosen as the dividing line between which size classes were efficiently killed and which were not. Using this criterion, it is evident that the larger the predator gerrid, generally the more prey size classes it can prey upon. The only exception to this is with size class 8 gerrids (adults of the three smaller species) which can efficiently kill more prey size classes than can size class 9 gerrids (fifth instar larvae of the two large species).

With respect to aggressiveness, it was found that the same relationship between predator and prey size class that occurs for kill efficiency does not always apply. Occasionally, a relatively large prey size class will suffer the same percent predation as will a small prey size class, even though the larger prey are not as easily captured. This was a result of the disproportionately large number of attacks large prey tend to elicit from a predator, counteracting the reduced efficiency on the part of the predator in handling these prey. This does not, however, account for the reduced total percent kill exhibited by the larger predators attacking very small prey. Here, the numbers of attacks made per predator were almost identical with that measured with slightly larger prey, but the kill efficiency was lower, suggesting that, like the larger prey items, a handling difficulty was present. It would thus seem
that these very small prey were smaller than the optimum prey size that these predators could handle efficiently.

C. Environmental complexity and kill success

The mean values of percent kill weighted for predator species' aggressiveness (see above) for each predator size class tested in each "microhabitat" are given in Table 26. The two trends to be noticed are that the larger the predator, the greater the percent kill, and that adult gerrids kill a greater number of prey than do larval gerrids. That large gerrids would kill more prey was expected, as in Section 4 it was noted that the larger the gerrid, the greater the swath through the environment the predator sweeps as it searches for food. Since a fixed container size and time period were used in this experiment, it follows that the larger the gerrid, the greater the chance that it will thus perceive the prey and hence capture it. In the previous experiment, larval and adult differences in aggressiveness were demonstrated. These are confirmed here, as in all four microhabitats, larval kills were less than the corresponding adult kills, even when the larvae were larger than the adults.

As equal numbers of trials for each gerrid size class were observed in each of the four microhabitats, comparisons of the mean values of both larvae and adult total percent kills are feasible. Larvae and adults were considered separately owing to their different average percent kills. Table 27 lists these values, and to permit a comparison between microhabitats, also
Table 26. The mean values of percent kill weighted for predator species aggressiveness for each predator size class tested in each of the four microhabitats.

<table>
<thead>
<tr>
<th>Predator size class</th>
<th>Number of n</th>
<th>Number of prey size classes</th>
<th>Microhabitats</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reeds 2.54 cm apart</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>16</td>
<td>13.0</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>16</td>
<td>13.0</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>16</td>
<td>6.0</td>
</tr>
<tr>
<td>6</td>
<td>2</td>
<td>32 ± 4.0</td>
<td>9.5 ± 3.5</td>
</tr>
<tr>
<td>7</td>
<td>3</td>
<td>48 ± 11.6</td>
<td>11.0 ± 2.0</td>
</tr>
<tr>
<td>8</td>
<td>5</td>
<td>80 ± 4.9</td>
<td>63.4 ± 5.4</td>
</tr>
<tr>
<td>9</td>
<td>4</td>
<td>64 ± 4.6</td>
<td>33.5 ± 8.5</td>
</tr>
<tr>
<td>10</td>
<td>7</td>
<td>113 ± 3.7</td>
<td>57.7 ± 8.8</td>
</tr>
</tbody>
</table>


Table 27. Mean values for instar and adult gerrid percent kills in each of the four microhabitats tested. Comparison coefficients are used to compare values in each microhabitat with that of the open water microhabitat.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>Larva Mean</th>
<th>Larva Coefficient</th>
<th>Adult Mean</th>
<th>Adult Coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open water</td>
<td>22.1 ± 4.1</td>
<td>1.00</td>
<td>77.1 ± 4.3</td>
<td>1.00</td>
</tr>
<tr>
<td>Reeds 5.08 cm apart</td>
<td>17.6 ± 4.5</td>
<td>0.80</td>
<td>60.1 ± 5.5</td>
<td>0.78</td>
</tr>
<tr>
<td>Reeds 2.54 cm apart</td>
<td>7.8 ± 2.5</td>
<td>0.35</td>
<td>31.5 ± 5.8</td>
<td>0.41</td>
</tr>
<tr>
<td>Algae</td>
<td>10.0 ± 4.1</td>
<td>0.45</td>
<td>40.7 ± 5.2</td>
<td>0.53</td>
</tr>
</tbody>
</table>
comparison coefficients. It is obvious from these data that the stage of development, ie. larvae or adult, has virtually no effect on relative microhabitat performance, with relative total percent kills for both larvae and adult in each microhabitat being almost identical. It is also obvious that the microhabitat greatly affects the percent kill, with the greatest percent kill being in open water; reeds 5.08 cm apart, algae and reeds 2.54 cm apart gave decreasing values.

In an effort to determine if vision was indeed a sense by which gerrids detected prey, trials were run in the dark on the open water habitat for one predator-prey size class combination. The results in Table 28 suggest that the absence of light does not drastically reduce the number of kills achieved, although the number of kills was ca. 10% less. Surface ripple detection, the only plausible means of prey detection under these conditions, would thus seem reasonably efficient, allowing gerrids to potentially hunt at night almost as well as during the day. In the field, the cooler night temperatures might reduce activity to an extent which would make this night predation insignificant, but the potential is nevertheless there.

D. Effect of predator choice of prey on predation

The design of the predation experiments thus far in this study have been such that only one prey item at a time was presented to a predator. This allowed determination of the ease with which a particular prey was handled, but did not allow
Table 28. The percent kill in the open water microhabitat for size class 10 predator gerrids preying on size class 2 prey gerrids in both illuminated and dark conditions.

<table>
<thead>
<tr>
<th>Illumination</th>
<th>n</th>
<th>Percent kill</th>
<th>Mean time required for kill</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present</td>
<td>56</td>
<td>76.8</td>
<td>23.0 ± 2.0</td>
</tr>
<tr>
<td>Absent</td>
<td>48</td>
<td>66.7</td>
<td>20.6 ± 1.9</td>
</tr>
</tbody>
</table>
determination of which prey item was actually preferred by a predator: only choice experiments can do this. Figure 40 presents the results of choice experiments in which adults of each species were presented with one of each of the prey size classes which that predator size class was known to capture efficiently (see above). Adults of the small species preferred the smaller prey items, whereas adults of the two large species, *G. notabilis* and *G. remigis*, selected larger prey items. The only significant departure in the data from the expected equal predation on each size class was for *G. remigis*. With this species, it appears that the middle-size to large prey were preferred, as the largest prey item presented was not preferentially chosen.

A one-to-one prey choice is not representative of the field situation, however, where characteristically more of the smaller instars are present. In an effort to provide a situation comparable to the field, two prey instar ratios where size class numbers were not equal were presented to the adult gerrids. The first unequal prey ratio tested consisted of prey ratioed, for nothing better, on the basis of leg length. The results of this experiment (Fig. 41) indicated no significant deviation away from the null hypothesis where the prey are killed according to the number present, although the trend was for the small adults to select the smaller prey and for the large adults to select medium-sized prey. In the other unequal prey ratio tested, prey items were ratioed on the basis of biomass, resulting in a greater difference between relative size class numbers.
Figure 40. The numbers of each prey size class killed by adults of each of the five species (shaded) when one of each of the prey size classes which that size class adult gerrid can kill efficiently are presented. The solid line represents the expected ratio.
G. incognitus

G. buenoi

PREY SIZE CLASS

NUMBER KILLED
G. incurvatus

NUMBER KILLED

PREY SIZE CLASS

1 2 3 4 5
Figure 41. The numbers of each prey size class killed by adult gerrids when the numbers of the prey size classes were ratioed as to total leg length present.
Unfortunately, the smallest prey size classes had to be omitted, but among those size classes that were presented, similar results as were obtained in the previous experiment were observed (Fig. 42). The small adults preferred the smaller size classes and the large adults preferred medium-sized prey. It should be noted that for both prey ratios, this selection was for both the size class killed and the size class attacked first. That the larger prey regardless of predator size were ignored is thus not a result of their being able to escape the predator gerrid, but is rather a result of a definite preference for smaller prey.

3. OTHER INSECT PREDATORS OF GERRIDS

The results of gyrinid predation are shown in Fig. 43a. Gyrinids are somewhat unusual predators in that on encountering a prey item, they tend to corral it by swimming quickly in tight circles around the prey, yet all the while launching attacks. The effect is for a disproportionately large number of attacks to be launched, and although they are only relatively efficient at capturing first instar gerrid larvae, for all the prey size classes, they were able to kill a relatively large number of the prey presented. Gyrinids were unable to kill gerrids larger than size class 6 owing to the great leg span of the larger gerrids. When attacking a large gerrid, the only portion of the gerrid that can be grasped by a gyrinid are the legs, as the body is suspended too high above the water surface. If only one
Figure 42. The numbers of each prey size class killed by adult gerrids when the numbers of the prey size classes present were ratioed as to total biomass present.
G. buenoi  G. incognitus  G. incurvatus

**TOTAL WET WEIGHT (mg)**

**NUMBER KILLED**

PREY SIZE CLASS

1  2  3  4  5
Figure 43. The total percent kill and percent kill/attack of 
(A) gyrinids, (B) fourth instar larvae notonectids and (C) adult 
notonectids when attacking each of the ten size classes of 
gerrids. ° = total percent kill; • = percent kill/attack; --- = 5% kill/attack threshold.
leg is grasped, the gerrid can usually free itself by jumping quickly, although part of the leg may be eaten. Gyrinids, possessing chewing mandibles, bite their prey and hence ingest their food relatively quickly. If both legs on one side of the body can be grasped simultaneously by the gyrinid, the gerrid is hobbled and cannot free itself. The gyrinid then eats its way up the gerrid's legs until it reaches the body, which is then also eaten.

The effectiveness of notonectids as gerrid predators are shown in Fig. 43b and 43c. Like the gyrinids, both sizes of notonectid tested were able to capture gerrid prey up to about size class 7. However, unlike the gyrinids, notonectids are relatively more efficient at catching gerrids, but they attack less. The net effect is for the total percent kill by notonectids to be slightly less than that for gyrinids. Regardless of relative effectiveness, however, these data demonstrate that both notonectids and gyrinids are effective predators of gerrids and have the potential to significantly influence their numbers.

DISCUSSION

The greater aggressiveness demonstrated by some of the species over the others may be related to the the specific habitats preferred by the species. The characteristically aggressive nature of G. remigis may thus be related to this species' preferred habitat being on streams, where food items
are presented only once, as they are swept by the current. It would seem of selective advantage for this species to check every item floating past. Whether or not the observed heterogeneity among the other species is a real phenomenon or not is open to question. The relatively large sample sizes involved support its validity, but why on the basis of whether larva or adult the different species should be ranked differently in terms of aggressiveness is not immediately obvious. All the instars of a species cohabit the same microhabitat and so would all presumably be exposed to the same problems relating to food capture. That G. buenoï and G. incognitus which do show larval-adult differences and which are the most aggressive of the pond species are those found closest inshore may be significant. Prey items in this microhabitat often result from insects falling off emergent vegetation or jumping off the shore, and with many potential surfaces to crawl out of the water on, they might be expected to leave the water surface relatively quickly. If this is indeed the case, then one might expect a generally higher level of aggressiveness for these two species as a whole, but not just for one particular stage.

Prey selection by a predator is influenced by many variables. Those characters of the prey in particular which determine the extent of predation are relative predator-prey size, mobility, defensive capabilities, palatability and the prey's relative abundance, both to the predator and to other potential prey items. The manner in which these parameters affect predation, however, vary. Some determine the efficiency
of attack, i.e. the number of kills made per unit number of attacks, whereas others determine the preference a predator has for a particular prey item, i.e. the total number of attacks which will be launched by the predator. Thus, a prey may be easily and efficiently captured, but because it is unpalatable, may be avoided and hence not preyed upon.

Kill efficiency and prey preference have been investigated in this study as both parameters influence the extent of cannibalism among gerrids. Gerrids are raptorial insects and like the mantid (Holling, 1966), one might expect that there should be a range of prey sizes which are grasped efficiently.

Terrestrial prey items are relatively helpless on the water surface and are often held immobile by the surface tension. This means that they do not always have to be actively subdued and hence, are often not grasped in the conventional manner. With such prey, a gerrid simply uses its forelegs to maintain position on the prey, thus permitting relatively small gerrids to eat very large prey. It is only with very small prey items and with prey which are also mobile on the water surface that grasping problems arise. Gerrids have never been observed to feed upon prey too small to be grasped and it would seem that they must hold such prey for insertion of the proboscis. Similarly, potential prey items such as other gerrids and velliids which are very active on the water surface have to be physically subdued before feeding can commence and so here too, grasping of the prey is often required. Thus, regardless of the nature of the prey, one would expect a minimum size threshold to
exist below which prey are not efficiently handled. One would expect a maximum size threshold to exist only for mobile prey, as only these prey items need to be subdued.

Maximum thresholds in prey size were determined for each gerrid size class studied, indicating that for any particular size gerrid, gerrids exist which although smaller than the predator, cannot be preyed upon. However, it was only with the largest and the smallest gerrid sizes studied together that an indication of a minimum size threshold became evident, and even here, the prey were efficiently caught. Thus, for the purpose of investigating cannibalism in this genus, the concept of a minimum size threshold need not be considered, as functionally, it does not exist.

Similar results have been reported for the coccinellid beetle *Adalia decempunctata* feeding on the aphid *Microlophium evansi* (Dixon, 1959). Each successive coccinellid instar larvae captured live first instar larvae aphids more efficiently than the previous coccinellid instar larvae, and was capable of capturing efficiently a greater number of aphid instars. The relative size difference between coccinellid and aphid was not great enough to indicate a minimum size threshold, but a maximum size threshold was evident for each coccinellid instar larvae.

With respect to prey preference, it is assumed that no difference in palatability exists between gerrids of different sizes and species. However, differences do exist between gerrids from the different size classes in amount of effort
required for subduing, potential gain in energy for the predator, and perhaps in stimuli presented to the predator. Obviously, for example, as a prey item approaches a predator in size, more and more effort will be required on the part of the predator to subdue the prey. Optimal foraging theory predicts that there should be a threshold equal to the average capture rate (energy gain) in the environment and that any prey encountered which gives a lower capture rate during its handling should be bypassed (Charnov, 1973). Thus, more energy might be gained over a unit time period when handling prey from a smaller size class, since small prey are characteristically more abundant than large prey, and so long as the prey are not too small, more efficiently captured. The average capture rate with these prey would thus often be relatively higher. It is suggested further that the internal state of the predator might be involved, as the potential energy gain can only be measured in terms of the average capture rate. Thus, if a predator is very hungry, i.e. has a low average capture rate, it might be likely to attack a larger prey which requires more subduing than would a predator having its gut 2/3 filled with food. It might chance the risk of losing the prey since any prey would represent an energy gain. In this respect, then, it is interesting to note that the five species of *Gerris* studied do not seem to prefer different size classes of prey at different levels of hunger. *G. remigis* and *G. bueno* kill roughly the same percentage of prey from each size class apparently regardless of state of hunger, whereas the other three species kill fewer prey at the lowest hunger level tested, but still
show no measurable preference for smaller prey. It would thus seem that in this situation, the energy gain on the part of the predator must always exceed the loss involved in capturing and subduing the prey. However, since the average capture rate under field conditions is unknown, predictions as to what size classes should be preferred in the field are impossible to assess.

It was originally thought that in the microhabitat with reeds 2.54 cm apart, the reeds might impede movement of the largest gerrids to an extent which would even further reduce their percent kill from that expected. However, the data do not support this hypothesis, as regardless of gerrid size, relative kill was not significantly different. It would thus seem that the main factor decreasing percent kill amongst the reeds was the cover they provided, not the impedement of pursuing predators. However, this does not explain the reduced predation in the algae habitat. There, visual cover was not decreased to too great an extent, as the algae did not protrude above the water surface very far. If prey detection was partly by surface ripple detection, however, cover functionally might be increased, as the ripples would not be able to move very far before being absorbed. Regardless of the reason, though, operationally, algae works to the advantage of the prey by reducing predator effectiveness.

The above experiments always involved the presentation of only one size class to the predator at a time. What do the results of choice experiments suggest concerning prey
preference? In trials where equal numbers (one) of each prey size class were presented, the two large gerrid species (G. remigis and G. notabilis) preferred the middle-to-large prey size classes and the three small species (G. bueno, G. incognitus and G. incurvatus) preferred the smallest prey size classes. Since the adults of the large species have been shown to exhibit handling problems with the smallest prey size classes, this preference for larger gerrids may result from avoidance of these small size classes. The small adults, having no such handling difficulties, would not be expected to avoid the smallest size classes, and this was observed. That the small adults and large adults both avoided the largest prey size classes in choice experiments where unequal prey size class numbers were presented supports this interpretation. It suggests that those prey size classes preferred are those which are most efficiently captured by that size class adult, as with both equal and unequal prey ratios, the largest prey size classes presented were avoided. Just as the smallest prey are slightly but nonetheless less efficiently caught, so are the largest prey, although for the purposes of this study, they are still relatively efficiently captured when compared to other gerrid size classes. That this is simply not just a result of the greater numerical abundance of the smaller prey in the latter experiments is suggested by the similarity of the results obtained from the equal prey size class numbers choice experiments.

The extent of cannibalism among gerrids, then, would seem
to depend on the availability of efficiently captured prey items. If the preferred prey is that which is most efficiently captured, nonmotile prey, particularly live prey trapped by the surface film, would likely be preferred over relatively large gerrids, as they can resist only weakly at best. Even *Drosophila* which do not break the surface film completely but rather act as if they stick to it, moving jerkily and with difficulty, can be readily captured by gerrids their own size.

Observations of potential prey items on water surfaces in the field suggest that on lakes and ponds, small potential prey items are likely always present. It may well be, however, that there is a shortage of food items for the larger gerrids. In the pond habitat under normal conditions, then, if cannibalism of gerrids where handling difficulties are present is occurring, it is likely at a relatively low level. Only the most efficiently caught gerrids would be preyed upon. That some cannibalism always occurs seems likely, as the ease with which these gerrids are caught approaches that with which nonmotile prey are captured. The situation may be different on streams, however, owing to the possible shortage of food that may exist in this habitat.

Mortality of the small to middle-size gerrids would also seem to result from predation by insects other than gerrids. Both gyrinids and notonectids are found in the same habitat as gerrids and both have been shown capable of preying on gerrids. Both insects, however, being in the water rather than on it, are restricted to water relatively free of floating debris and
algae. Gerrids may thus have a refuge away from these predators in that they can move over and live in debris-choked waters, a habitat largely avoided by these two predators.
SECTION 6. THE MODEL

INTRODUCTION

That the species of *Gerris* studied are not ecological homologues has been demonstrated. However, owing to the great number of differences between the species and the characteristics of the genus as a whole, the consequences arising when different species coexist are not immediately obvious. Which specific differences between the species are likely to weigh most heavily in coexisting situations, and how important cannibalism might be among gerrids are unknown.

In an attempt to answer these questions, it was decided to construct a computer model capable of simulating coexisting species. This section is concerned with the organization of the data described in the preceding sections to create such a model and in the model's predictions. The main interests here, therefore, lie not in the species themselves, but in the ecological relationships between the species.

MATERIALS AND METHODS

The model described here was designed for use on the I.R.M. model 360 computer. Fortran IV was the language used in programming the model. All the data used in the model was derived from experiments and observations in the five preceding
sections.

An experimental components analysis type of approach as developed by Holling (1965, 1966) was used in the construction of a mechanistic model (Fig. 44 and Appendix 1). The model was simplified whenever possible, but as it simulated the interactions of five potentially coexisting species, a certain amount of complexity was unavoidable. Many of the same components used by Holling were contained in the model and like Holling's models, the present model describes the predator's activities once it has reached the site where it did its hunting. It does not include the location of these hunting areas by the predator.

The same four basic primary components used by Holling (1966) were used in this model, namely: (1) rate of successful search, (2) time predators are exposed to prey, (3) time spent handling prey and (4) hunger. All the equations and submodels used in the model were involved in the derivation and modification of these primary components.

The values for the parameters used in the basic version of the model are shown in Appendix 2. Descriptions of the major processes in the model are as follows:
Figure 44. A simple flow diagram describing the model constructed in the present study.
Input arrays; Initialize

Input newly hatched young

Organize species-instars into size classes

Determine hunger, etc. of the size classes

Determine potential predation

Determine actual predation

Determine new hunger, etc. of the size classes

Subtract mortality

Daily output

Seasonal output
A. Growth and moulting

Species instar growth was based on the number of degree-days accumulated each day measured in the water at Area 3 on Marion Lake in 1971. These values were determined for each day by plotting a sine curve between the maximum and minimum temperatures measured in the field. Since gerrids are on the water surface and are not in the water, on sunny days, their body temperatures became greater than water temperatures. A multiplication coefficient of 3.0 was found most realistic in simulating what the accumulated degree-days by gerrids might have been. This coefficient was maximal on the summer solstice (June 21) and decreased by 0.01 every day away from this date. The number of degree-days accumulated in this manner by the gerrids of each daily cohort of each species was monitored, and at the beginning of each iterative day, the instar of each cohort was determined from these data. Ecdyses and input of first instar gerrids following eclosion was thus at a specific time once each iterative day.

B. Predator-prey units

The 30 species-instars of the five gerrid species were each assigned into one of ten size classes on the basis of leg length as described in Section 4. Predation was between the gerrids comprising these size classes, with the gerrids in each size class capable of preying only on gerrids in its own or a smaller size class. Since each species responded to temperature differently, it was necessary to weight the response to
temperature by the size class according to the numbers of the different species comprising that size class. This weighting of size class parameters was required whenever species differences existed, with maximum gut capacity, food desired, rate of movement and aggressiveness examples of other weighted size class values. Those parameters such as maximum reactive distance, stride length and kill efficiency which were felt characteristic of the size of a gerrid irrespective of species were not weighted.

C. Number of predators and prey

Since the model was designed to simulate the interactions over an entire season, the initial gerrids fed into the system were overwintered adults. These adults commenced breeding immediately in all the species except G. notabilis, which required a temperature threshold to be exceeded before breeding could commence (although the field data suggested that this should be 15°C. 20°C. was used in an attempt to correct for actual body temperatures experienced). Oviposition rate was based on accumulated degree-days.

A daily mortality factor of 1% of the number present in each daily cohort, in addition to that resulting from potential predation by gerrids, was applied to every instar of each species on the basis of data obtained by Vepsalainen (1971c). Following breeding, mortality of the overwintered adults increased greatly, and in the model, all the adults were presumed dead 10 days after 90% of their eggs had been laid.
The effect of this latter mortality was to temporally separate the overwintered adults from the summer adults, as the number of degree-days required for gerrids to lay 90% of their eggs was less than that required by the larvae to reach maturity.

In all the species except *G. remigis*, following completion of development as an adult, those adults destined for overwintering (macropters in the bivoltine species) were assumed to leave the lake, as gerrids overwinter in a terrestrial habitat. In the bivoltine species, however, those gerrids which had developed during their fourth instar under long days with an incremental change of daylength were used to suggest which adults became summer breeding imagos. It was these latter gerrids that gave rise to a partial second generation. This mechanism for morph determination was reported for *G. odontogaster* by Vepsalainen (1971b), and since the actual mechanism in the gerrids studied is unknown, this was adopted. A half hour decrease in day length following the summer solstice was used to set a date after which any instar not already advanced to the adult stadium would become an overwintering adult. Thus, any gerrid which had reached this stage by this date will breed as soon as it matures, and any gerrid which has not reached this stage by this date will overwinter.
D. Temporal pattern of hunting bouts

The basic iterative unit of the model was one hour. Predation, the number of kills made by each predator size class on each prey size class, was determined each hour for 24 hr, as it was assumed that gerrids hunt both at night and during the day. Both feeding experiments and predation experiments indicated that the presence of light was not required for these actions to occur. Operationally, however, less predation would usually occur at night owing to the typically cooler temperatures and hence lower metabolism of the gerrids.

E. Calculation of food in the gut

The amount of food in the gut was determined in each iteration hour. If the food volume present in the gut at the beginning of the iteration was less than a specified percent of the maximum gut capacity, the amount of food present in the gut was set equal to this amount. The specified amount of food always present represented the food obtained from food items other than gerrids. At the end of each iteration hour, the amount of food initially present plus that obtained during the hour was digested, i.e. reduced, by an amount determined from the negative exponential equation in Section 3. Digestive rate varied, depending on whether the gerrids were larvae or adults, and was modified by temperature according to its effect on food consumption.
F. Estimated handling time and area searched

Handling time comprised the amount of time spent feeding plus capture time (the amount of time spent searching for a prey item). Feeding time was a maximum of two hours for the largest gerrids tested if they were maximally starved. Since this time period exceeded the length of the basic iterative unit (one hour), the gerrids in each size class were assigned to one of two states: those feeding and those not feeding. Those feeding were not capable of hunting, and hence the amount of time spent hunting by the gerrids in each size class varied, as time spent hunting per gerrid was the average among all the gerrids present in the size class.

Since both predator and prey gerrid moved, the operational rate of movement between any two size classes was the square root of the sum of the squares of their respective rates of movement. Size class rates of movement were influenced by both species and the amount of food present in the gut.

Reactive distance of the predator was also influenced by the amount of food present in the gut. Combining this value with the operational rate of movement allowed calculation of the swath through the environment swept by the gerrid. Since a finite area (50 m²) of water surface was being simulated, the area unswept was $e^{-s}$, where $S$ represents the area swept divided by 50.
G. Calculation of potential number of prey killed

A random distribution of the gerrids over the 50 m² simulation area was assumed. The number of encounters between each predator-prey size class combination was determined from the area swept and the prey density. The number of these encounters which resulted in kills depended on the efficiency with which the prey was killed, predator aggressiveness, prey preference by the predator, the degree of environmental complexity, and the amount of food desired by the predator. The mean size of the prey relative to the mean amount of food desired by the predator determined whether a predator could kill more than one prey item per iteration interval.

H. Calculation of actual number of prey killed

The potential number of each prey size class killed by each predator size class was determined assuming that these two size classes interacted independently of the other eight size classes. Hence, depending on the number of gerrids in all ten size classes, the total number of gerrids in all the size classes killed by a size class could easily exceed the number which that size class was actually capable of killing. Similarly, the total number of prey in a size class killed by all its potential predator size classes could exceed the number of prey actually present in that size class. The potential number of each prey size class killed by each predator size class was thus modified by the number of predators and prey actually present, to provide the actual numbers of each size
class killed. The distribution of this actual mortality over the species comprising the prey size class was weighted as to the number of each species present in that size class. The numbers killed were subtracted from each size class at the end of each hourly iteration.

Once the actual numbers killed by each size class had been determined, the actual volume of food gained and the actual handling time was determined in preparation for the next iteration.

RESULTS

Figure 45 demonstrates the temporal pattern of breeding by each species when alone in 1971 as predicted by the model. It can be seen that although the predicted dates of the first appearance of first instar larvae of each species agree reasonably well with the observed field data, differences exist, indicating that the measure of degree-days accumulated by the gerrids was only approximated. This was expected, for whenever a value has to be guessed, as with the coefficient relating water temperatures to gerrid body temperatures, errors arise. More attention is thus obviously needed in determining the actual body temperatures experienced by gerrids in the field situation if a more exact simulation of the observed field data is desired.

The prediction of greatest interest here is that G.
Figure 45. The predicted occurrence and numbers of first instar larvae of each of the five species produced when each species was considered separately and the stomachs were always 75% full.
incognitus is a trivoltine species. This was not initially obvious from the field data, as no attempt was made to distinguish between summer generations. Restudying the field data, however, supports the model's predictions that G. incognitus might be trivoltine in at least some habitats, as summer adults were collected on Marion L. as early as June 8 in 1972.

Since the data in Fig. 45 are the predicted results when each of the five species was run separately in the model, the numbers of first instar larvae present reflect only the consequences of intraspecific cannibalism. Unfortunately, the actual numbers of first instar larvae predicted cannot accurately be related to the field data, as the data obtained in the model represent the total number of gerrids present in the 50 m² simulated area. Observed field numbers were based on five, 1 m² samples, and since the distribution of gerrids in the field is somewhat contagious, depending on the vegetation pattern, accurate values representing the total number of gerrids present may not have been obtained. Nevertheless, the predictions are of interest, as they suggest when peaking of numbers may have occurred for each of the species in the field. Only numbers of G. buenoï and G. incurvatus are predicted to peak in late summer, in agreement with the observed field data. It should be noted, however, that since development, like egg laying, is temperature dependent, the model's predictions here, like those above, are only as valid as the assumptions used in the model. One would therefore not expect the model's
predictions to exactly duplicate the field observations.

For comparison of different simulations, perhaps the best measure of how the species are affected is in terms of the number of adult females produced during the course of the season. If two ecological homologues in equal numbers happen to invade or are simulated to invade a new habitat simultaneously, then the winning species eventually will be that which produces the greatest number of female progeny which survive to reproduce per unit time. In this model, unit time would be one summer, as the model has not been constructed to include overwintering. In the bivoltine species, adult females are of two types: those which breed the same season they mature, and those that will overwinter to breed the following spring. To distinguish the relative numbers of each female type, the pattern of presentation shown in Fig. 46 will be used in the following tables to present the results of each run of the model. Two measures of species success are thus available: the total number of females produced, i.e. including both female types, and the total number of females which will overwinter and establish the species' populations in the following year.

Table 29 shows the predicted effect of hunger level on the number of adult females produced when each species was run separately in the model. Mean hunger level of each gerrid was controlled in the model by modifying the percent of the maximum gut capacity. It should be noted that if the guts of the gerrids were always filled with food, no cannibalism would occur, and the greatest number of females would be produced.
Figure 46. The manner of presentation of predicted numbers of adult female progeny produced during the season by any one species.
Overwintered adults

Adult female spring offspring

Breeding offspring

Overwintering offspring

Adult female summer offspring

Breeding offspring

Overwintering offspring

Adult female fall offspring

Overwintering offspring

Total breeding offspring

Total overwintering offspring
Table 29. The predicted number of adult female progeny produced at the end of the summer at each of three hunger levels when each species was considered separately.

<table>
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<th>Gut 50% full</th>
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Since no animal in the field is always satiated, however, this condition was never simulated. Among the hunger levels simulated (guts 1/4, 1/2 and 3/4 filled with food), the predictions here are of interest. *G. incognitus*, *G. remigis* and *G. notabilis* should each produce the greatest number of female progeny when food is in short supply, whereas the greatest number of *G. incurvatus* and *G. buenoi* females to survive would be when food was only slightly limiting. These predictions presumably reflect the intraspecific interactions resulting from the observed different effects of hunger on species aggressiveness and species kill efficiency.

Table 30 presents the predicted results when *G. notabilis* was considered alone at three initial densities of overwintered adults. In all three simulations, the gut was assumed 3/4 filled with food. It can be seen that although the number of progeny produced increases with increasing initial numbers of gerrids, the rate of progeny increase declines. This suggests, as was expected, that there is a threshold of number of overwintered adults present above which a further increase in number will have no effect on the number of progeny produced. The main feature to be noted here, however, is that the total densities of overwintered adult females used in most of the model's simulations (20-100) are well below this threshold. These densities were also those commonly observed in the field situation.

The consequences of all the species coexisting in the same
Table 30. The predicted number of adult female progeny produced at the end of the season from varying numbers of overwintered *G. notabilis*.

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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>830</td>
</tr>
</tbody>
</table>
microhabitat are shown in Table 31. At a low hunger level (gut 3/4 filled), only *G. incognitus* is successful in producing a large number of young, and *G. incurvatus* is eliminated entirely from the system. Increasing hunger has no effect in altering the outcome, but results in an even better survival of *G. incognitus* females, and the additional elimination of both *G. remigis* and *G. buenoi* from the system. The explanation for the success of *G. incognitus*, considering its relatively low fecundity, is the low minimum temperature for growth demonstrated by this species and hence the early start to breeding. In the early spring, the larvae of other species grow only very slowly if at all owing to the cool temperatures whereas *G. incognitus* larvae grow relatively quickly. *G. incognitus* larvae are thus able to reach a size which allows them to prey on the instars of the other species, and this combined with its ability to have three generations, would seem sufficient to effectively eliminate the other coexisting species.

In the following simulated situations, hunger is always low, with the gut always 3/4 filled with food. The predictions made by the model should thus be interpreted with this in mind.

It is not realistic to simulate *G. remigis* coexisting with other species on the pond habitat, since it occurs primarily on streams. Table 32 presents the predictions obtained when only the four pond species are thus considered. It can be seen that *G. incognitus* is still dominant, although the other three species do produce slightly more progeny and no species is
Table 31. The predicted number of adult female progeny produced at the end of the season at each of three hunger levels when all five species are considered together.

<table>
<thead>
<tr>
<th>Species</th>
<th>Gut 25% full</th>
<th>Gut 50% full</th>
<th>Gut 75% full</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. incurvatus</em></td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>G. incognitus</em></td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>37</td>
<td>38</td>
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</tr>
<tr>
<td></td>
<td>214</td>
<td>214</td>
<td>0</td>
</tr>
<tr>
<td><em>G. notabilis</em></td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>10</td>
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<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
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</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td><em>G. buenoi</em></td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>0</td>
<td>0</td>
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<td></td>
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<td>1</td>
</tr>
</tbody>
</table>
Table 32. The predicted number of adult female progeny produced at the end of the season when only the four pond species are considered together.

<table>
<thead>
<tr>
<th></th>
<th>G. notabilis</th>
<th>G. incurvatus</th>
<th>G. buenoi</th>
<th>G. incognitus</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
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<td>8</td>
<td>8</td>
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<td>8</td>
</tr>
<tr>
<td></td>
<td>43</td>
<td>0</td>
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</tr>
<tr>
<td></td>
<td>261</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| (ii)    |              |               |           |              |
| 10      | 16           | 10            | 10        | 5            |
|         | 0            | 16            | 0         | 1            |
|         | 0            | 1             | 0         | 6            |
|         | 6            | 6             | 0         | 35           |
|         | 35           | 0             |           |              |
|         | 229          |               |           |              |
|         | 1            | 228           |           | 7            |
|         | 0            |               |           | 36           |
|         | 7            |               |           | 235          |

| (iii)   |              |               |           |              |
| 10      | 24           | 10            | 10        | 3            |
|         | 0            | 24            | 0         | 5            |
|         | 0            | 10            | 0         | 10           |
|         | 10           | 24            | 0         | 24           |
|         | 148          |               |           | 148          |
|         | 0            |               |           | 24           |
|         | 148          |               |           | 148          |

| (iv)    |              |               |           |              |
| 20      | 17           | 20            | 20        | 10           |
|         | 0            | 17            | 0         | 0            |
|         | 0            | 0             | 0         | 3            |
|         | 3            | 3             | 0         | 43           |
|         | 43           | 0             |           |              |
|         | 258          |               |           | 257          |
|         | 1            | 257           |           | 11           |
|         | 0            |               |           | 44           |
|         | 11           |               |           | 268          |

(continued)
<table>
<thead>
<tr>
<th></th>
<th><em>G. notabilis</em></th>
<th><em>G. incurvatus</em></th>
<th><em>G. buenoi</em></th>
<th><em>G. incognitus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>(v)</strong></td>
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</tr>
<tr>
<td></td>
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<td>140</td>
<td>0</td>
</tr>
<tr>
<td><strong>(vi)</strong></td>
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<td>25</td>
<td>25</td>
<td>25</td>
</tr>
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<td>188</td>
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<td></td>
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<td>8</td>
</tr>
<tr>
<td></td>
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<td>19</td>
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</tr>
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<td>19</td>
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<td>8</td>
</tr>
<tr>
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</tr>
<tr>
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<td>208</td>
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<tr>
<td></td>
<td>64</td>
<td>64</td>
<td>64</td>
<td>64</td>
</tr>
</tbody>
</table>
entirely eliminated from the system.

In an effort to determine what the ratio of *G. incognitus* must be relative to the other species present to allow coexistence of all four species, the model was run with varying proportions of the four pond species present. Only at the lowest *G. incognitus* density tested, when only one pair of *G. incognitus* was initially present compared to 25 pairs of each of the other three species, was the effect of its initial headstart reduced enough to permit even a moderate establishment of the other three species in the system. The advantage established by the low minimum growth threshold of *G. incognitus* is thus of major significance. It should be noted that considering only the three small species together (*G. incognitus*, *G. incurvatus* and *G. buenoi*) the results show again dominance by *G. incognitus*, indicating that *G. buenoi* and *G. incurvatus* numbers were not decimated by *G. notabilis*.

Table 33 presents the predicted results when only the species inhabiting the open water pond habitat (*G. buenoi*, *G. incurvatus* and *G. notabilis*) are considered together. All three species are capable of coexisting, even when only one pair of each of the three species are considered. The ability of *G. notabilis* to grow at lower temperatures than the other two species seems to have little effect here, presumably because the univoltine nature of *G. notabilis*, leaves it unable to follow up the advantage initially obtained. If the suggested 15°C. threshold which must be exceeded before breeding of *G. notabilis* can commence is removed, the results are still the same. The
Table 33. The predicted number of female progeny produced when only the open water pond species are considered together. * = the temperature threshold which must be exceeded for G. notabilis to commence breeding has been removed.

<table>
<thead>
<tr>
<th></th>
<th>G. notabilis</th>
<th>G. incurvatus</th>
<th>G. buenoi</th>
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<tbody>
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<td>107</td>
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<td>107</td>
</tr>
<tr>
<td></td>
<td></td>
<td>739</td>
<td></td>
</tr>
</tbody>
</table>
slight temporal breeding separation produced by this threshold thus has little effect.

Simulation of coexistence of the two univoltine species (Table 34), *G. notabilis* and *G. remigis*, suggests that *G. notabilis* would dominate, presumably owing to the greater fecundity of this species. The greater aggressiveness of *G. remigis* would not help, as it would be directed against its own young as well. The delayed initiation of breeding by *G. notabilis* again has little effect on the final outcome.

DISCUSSION

The main concern of this section has been the synthesis of much of the data obtained in the preceding five sections into a working model designed to simulate the interactions between gerrids. Models can be very valuable and elegant tools, in that they allow testing of hypotheses which, owing perhaps to their complexity and length, would be impractical to study using more conventional techniques. However, the value of a model and its predictions can only be realized if the right criteria are used to assess it.

The number of reproducing adult females in one generation per unit female of the preceding generation has been used as a measure of the relative success of a species in a number of studies (DeBach, 1969; Gilbert and Hughes, 1971). One main advantage of this criterion is that it takes into account
Table 34. The predicted number of female progeny produced at the end of the season when the three small species and the two large species are considered separately. * = the temperature threshold which must be exceeded before *G. notabilis* can commence breeding has been removed.

<table>
<thead>
<tr>
<th>(i)</th>
<th><em>G. incurvatus</em></th>
<th><em>G. buenoi</em></th>
<th><em>G. incognitus</em></th>
</tr>
</thead>
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<tr>
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<th><em>G. notabilis</em></th>
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<table>
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<th>(iii)</th>
<th><em>G. notabilis</em></th>
<th><em>G. remigis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>10*</td>
<td>413</td>
<td>18</td>
</tr>
<tr>
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<td>0</td>
</tr>
<tr>
<td>0</td>
<td>18</td>
<td>0</td>
</tr>
</tbody>
</table>
mortality of the immature stages because only the female progeny which mature are counted. In this study, this criterion per se could not be strictly used, as no data on overwintering survival of each of the species were available. If the number of females destined for overwintering are used, and winter survival discriminates against the species differently, then any conclusions derived from fall numbers would be wrong. For comparative purposes, however, the only measure available in this study were the number of adult females which mature, and so the assumption here is that winter survival does not discriminate against the species differently. Obviously this is a major assumption, and one which certainly needs future investigation.

Another consideration is that the breeding success of a female depends on when in the season the female breeds. Thus, an overwintering female of a bivoltine species might produce, owing to heavy cannibalism in the spring, only a few females, of which some will be destined to overwinter and some will be destined to breed again the same year. The latter females, perhaps owing to an absence of other gerrids in late summer, might be very successful, producing many adult female progeny. What criterion should thus be used to assess reproductive success of the population of a species during the season? Gilbert and Gutierrez (1973) recognized this problem when they stated that "maximizing individual "fitness" is certainly not the same thing as minimizing the probability of extinction". The problem here is weighting the success of an individual
against the probability of the species going extinct. To avoid this, Gilbert and Gutierrez (1973) have determined the "fitness" of the population for a number of time-intervals, and it is the sum of all these "fitnesses" which the population should, in theory, attempt to maximize. In a sense, this has been done here, with the time intervals in the bivoltine and trivoltine species being one generation. The number of adult daughters produced by the adult female offspring of the overwintered females have been considered as progeny of the overwintered females, thereby establishing a population concept. Since it has already been assumed that winter survival has no relative effects, the success of a species can thus be measured in terms of the number of overwintering adults.

One important point to stress with respect to the present model is the fact that the data used in the construction of the model were obtained from laboratory experiments. Only the environmental temperature data were taken from the field results. It is therefore of interest to note that the predictions of the present model agree favourably with those results observed in the field. Since no effort was made to formulate a model, and then through varying the parameters, obtain good approximations of census histories, the present model is felt to indicate some of the mechanisms controlling the system being studied. Cannibalism in Gerris would thus seem to be an important process whereby population numbers may be regulated. It can lead to species extinctions in coexisting situations, and where only one species is present, results in a
lower number of surviving progeny.
GENERAL DISCUSSION

A considerable body of information concerning the biology of gerrids has been accumulated in this study. It has been shown that the five species of *Gerris* are not ecological homologues and that both temporal and spatial differences exist between the species. Two of the species, *G. remigis* and *G. incognitus*, prefer specific habitats unique to that species, and where the species prefer the same habitat, as do *G. notabilis, G. incurvatus* and *G. buenoi*, microhabitat differences exist. This information, however, does not demonstrate why these differences may exist and what the consequences might be if the species did not have such habitat differences. Such questions can only be framed in a model, as only in a model is it practical to simulate the numerous interactions of all the combinations of coexisting species which are of interest. It is of value, therefore, to consider the implications of the predictions of the model in terms of how do the differences between the species influence coexistence. It should be pointed out once again that, the various bits and pieces of data that went into the model were derived from independent study of thousands of gerrids in the laboratory. The model is thus nothing but a tool designed to answer biological questions based on the above data, and by itself, has no intrinsic value.

The first major prediction by the model is that in a habitat in which *G. incognitus* breeds throughout the season, no other species produces a significant number of adult female progeny. Even a few breeding *G. incognitus* is sufficient to
establish this one as the dominant species. This prediction is supported by the observed field data. On C Inlet, the only area studied where *G. incognitus* bred throughout the season, *G. incognitus* was dominant. On Marion Lake and Gate Pond, where other species were present, *G. incognitus* was only present early in the season and largely left these areas in late June for some reason. Thus the success of *G. incognitus* in a coexisting situation is because of (1) its ability to utilize temperatures for growth lower than those capable of being utilized by the other species, and (2) its potential for being bivoltine and even perhaps trivoltine, which allows it to capitalize on the headstart created in (1). Hence, only in areas where *G. incognitus* is present all summer does it eliminate the other species present. *G. notabilis*, which has a minimum temperature for growth only slightly above that of *G. incognitus*, is univoltine and hence is unable to exploit any advantages obtained from an early start.

The second major prediction of the model is that *G. notabilis*, *G. incurvatus* and *G. buenoi* are capable of coexisting together in the same habitat for at least one season. Long term coexistence was not studied in the present study. It is thus of interest to note that in the field on the open water habitat, where all three species coexist, spatial separation (expressed in terms of preferred distance from shore) was found to exist. This supports the competitive displacement principle, and may be the mechanism which allows coexistence between these species over a number of years. If they were to coexist in the same
microhabitat, in theory at least, given enough time, the species producing the greatest number of reproducing female progeny would be expected to gradually eliminate the other two species. Unfortunately, however, as in the case of Mitchell's (1969) study, the evolutionary histories of the species being studied are unknown. Hence, although it has been shown that in theory the three open water pond species can coexist in the same habitat for at least one season, it must be concluded that there is no basis for arguing that competition in the past caused species of Gerris to specialize so as to divide resources among them.

Finally, G. remigis would seem to demonstrate adaptive radiation within the genus to exploit a new habitat. It is capable of coexisting with the pond species in theory, but it appears that it has gone its own way and has specialized to exploit the stream habitat.

In conclusion, cannibalism would seem to be a major factor capable of influencing coexistence in Gerris. It can determine which species are capable of coexisting together. Figure 47 summarizes the characteristics of the five species which appear important in their coexistence. Many problems still remain to be investigated and the model should be put to independent experimental verification. Much data is still needed before the model can be expected to run for several seasons. Only then can a complete understanding of coexistence in Gerris be attained. The data presented here, however, are felt to lay the groundwork for future study, and like most biological studies, in doing so,
Figure 47. A summary of the characteristics of the five species which seem of major importance in their coexistence.
**G. remigis**
Isolated by stream and cold water preferences.

**G. incognitus**
Isolated by preference for littered water surface habitat. Dominates in sympatric situations owing to initial headstart obtained in breeding.

**G. buenoi**
**G. incurvatus**
**G. notabilis**
Prefer open water habitat. Able to coexist in short-term situations. Preference for different distances from shore may be important in long-term coexistence.
have exposed perhaps more questions than were answered.
REFERENCES


Dixon, A. F. G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle Adalia


Riley, C.F.C. 1922. Droughts and cannibalistic responses of the


APPENDIX 1

SUBROUTINE EGG(DTEMP,N,NAF,NINAA,M,NEG,KN,XMORT)
C AEG = MAXIMUM ACCUMULATIVE NUMBER OF EGGS LAID BY EACH SPECIES
C BEG = Y - INTERCEPT OF EGGLAYING EQUATION
C NEDA = NUMBER OF DEGREE - DAYS AT DAY M
C NENA = NUMBER OF MATURE FEMALES AT DAY M
C NINAA = NUMBER OF EGGS LAID BY EACH SPECIES ON DAY M
C SEG = SLOPE IN EGGLAYING EQUATION
DIMENSION NEG (5)
DIMENSION DTEMP (5,1)
DIMENSION NEDA (5,100), NENA (5,100), M (5), SEG (8), BEG (8)
DIMENSION AEG (8)
DIMENSION NAF (5), NINAA (5)
IF (KN .NE. 0) GO TO 1
C INITIALIZES PARAMETERS
10=6
IN=5
999 FORMAT (8F6.2)
998 FORMAT (F6.0)
997 FORMAT (8F6.4)
DO 3 J = 1,5
 M (J) = 0
 DO 3 JJ = 1,100
 NENA (J, JJ) = 0
3 NENA (J, JJ) = 0
READ(IN,997) (SEG(J), J=1,8)
READ(IN,999) (AEG(J), J=1,8)
READ(IN,999) (BEG(J), J=1,8)
C TERM = MAXIMUM NUMBER OF DAYS OVER-WINTERING ADULTS LAY EGGS BEFORE
C OLD AGE MORTALITY COMMENCES AND DATE OF SWITCH TO 2ND GENERATION
C EGGLAYING
READ(IN,998) TERM
TERM = TERM + 10.
GO TO 9
C IF THE FEMALES ARE TURNED ON, THE NUMBER OF DEGREE-DAYS SINCE THEY
C WERE TURNED ON IS DETERMINED AND THE NUMBER OF EGGS TO BE ADDED TO
C THE SYSTEM IS CALCULATED
1 DO 25 JL = 1,5
30 M(JL) = M(JL) + 1
 IF (NEG(JL)) 25,25,26
26 M(JL) = M(JL) + 1
 IF (M(JL) .GT. 99) M(JL) = 99
MM = M(JL)
C ADD DEGREE-DAYS TO DAILY TOTALS AND MOVE TOTALS AHEAD ONE DAY
DEGEG = DTEMP(JL,N)
 IF (DEGEG .LT. 0.) DEGEG = 0.
NMN = DEGEG + 0.5
 IF (MM-1)30,30,31
31 DO 24 J = 2,MM
 JE = J - 1
 IF (JE.EQ.1) NXEDA = NEDA(JL,JE)
 NEDA = NXEDA
 NXEDA = NEDA(JL,J)
 IF (JE.EQ.1) NEDA(JL,JE) = DEGEG + 0.5
24 NEDA(JL,J) = NEDA + DEGEG + 0.5
30 IF (MM .EQ. 1) NEDA(JL,MM) = DEGEG + 0.5
C MOVES TOTALS OF MATURE FEMALES FOR EACH DAY AHEAD ONE DAY AND INPUTS
C NEW ADULTS
   IF (MM - 1) 32, 32, 33
33 DO 34 J = 2, MM
   JEN = J - 1
   IF (JEN .EQ. 1) NXENA = NENA(JL,JEN)
   NNENA = NXENA
   NXENA = NENA(JL,J)
   IF (JEN .EQ. 1) NENA(JL,JEN) = NAF(JL)
34 NENA(JL,J) = NNENA
C DETERMINES DAILY AND OLD AGE MORTALITY
   OLD = 0.
   DO 2 J = 1, MM
      NDAI = (NENA(JL,J) * XMORT) + 0.5
      NENA(JL,J) = NENA(JL,J) - NDAI
      NNED = NEDA(JL,J)
      IF (JL .EQ. 1 .AND. NNED .GT. 295) OLD = ((NNED - 295) / 5.) * 0.05
      IF (JL .EQ. 2 .AND. NNED .GT. 225) OLD = ((NNED - 225) / 5.) * 0.05
      IF (N .GT. TTERM) GO TO 4
      IF (JL .EQ. 3 .AND. NNED .GT. 211) OLD = ((NNED - 211) / 5.) * 0.05
      IF (JL .EQ. 4 .AND. NNED .GT. 155) OLD = ((NNED - 155) / 5.) * 0.05
      IF (JL .EQ. 5 .AND. NNED .GT. 198) OLD = ((NNED - 198) / 5.) * 0.05
      GO TO 5
4 IF (JL .EQ. 3 .AND. NNED .GT. 259) OLD = ((NNED - 259) / 5.) * 0.05
   IF (JL .EQ. 4 .AND. NNED .GT. 180) OLD = ((NNED - 180) / 5.) * 0.05
   IF (JL .EQ. 5 .AND. NNED .GT. 286) OLD = ((NNED - 286) / 5.) * 0.05
5 NOLD = (OLD * NENA(JL,J)) + 0.5
      NENA(JL,J) = NENA(JL,J) - NOLD
      IF (NENA(JL,J) .LT. 0.) NENA(JL,J) = 0
   2 CONTINUE
32 IF (MM .EQ. 1) NENA(JL,MM) = NAF(JL)
C DETERMINES NUMBER OF EGGS LAID ON BASIS OF SUMMED DEGREE-DAYS AND
C NUMBER OF MATURE FEMALES
   NOTEG = 0.
   IF (N .LT. TTERM .OR. N .GT. TTERM) GO TO 40
   DO 41 JN = 3, 5
      JJ = JN + 3
      SEG(JN) = SEG(JJ)
      AEG(JN) = AEG(JJ)
   41 BEG(JN) = BEG(JJ)
   40 DO 36 J = 1, MM
      IF (NENA(JL,J) .EQ. 0) GO TO 36
      XEG = NEDA(JL,J)
      YEG = AEG(JL) / (1. + EXP(BEG(JL) - (SEG(JL) * XEG))
      IF (JL .EQ. 1 .AND. YEG .GT. 203.) YEG = 203.
      IF (JL .EQ. 2 .AND. YEG .GT. 98.) YEG = 98.
      IF (JL .EQ. 3 .AND. YEG .GT. 72.) YEG = 72.
      IF (JL .EQ. 4 .AND. YEG .GT. 123.) YEG = 123.
      IF (JL .EQ. 5 .AND. YEG .GT. 153.) YEG = 153.
      IF (YEG .LT. 0.) YEG = 0.
      YEG = YEG * NENA(JL,J)
      XXEG = NEDA(JL,J) - NMN
      ZEG = AEG(JL) / (1. + EXP(BEG(JL) - (SEG(JL) * XXEG)))
IF (JL.EQ.1.AND.ZEG.GT.203.) ZEG = 203. - 0.5
IF (JL.EQ.2.AND.ZEG.GT.98.) ZEG = 98. - 0.5
IF (JL.EQ.3.AND.ZEG.GT.72.) ZEG = 72. - 0.5
IF (JL.EQ.4.AND.ZEG.GT.123.) ZEG = 123. - 0.5
IF (JL.EQ.5.AND.ZEG.GT.153.) ZEG = 153. - 0.5
IF (ZEG.LT.0.) ZEG = 0.
ZEG = ZEG * NENA(JL,J)
IF (N.GT.40. AND E. MOD (N , 160) .EQ.0) WRITE (10,995) YEG, ZEG
995 FORMAT (4X,2 (F6.2,2X))
NOTE = NOTE + YEG - ZEG + 0.5
36 CONTINUE
NINAA(JL) = NOTE
25 CONTINUE
9 RETURN
END
C*AD = SLOPE IN HUNGER EQUATION (INSTAR OR ADULT)
C*ADI = SPECIES INSTAR MAXIMUM DAILY INTAKE AT 26 C.
C*AHU = SPECIES INSTAR MAXIMUM GUT CAPACITY
C*ASYM = MEAN SIZE CLASS MAXIMUM GUT CAPACITY
C*AT = Y-INTERCEPT OF TEMPERATURE REGRESSION
C*BT = UNIT INCREMENT OF TEMPERATURE REGRESSION
C*DV = SIZE CLASS PREFERENCE VALUE
C*EFF = SIZE CLASS KILL EFFICIENCY
C F = FOOD IN GUT
C FDES = MEAN SIZE CLASS FOOD DESIRED (SIZHG - F)
C FFDES = INITIAL MEAN SIZE CLASS FOOD DESIRED (SIZHG - F)
C*HA = SPECIES CONSTANT IN EFFECT OF HUNGER ON % KILL
C*HB = SPECIES CONSTANT IN EFFECT OF HUNGER ON % KILL
C*HP = SPECIES % KILL COEFFICIENT RELATIVE TO NO FOOD IN GUT
C*HUIN = MEAN INSTAR FOOD NEEDED
C L = NUMBER OF CONSECUTIVE DAYS WITH TEMPERATURE ABOVE THE THRESHOLD
C REQUIRED TO COMMENCE EGGLAYING
C M = NUMBER OF DAYS SINCE SPECIES COMMENCED EGGLAYING
C MICRO = DAY THRESHOLD BEFORE WHICH IMAGOS OF BIVOLTINE SPECIES
C ARE SHORTWING
C MISC = NUMBER OF KILL ITEMS OF BIOMASS WT1 DISCARDED
C MWK = MEAN WEIGHT OF KILL ITEM BY SIZE CLASS
C NAP = NUMBER OF FEMALES TO MATURE ON EACH DAY
C NAPB = NUMBER OF EACH SPECIES MATURING TO BREED ON DAY N
C*NDM = NUMBER OF DEGREE DAYS BETWEEN SPECIES - INSTARS MOULTS
C NDIAP = NUMBER OF SPECIES-ADULTS THAT ENTER DIAPAUSE ON DAY N
C NDP = NUMBER OF EACH SPECIES ENTERING DIAPAUSE ON DAY N
C NEG = OFF - ON SWITCH FOR SPECIES TURNED ON TO REPRODUCTION
C NIDA = NUMBER OF SPECIES- DEGREE DAYS ON DAY N
C NGER = NUMBER OF SPECIES-INSTARS IN DIAPAUSE ON DAY N
C NIN = NUMBER IN SPECIES-INSTAR COHORT ON DAY (N-1)
C*NINA = NUMBER OF ANIMALS AT DAY N
C NINS = NUMBER IN SPECIES - INSTAR COHORTS
C NK = NUMBER OF PREY POTENTIALLY KILLED
C NKT = TOTAL NUMBER ACTUALLY KILLED BY SIZE CLASS
C NOSIZ = INSTAR SIZE CLASS NUMBER
C NRR = NUMBER OF MATURE ADULTS THAT ARE KILLED THROUGH PREDATION EACH
C DAY
C NSIOO = NUMBER IN SIZE CLASS AT BEGINNING OF DAY
C NSIZ0 = NUMBER IN SIZE CLASS COHORTS
C NSIZ1 = SIZE CLASS NUMBER STILL FEEDING AT TIME (T + 1)
C NWT = TOTAL BIOMASS OF KILL BY SIZE CLASS
C PROX = PROPORTION NO. PREDATORS PRESENT IS TO NUMBER
C POTENTIALLY OBTAINED
C PROY = PROPORTION NO. PRESENT IS TO NO. POTENTIALLY OBTAINED
C*RATES = SPECIES-INSTAR RATE OF MOVEMENT (M/HR)
C RATE = SIZE CLASS RATE OF MOVEMENT (M/HR) - GUT FULL
C RATT = PROPORTION OF EACH SIZE CLASS SURVIVING AT THE END OF THE DAY
C*RFW = SIZE CLASS MAXIMUM REACTIVE DISTANCE (CM)
C RRATE = SIZE CLASS RATE OF MOVEMENT ADJUSTED FOR HUNGER
C SIZHG = MEAN SIZE CLASS FOOD NEEDED
C SIZHM = MAXIMUM SIZE CLASS FOOD NEEDED
C*SPF = SIZE CLASS % KILL COEFFICIENTS RELATIVE TO POND SPECIES
C T = NUMBER OF MINUTES OUT OF THE HOUR THE PREDATORS ARE HUNTING
C*TEMP = TEMPERATURE FOR DAY N
C TH = TEMPERATURE COEFFICIENT (% OF MAXIMUM DESIRED)
C TINS = DAILY BREEDING ADULT CHANCE MORTALITY
C TOLD = DAILY BREEDING ADULT OLD AGE MORTALITY
C TTH = MEAN SIZE CLASS TEMPERATURE COEFFICIENT
C W = USEABLE DRYWEIGHT BIOMASS
C*WX = USEABLE BIOMASS OF EACH SIZE CLASS (DRIYWEIGHT PERCENT)
C WT1 = BIOMASS OF KILL NOT ASSIMILATED
C*WW = WET WEIGHT OF EACH SPECIES-INSTAR
C WZ = WET WEIGHT OF MEAN SIZE CLASS INDIVIDUAL
C*XDDGH = SPECIES TEMPERATURE THRESHOLD FOR EGGLAYING
C XEF = SIZE CLASS % KILL COEFFICIENTS RELATIVE TO G. BUENOII
C XNK = NUMBER OF PREY SIZE CLASS ACTUALLY KILLED BY PREDATOR SIZE CLASS
C YEF = SIZE CLASS % KILL COEFFICIENTS RELATIVE TO MAXIMUM % KILL
REAL MWK,NWT
DIMENSION NKT(10),MWK(10),SIZHM(10)
DIMENSION AT(5),BT(5),FDES(10)
DIMENSION T(10),T1(10),NSIZ1(10),F1(10),NK(10,10),WX(10),WZ(10)
DIMENSION PROY(10),HUGIN(5,8)
DIMENSION TH(5),SIZHG(10),PPDES(10),DV(10,10),XNK(10,10),PROX(10)
DIMENSION NWT(10),AD(2)
DIMENSION NOSIZ(5,7),AHU(5,8),ASYM(10),F(10),RATES(5,7),EFF(110,10),RFW(10,10)
DIMENSION NKDT(10),WW(5,7),RATE(10)
DIMENSION NSIZ0(10),NSIOO(10)
DIMENSION RATT(10),WT1(10),MISC(10)
DIMENSION TINS(5),TOLD(5),TTH(10)
DIMENSION NKST(10),W(10),RRATE(10)
DIMENSION NIN(5),ADI(5,8),MICRO(5),NDIAP(5)
DIMENSION NAP(5),XDDGH(5),NEG(5),L(5),M(5)
DIMENSION NIDA(5,150),NINA(5,150),NDDM(5,9),NINS(5,8),NSIZ(12),
1 TEMP(154),NAPB(5,155)
DIMENSION NRR(5),NDP(5,155),NGER(5,8,155)
DIMENSION SPF(10),XEP(10),HA(5,3),HB(5,3),HP(5),YEF(10)
DIMENSION NINAA(5),DTEMP(5,154)
EQUIVALENCE (NINS(1,1),N11), (NINS(2,1),N21), (NINS(3,1),N31), (NINS(4,1),N41), (NINS(5,1),N51)
EQUIVALENCE (HUGIN(3,2),H32), (HUGIN(4,2),H42), (HUGIN(5,2),H52),
1 (HUGIN (1, 2), H12), (HUGIN (2, 2), H22), (HUGIN (3, 3), H33),
( HUGIN (4, 3), H43), (HUGIN (5, 3), H53), (HUGIN (1, 3), H13),
( HUGIN (2, 3), H23), (HUGIN (3, 4), H34),
( HUGIN (4, 4), H44), (HUGIN (5, 4), H54), (HUGIN (3, 5), H35)
1 (HUGIN (5, 5), H55), (HUGIN (1, 4), H14), (HUGIN (2, 4), H24),
( HUGIN (4, 5), H45), (HUGIN (3, 6), H36), (HUGIN (5, 6), H56),
( HUGIN (1, 5), H15),
EQUIVALENCE (HUGIN (4, 6), H46), (HUGIN (3, 7), H37),
(HUGIN (4, 7), H47)
1 (HUGIN (5, 7), H57), (HUGIN (3, 8), H38), (HUGIN (4, 8), H48),
( HUGIN (5, 8), H58), (HUGIN (1, 6), H16), (HUGIN (2, 6), H26),
( HUGIN (1, 7), H17),
EQUIVALENCE (NINS (3, 2), N32), (NINS (4, 2), N42), (NINS (5, 2), N52),
1 (NINS (1, 2), N12), (NINS (2, 2), N22), (NINS (3, 3), N33),
( NINS (4, 3), N43),
1 (NINS (5, 3), N53), (NINS (1, 3), N13), (NINS (2, 3), N23), (NINS (3, 4), N34)
1, (NINS (4, 4), N44), (NINS (5, 4), N54), (NINS (3, 5), N35),
( NINS (5, 5), N515), (NINS (1, 4), N14), (NINS (2, 4), N24),
( NINS (4, 5), N45), (NINS (3, 6),
1 N36), (NINS (5, 6), N56), (NINS (1, 5), N15), (NINS (2, 5), N25)
EQUIVALENCE (NINS (4, 7), N47), (NINS (5, 7), N57), (NINS 3
1,8), N38), (NINS (4, 8), N48), (NINS (5, 8), N58), (NINS (1, 6), N16),
( NINS (2, 6), N26), (NINS (1, 7), N17), (NINS (2, 7), N27),
( NINS (1, 8), N18),
1 (NINS (2, 8), N28)
EQUIVALENCE (HUGIN (2, 5), H25), (NINS (4, 6), N46),
( NINS (3, 7),
1 N37)
EQUIVALENCE (TH (1), TH1), (TH (2), T2), (TH (3), T3), (TH (4), T4),
1 (TH (5), T5)
EQUIVALENCE (SPF (1), E1), (SPF (2), E2), (SPF (3), E3), (SPF (4), E4),
1 (SPF (5), E5), (SPF (6), E6), (SPF (7), E7), (SPF (8), E8),
( SPF (9), E9),
1 (SPF (10), E10)
EQUIVALENCE (XEF (1), X1), (XEF (2), X2), (XEF (3), X3), (XEF (4), X4),
1 (XEF (5), X5), (XEF (6), X6), (XEF (7), X7), (XEF (8), X8),
( XEF (9), X9),
1 (XEF (10), X10)
EQUIVALENCE (YEF (1), Y1), (YEF (2), Y2), (YEF (3), Y3), (YEF (4), Y4),
1 (YEF (5), Y5), (YEF (6), Y6), (YEF (7), Y7), (YEF (8), Y8),
( YEF (9), Y9),
1 (YEF (10), Y10), (HP (1), G1), (HP (2), G2), (HP (3), G3),
( HP (4), G4),
1 (HP (5), G5)
EQUIVALENCE (NSIZ (1), NS1), (NSIZ (2), NS2), (NSIZ (3), NS3),
1 (NSIZ (4),
1 NS4), (NSIZ (5), NS5), (NSIZ (6), NS6), (NSIZ (7), NS7), (NSIZ (8), NS8),
1 (NSIZ (9), NS9), (NSIZ (10), NS10)
\text{KN} = 0
\text{IN} = 5
\text{IO}=6
\text{TI} = 24.
\text{C SETS NUMBER OF DEGREE-DAYS AT DAY J AND NUMBER OF SPECIES AT DAY J = 0}
\text{C J=1 NOTABILIS; J=2 REMIGIS; J=3 INCOGNITUS; J=4 INCURVATUS; J=5 BUENOI}
\text{DO 1 JJ=1,5}
\text{DO 1 J = 1,150}
\text{NAFB (JJ, J)=0}
\text{NDP (JJ, J)=0}
1 \text{NIDA (JJ, J) = 0}
\text{DO 2 J = 1,5}
\text{DO 2 JJ = 1,150}
2 \text{NINA (J, JJ) = 0}
\text{C SETS NUMBERS OF SPECIES-INSTARS AT DAY J = 0}
\text{DO 3 J = 1,5}
\text{DO 3 JJ = 1,8}
3 \text{NINS (J, JJ) = 0}
\text{C SETS NUMBER OF MATURE FEMALES AT DAY -1 = 0}
DO 11 J = 1, 5
L(J) = 0
NRR(J) = 0
MICRO(J) = 0
NEG(J) = 0
NIN(J) = 0
11 NAF(J) = 0
C READS IN MAXIMUM GUT CAPACITIES
DO 89 J = 1, 5
89 READ (IN, 999) (AHU(J, K), K = 1, 8)
C READS IN TEMPERATURE REGRESSION PARAMETERS,
C HUNGER CURVE SLOPES, RATE, RFW, AND W
READ (IN, 3000) AT
READ (IN, 3000) BT
READ (IN, 3001) AD
READ (IN, 3004) (SPF(J), J = 1, 10)
DO 4113 J = 1, 5
4113 READ (IN, 3006) (HA(J, K), K = 1, 3)
READ (IN, 3006) (HB(J, K), K = 1, 3)
DO 96 J = 1, 5
96 READ (IN, 3002) (WW(J, K), K = 1, 7)
READ (IN, 3003) (RATES(J, K), K = 1, 7)
DO 240 J = 1, 10
240 READ (IN, 3004) (RFW(J, K), K = 1, 10)
READ (IN, 3004) WX
C READS IN SIZE CLASS PREFERENCE VALUES, SIZE CLASS KILL EFFICIENCIES,
C AND INSTAR SIZE CLASS VALUES
DO 88 J = 1, 10
88 READ (IN, 3004) (DV(K, J), K = 1, 10)
DO 87 J = 1, 10
87 READ (IN, 3004) (EFF(K, J), K = 1, 10)
DO 86 J = 1, 5
86 READ (IN, 1002) (NOSIZ(J, K), K = 1, 7)
C SETS NUMBERS IN SIZE CLASSES = 0
DO 5 J = 1, 12
5 NSIZ(J) = 0
READ (IN, 3000) (XDDGH(J), J = 1, 5)
C READS IN NUMBER OF DEGREE-DAYS AT WHICH SPECIES-INSTARS MOULT
C AND OVERWINTERED ADULTS
READ (IN, 1001) (NINA(J, 1), J = 1, 5)
DO 4 J = 1, 5
4 READ (IN, 1000) (NDDM(J, K), K = 1, 9)
1000 FORMAT (9(I4, 2X))
1001 FORMAT (5(I3, 3X))
1002 FORMAT (7(I2, 4X))
3000 FORMAT (5F6.2)
3001 FORMAT (5F6.3)
3002 FORMAT (7F6.0)
3003 FORMAT (7F6.2)
3004 FORMAT (10F6.3)
3005 FORMAT (10F8.0)
3006 FORMAT (3F6.2)
2224 FORMAT (1X, I3, 3X, I9, 5X, I9, 8X, I9, 6X, I9, 4X, I9)
2223 FORMAT (//4X, 'G. NOTABILIS', 4X, 'G. REMIGIS', 4X, 'G. INCOGNITUS', 2X,
1 'G. INCURVATUS', 4X, 'G. BUENOI')
READ(IN,3001) XY,XMORT,ENVIR,TC,TCC
C XMORT = % DAILY MORTALITY; NTERM = MAXIMUM NUMBER OF DAYS GERRIDS LIVE
READ(IN,1003) NTERM,(MICRO(J),J=3,5)
1003 FORMAT(4(I3,3X))
C READS IN DAILY TEMPERATURES
N=0
DO 529 JJ=1,154
529 READ(IN,3000) (DTEMP(J,JJ),J=1,5)
READ(IN,3014) TEMP
3014 FORMAT(10F6.2)
999 FORMAT(8F6.0)
DO 95 J=1,5
95 READ(IN,999) (ADI(J,K),K=1,8)
READ(IN,3005) TWET
NTWET=TWET
10 N=N+1
IF(N.EQ.160.AND.MOD(N,1).EQ.0) WRITE(IO,106)
106 FORMAT(4X,'DAY',4X,13)
LJ=0
DO 733 J=1,5
DO 732 JJ=1,N
IF(NINA(J,JJ).EQ.0) LJ=LJ+1
732 CONTINUE
733 CONTINUE
LLJ=5*N
IF(LJ.EQ.LLJ) WRITE(IO,731)
731 FORMAT(2X,'ALL SPECIES NUMBERS EQUAL ZERO')
IF(LJ.EQ.LLJ) GO TO 201
C ADDS DEGREE DAYS TO DAILY TOTALS AND MOVES TOTALS AHEAD ONE DAY
TEMP(N)=TEMP(N)+TCC
IF(N.GT.52) NTN=N-52
IF(N.EQ.52.OR.N.LT.52) NTN=52-N
DO 991 JT=1,5
DO 20 JJ=2,N
JN=JJ-1
IF(JN.EQ.1) NXIDA=NIDA(JT,JN)
NNIDA=NXIDA
NXIDA=NIDA(JT,J)
IF(JN.EQ.1) NIDA(JT,JN)=DEGDY+0.5
12 NIDA(JT,J)=NNIDA+DEGDY+0.5
7 IF(N.EQ.1) NIDA(JT,N)=NDDM(JT,8)+1
991 CONTINUE
C MOVES TOTAL OF ANIMALS FOR EACH DAY AHEAD ONE DAY
IF(N.EQ.1)9,9,8
8 DO 17 J=1,5
DO 20 JJ=2,N
JN=JJ-1
IF(JN.EQ.1) NXINA=NINA(J,JN)
NNINA=NXINA
NXINA=NINA(J,JJ)
IF(JN.EQ.1) NINA(J,JN)=NINAA(J)
C DETERMINES NUMBER OF ADULTS GOING INTO DIAPAUSE AND SUMMER BREEDING
C ADULTS
DO 245 J = 1, 5
NDIAP(J) = 0.
NAF(J) = 0
IF(NEG(J) .EQ. 0) GO TO 247
DO 242 JJ = 1, N
IF(NIDA(J, JJ) .LT. NDDM(J, 8)) GO TO 242
NXY = NIDA(J, JJ) - DEGD
IF(NXY .EQ. NDDM(J, 8) .OR. NXY .GT. NDDM(J, 8)) GO TO 242
IF(N.LT.MICRO(J)) GO TO 29
NDIAP(J) = NDIAP(J) + NINA(J, JJ)
IF(J .EQ. 2) GO TO 242
NINA(J, JJ) = 0
GO TO 242
29 IF(NEG(J) .EQ. O .OR. NEG(J) .LT. O) GO TO 242
NAF(J) = NAF(J) + (NINA(J, JJ) / 2)
242 CONTINUE
247 NDP(J, N) = NDIAP(J)
NAFB(J, N) = NAF(J)
245 CONTINUE
IF(N .EQ. 160 .AND. MOD(N, 1) .EQ. 0) WRITE(10, 1001) NDIAP
C DETERMINES OLD AGE MORTALITY OF BREEDING ADULTS
C GERRIDS LIVE A MAXIMUM OF (TERM) DAYS
TERM = NTERM + 10
DO 932 I = 1, 5
TOLD(I) = 0.
DO 933 II = 1, N
OLD = 0.
NID = NIDA(I, II)
IF(I .EQ. 1 .AND. NID .GT. 1045) OLD = ((NID - 1045) / 5.) * 0.05
IF(I .EQ. 2 .AND. NID .GT. 900 .AND. N .LT. 75) OLD = ((NID - 1900) / 5.) * 0.05
IF(I .EQ. 3 .AND. NID .GT. 896) OLD = ((NID - 896) / 5.) * 0.05
IF(I .EQ. 4 .AND. NID .GT. 777) OLD = ((NID - 777) / 5.) * 0.05
IF(I .EQ. 5 .AND. NID .GT. 808) OLD = ((NID - 808) / 5.) * 0.05
GO TO 130
131 IF(I .EQ. 3 .AND. NID .GT. 944) OLD = ((NID - 944) / 5.) * 0.05
IF(I .EQ. 4 .AND. NID .GT. 802) OLD = ((NID - 802) / 5.) * 0.05
IF(I .EQ. 5 .AND. NID .GT. 896) OLD = ((NID - 896) / 5.) * 0.05
GO TO 130
130 IF(OLD .GT. 1.) OLD = 1.
NOLD = (NINA(I, II) * OLD) + 0.5
NINA(I, II) = NINA(I, II) - NOLD
933 TOLD(I) = TOLD(I) + NOLD
932 CONTINUE
IF(N .EQ. 160 .AND. MOD(N, 1) .EQ. 0) WRITE(10, 3000) TOLD
C Assigns numbers to instars on the basis of the summed degree-days
C and determines total instar food needed at 26 degrees centigrade
C corrects for position within stadium
C Instar 7=Adult stadium; Instar 8=Mature adult; Instar 1=egg
9 DO 14 J = 1, 5
DO 21 JJ = 1, 8
NINS(J,JJ) = 0
CFF = 0.
JJJ = JJ + 1
DO 16 K = 1, N
   IF (NIDA(J,K) - NDDM(J,JJ)) 16, 16, 15
   IF (NIDA(J,K) - NDDM(J,JJJ)) 32, 32, 16
15 NINS(J,JJ) = NINS(J,JJ) + NINA(J,K)
   IF (JJ.EQ.8) CFF = 0.
   IF (JJ.EQ.8) GO TO 16
   NDIFF = NDDM(J,JJJ) - NDDM(J,JJ)
   DIF = NIDA(J,K) - NDDM(J,JJ)
   CF = (DIF/NDIFF) * 100.
   IF (CF.LT.0.40. OR. CF.EQ.0.40) CFH = (32.3 + (1.5 * CF))/100.
   IF (CF.GT.0.40) CFH = (102.4 - (0.25 * CF))/100.
   CFH = ADI(J,JJ) * CFH * NINA(J,K)
   CFF = CFF + CFH
16 CONTINUE
   HUGIN(J,JJ) = CFF
   NGER(J,JJ,N) = NINS(J,JJ)
21 CONTINUE
14 CONTINUE
C FOR THE ADULTS, IT IS ASSUMED THAT THE NUMBER OF MALES EQUALS THE
C NUMBER OF FEMALES, HENCE ADI IS THE AVERAGE OF BOTH SEXES
H18 = ADI(1,8) * N18
H28 = ADI(2,8) * N28
H38 = ADI(3,8) * N38
H48 = ADI(4,8) * N48
H58 = ADI(5,8) * N58
   IF (N.EQ.160.AND.MOD(N,1).EQ.0) WRITE(IO,1000) NINS
   IF (N.EQ.160.AND.MOD(N,1).EQ.0) WRITE(IO,400) HUGIN
400 FORMAT(10(F7.1,2X))
C DETERMINES DAILY MORTALITY
   DO 931 I=1,5
      TINS(I) = 0.
      DO 930 II=1,8
         MMORT = 0.5 + (XMORT * NINS(I,II))
         NINS(I,II) = NINS(I,II) - MMORT
      930 CONTINUE
   931 CONTINUE
   IF (N.EQ.160.AND.MOD(N,1).EQ.0) WRITE(IO,3000) TINS
C CHECKS TO SEE IF FEMALES HAVE BEEN TURNED ON TO REPRODUCTION - THIS
C REQUIRES FIVE CONSECUTIVE DAYS WITH TEMPERATURES ABOVE THE
C THRESHOLD DESIGNATED FOR THAT SPECIES (XDDGH(SP))
   DO 18 K = 1, 5
      IF (NEG(K)) 19, 19, 18
   19 NCF = 0
      IF (TEMP(N).GT.XDDGH(K)) NCF = 1
      IF (NCF) 13, 13, 22
   13 L(K) = 0
      GO TO 18
   22 L(K) = L(K) + 1
      IF (L(K).EQ.5) NEG(K) = 1
      IF (L(K).EQ.5) M(K) = 0
18 CONTINUE
C DETERMINES NUMBER OF ADULT FEMALES THAT HAVE MATURED
IF (N.EQ.160. AND. MOD(N,1).EQ.0) WRITE (IO,1019) NER
DO 35 J =1,5
IF(NEG(J)) 35,35,248
248 IF (M(J).NE.0) GO TO 35
NAF(J)=NINS(J,8)/2
NAFB(J,N)=NAF(J)
35 CONTINUE'
IF (N.EQ.160. AND. MOD (N, 1) .EQ. O) WRITE
(10,1019) NIN
IF (N.EQ. 1 60. AND.MOD (N, 1) .EQ.O) WRITE
(10,1019) NAF
DO 31
J =1,5
31 NINAA(J) = 0
CALL EGG(DTEMP,N,NAF,NINAA,M,NEG,KN,XMORT)
IF (N. EQ. 160.AND.BOD(N, 1) .EQ.O) WRITE
(10,1019) NINAA
1019 FORMAT (5(I3,2X))
KN = KN +1
C SUMS SPECIES-INSTARS TO FORM SIZE CLASSES
NS 1 = N32 + N42 + N52
NS 2 = N12 * N22 + N33 + N43 + N53
NS 3 = N13 + N23 + N34 + N44 + N54
NS 4 = N35 + N55
NS 5 = N14 + N24 + N45
NS 6 = N36 + N56
NS 7 = N15 + N25 + N46
NS 8 = N37 + N47 + N57 + N38 + N48 + N58
NS 9 = N16 + N26
NS10 = N17 + N27 + N18 + N28
NSIZ (11) = N11 + N21 + N31 + N41 + N51
C DETERMINES SIZE CLASS AGGRESIVENESS AT MAXIMUM STARVATION
C CORRECTED FOR RELATIVE RATES OF MOVEMENT AND REACTIVE DISTANCE (B=1)
DO 80 J=1,10
80 IF(NSIZ(J).EQ.0)NSIZ(J)=10000000
X1= ( (N32*E3) + (N42*E4) + (N52*E5) )/NS1
X2= ( (N12*E1) + (N22*E2) + (N33*E3) + (N43*E4) + (N53*E5) )/NS2
X3= ( (N13*E1) + (N23*E2) + (N34*E3) + (N44*E4) + (N54*E5) )/NS3
X4= ( (N35*E3) + (N55*E5) )/NS4
X5= ( (N14*E1) + (N24*E2) + (N45*E4) )/NS5
X6= ( (N36*E3) + (N56*E5) )/NS6
X7= ( (N15*E1) + (N25*E2) + (N46*E4) )/NS7
X8= ( (N37+N38)*E8) + ( (N47+N48)*E9) + ( (N57+N58)*E10) )/NS8
X9= ( (N16*E1) + (N26*E2) )/NS9
X10= (((N17+N18)*E6) + ((N27+N28)*E7))/NS10
C DETERMINES TEMPERATURE COEFFICIENT FOR EACH SPECIES
DO 33 J = 1,5
TH(J) = (AT(J) + (BT(J) * TEMP(N))) / (AT(J) + (BT(J) * 26.))
IF(J.LE.2) GO TO 33
IF(TEMP(N).LT.19.) GO TO 33
TH(2) = (1916. - (27.38 * TEMP(N)))/(1916. - (27.38 * 26))
33 CONTINUE
IF(N.EQ.160. AND. MOD(N,1).EQ.0) WRITE (IO,401)TH
401 FORMAT (5(F7.2 ,2X))
C DETERMINES MEAN SIZE CLASS FOOD NEEDED
SIZHG(1) =((H32 * T3) + (H42 * T4) + (H52 * T5)) / NS1
SIZHG(2) =((H12 * TH1) + (H22 * T2) + (H33 * T3) + (H43 *
```
1T4) + (H53 * T5)) / NS2
SIZHG(3) = (H13 * TH1) + (H23 * T2) + (H34 * T3) + (H44 * T4) + (H54 * T5)) / NS3
SIZHG(4) = (H35 * T3) + (H55 * T5)) / NS4
SIZHG(5) = (H14 * TH1) + (H24 * T2) + (H45 * T4)) / NS5
SIZHG(6) = (H36 * T3) + (H56 * T5)) / NS6
SIZHG(7) = (H15 * TH1) + (H25 * T2) + (H46 * T4)) / NS7
SIZHG(8) = (H37 * T3) + (H47 * T4) + (H57 * T5) + (H38 * T4) + (H58 * T5)) / NS8
SIZHG(9) = (H16 * TH1) + (H26 * T2)) / NS9
SIZHG(10) = (H17 * TH1) + (H27 * T2) + (H18 * TH1) + (H28 T2) / NS10

IF (N.EQ. 160 AND MOD (N, 1). EQ. 0) WRITE (IO, 400) SIZHG
```

```
C DETERMINES MAXIMUM SIZE CLASS FOOD NEEDED
SIZHM(1) = (H32 + H42 + H52) / NS1
SIZHM(2) = (H12 + H22 + H33 + H43 + H53) / NS2
SIZHM(3) = (H13 + H23 + H34 + H44 + H54) / NS3
SIZHM(4) = (H35 + H55) / NS4
SIZHM(5) = (H14 + H24 + H45) / NS5
SIZHM(6) = (H36 + H56) / NS6
SIZHM(7) = (H15 + H25 + H46) / NS7
SIZHM(8) = (H37 + H47 + H57 + H38 + H48 + H58) / NS8
SIZHM(9) = (H16 + H26) / NS9
SIZHM(10) = (H17 + H27 + H18 + H28) / NS10

IF (N.EQ. 160 AND MOD (N, 1). EQ. 0) WRITE (IO, 400) SIZHM
```

```
DO 81 J = 1, 10
IF (NSIZ (J) . NE. 10000000) GO TO 81
SIZHM(J) = 0.
SIZHG(J) = 0.
NSIZ(J) = 0
XEX(J) = 0.
81 CONTINUE

TAREA = 50.
```

```
C DETERMINES MEAN SIZE CLASS MAXIMUM GUT CAPACITY

DO 42 J = 1, 10
IF (NSIZ (J) . EQ. 0) ASYM (J) = 0.
IF (NSIZ (J) . EQ. 0) GO TO 42
XNO = 0.

DO 409 K = 1, 5
DO 410 KK = 2, 8
JK = KK - 1
IF (NOSIZ (K, JK) - J) 410, 43, 410
43 XNO = (NINS (K, KK) * AHU (K, KK)) * XNO
410 CONTINUE
409 CONTINUE

ASYM (J) = XNO / NSIZ (J)
```

```
42 CONTINUE
IF (N.EQ. 160 AND MOD (N, 1). EQ. 0) WRITE (IO, 400) ASYM
```

```
DO 74 J = 1, 10
T1(J) = 0.
F1(J) = 0.
NSIZ1(J) = 0.
NS100(J) = NSIZ(J)
F(J) = XY * ASYM (J)
WZ (J) = 0
```
TTH(J) = 0.
RATE(J) = 0.
W(J) = 0.

C DETERMINES SIZE CLASS RATE OF MOVEMENT AND SIZE CLASS USEABLE
C DRYWEIGHT BIOMASS
DO 263 I = 1, 5
DO 264 IJ = 2, 8
JJ = IJ - 1
IF (NINS(I, IJ) .EQ. 0) GO TO 264
JJJ = NOSIZ(I, JJJ)
RATE(JJJ) = (NINS(I, IJ) * RATES(I, JJJ) * TH(I)) + RATE(JJJ)
WZ(JJJ) = (NINS(I, IJ) * WW(I, JJJ)) + WZ(JJJ)
TTH(JJJ) = (NINS(I, IJ) * TH(I)) + TTH(JJJ)
264 CONTINUE
263 CONTINUE
DO 265 I = 1, 10
IF (NSIZ(I) .EQ. 0) GO TO 265
TTH(I) = TTH(I) / NSIZ(I)
WZ(I) = WZ(I) / NSIZ(I)
W(I) = WX(I) * WZ(I) * 0.01
RATE(I) = RATE(I) / NSIZ(I)
265 CONTINUE
IF (N.EQ. 160. AND. MOD(N, 1) .EQ. 0) WRITE(IO, 3005) W
IF (N.EQ. 160. AND. MOD(N, 1) .EQ. 0) WRITE(IO, 3004) RATE
C MAXIMUM VALUE OF MJ EQUALS NUMBER OF ITERATIONS PER DAY
DO 52 MJ = 1, 24
DO 3402 J = 1, 10
3402 NSIZO(J) = NSIZ(J)
IF (N.EQ. 160. AND. MOD(N, 1) .EQ. 0. AND. MJ .EQ. 1) WRITE(IO, 405) NSIZO
C J EQUALS PREDATOR SIZE CLASS
DO 411 J = 1, 10
IF (NSIZ(J) .NE. 0) GO TO 350
DO 351 JJ = 1, 10
351 NK(J, JJ) = 0
350 IF (NSIZ(J) .EQ. 0) GO TO 411
C JJ EQUALS PREY SIZE CLASS
DO 40 J = 1, 10
IF (NSIZ(JJ) .EQ. 0) NK(J, JJ) = 0
IF (NSIZ(JJ) .EQ. 0) GO TO 40
IF (J - J) 121, 121, 40
121 R = 0.
C R = CODE INDICATING POTENTIAL NUMBER KILLED GREATER THAN NUMBER
C OF PREDATORS
C MN = NUMBER OF POTENTIAL PREY PREDATOR HAS EATEN IN HOUR
MN = 0
C DETERMINES INITIAL PARAMETERS
C NOTE: ANIMALS ALWAYS HAVE XY % OF THEIR GUT FULL FROM FEEDING ON
C OTHER FOOD ITEMS BESIDES GERRIDS
IF (N.EQ. 160. AND. MOD(N, 1) .EQ. 0. AND. MJ .EQ. 1) WRITE(IO, 405) NSIZ
IF (N.EQ. 160. AND. MOD(N, 1) .EQ. 0. AND. MJ .EQ. 1) WRITE(IO, 405) NSIZ
405 FORMAT(10I6)
NHUNT = NSIZ(J) - NSIZ1(J)
T(J) = 60. * (((60. * NHUNT) + (T1(J) * NSIZ1(J))) / (60. * (NHUNT
1 + NSIZ1(J))))
F(J) = (((NHUNT * F(J)) + (NSIZ1(J) * F1(J))) / NSIZ(J)
\[ FR = \frac{F(J)}{ASYM(J)} \]

IF \((FR \lt XY)\) \(F(J) = XY \times ASYM(J)\)

C DETERMINES SIZE CLASS AGGRESIVENESS IN RELATION TO FOOD IN GUT

C ASSUMED MAXIMUM ENCOUNTERS ATTACKED WHEN % KILL IS AT MAXIMUM

\[ FR = \frac{F(J)}{ASYM(J)} \]

IF \((FR \lt 0.33)\) \(NF = 1\)

IF \((FR \gt 0.32 \text{ AND } FR \lt 0.66)\) \(NF = 2\)

IF \((FR \gt 0.65)\) \(NF = 3\)

DO 3407 \(JK = 1, 5\)

3407 \(HP(JK) = HA(JK, NF) + (HB(JK, NF) \times FR)\)

DO 4316 \(JZ = 1, 10\)

IF \((NSIOO(JZ) \cdot EQ. 0)\) \(NSIOO(JZ) = 10000000\)

4316 CONTINUE

\[
Y_1 = \frac{(G_3 \times N_{32}) + (G_4 \times N_{42}) + (G_5 \times N_{52})}{NSIOO (1)}
\]

\[
Y_2 = \frac{(G_1 \times N_{12}) + (G_2 \times N_{22}) + (G_3 \times N_{33}) + (G_4 \times N_{43}) + (G_5 \times N_{53})}{NSIOO (2)}
\]

\[
Y_3 = \frac{(G_1 \times N_{13}) + (G_2 \times N_{23}) + (G_3 \times N_{34}) + (G_4 \times N_{44}) + (G_5 \times N_{54})}{NSIOO (3)}
\]

\[
Y_4 = \frac{(G_3 \times N_{35}) + (G_5 \times N_{55})}{NSIOO (4)}
\]

\[
Y_5 = \frac{(G_1 \times N_{14}) + (G_2 \times N_{24}) + (G_4 \times N_{45})}{NSIOO (5)}
\]

\[
Y_6 = \frac{(G_3 \times N_{36}) + (G_5 \times N_{56})}{NSIOO (6)}
\]

\[
Y_7 = \frac{(G_1 \times N_{15}) + (G_2 \times N_{25}) + (G_4 \times N_{46})}{NSIOO (7)}
\]

\[
Y_8 = \frac{(G_3 \times (N_{37} + N_{38})) + (G_4 \times (N_{47} + N_{48})) + (G_5 \times (N_{57} + N_{58}))}{NSIOO (8)}
\]

\[
Y_9 = \frac{(G_1 \times N_{16}) + (G_2 \times N_{26})}{NSIOO (9)}
\]

\[
Y_{10} = \frac{(E_1 \times (N_{17} + N_{18})) + (E_2 \times (N_{27} + N_{28}))}{NSIOO (10)}
\]

DO 4317 \(JZ = 1, 10\)

IF \((NSIOO(JZ) \cdot EQ. 10000000)\) \(YEF(JZ) = 0.\)

4317 IF \((NSIOO(JZ) \cdot EQ. 10000000)\) \(NSIOO(JZ) = 0\)

IF \((N \cdot EQ. 160 \text{ AND } MOD(N, 1) \cdot EQ. 0 \text{ AND } MJ \cdot EQ. 1)\) WRITE(IO, 2003) \(J, JJ\)

2003 FORMAT(2X, I2, 2X, I2)

IF \((N \cdot EQ. 160 \text{ AND } MOD(N, 1) \cdot EQ. 0 \text{ AND } MJ \cdot EQ. 1)\) WRITE(IO, 1006) \(T(J)\)

1006 FORMAT(2X, 10F10.2)

C DETERMINES AREA SEARCHED

DO 992 \(JR = 1, 10\)

992 \(RRATE(JR) = (0.29 + (0.71 \times FR)) \times RATE(JR)\)

FF = \(F(J)\)

41 \(RVEL1 \times RRATE(J)\)

\(RVEL2 \times RRATE(JJ)\)

\(RVEL = \{(RVEL1 \times RVEL1) + (RVEL2 \times RVEL2)\} \times 0.5\)

\(RZW = RFW(J, JJ) \times (0.69 + (0.31 \times FR)) \times 0.02\)

\(ASER = RVEL \times RZW\)

\(ASER = ASER / TAREA\)

\(UNSWP = EXP(-ASER)\)

\(ASER = TAREA - (TAREA \times UNSWP)\)

C DETERMINES NUMBER OF ENCOUNTERS

\(DEN = NSIZ(JJ) \times TAREA\)

\(ENC = ASER \times DEN \times T(J) / 60. \times NSIZ(J)\)

IF \((N \cdot EQ. 160 \text{ AND } MOD(N, 1) \cdot EQ. 0 \text{ AND } MJ \cdot EQ. 1)\) WRITE(IO, 3403) \(ENC\)

3403 FORMAT(F8.3)

C DETERMINES POTENTIAL NUMBER OF JJ KILLED BY J

C AGGRESIVENESS DETERMINES TOTAL NUMBER OF ENCOUNTERS WHICH

C ACTUALLY RESULT IN AN ATTACK

\(PDES(J) = (SIZHG(J) - F(J))\)

IF \((MN \cdot EQ. 0)\) \(FPDES(J) = PDES(J)\)

\(DV(J, JJ) = 1.\)
ZEFF = ENC * XEF(J) * YEF(J)
NK(J,JJ) = (EFF(J,JJ) * ZEFF * DV(J,JJ) * ENVIR) + 0.5
IF(N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1)WRITE(IO,1010)
1EFF(J,JJ),DV(J,JJ)
1010 FORMAT(2X,2F10.2)
IF(NK(J,JJ).GT.NSIZ(J)) R=1.
C DETERMINES IF NUMBER KILLED IS GREATER THAN NUMBER OF PREDATORS
IF(NK(J,JJ).GT.NSIZ(J)) NK(J,JJ) = NSIZ(J)
IF(R.EQ.0.) NK(J,JJ) = (MN * NSIZ(J)) + NK(J,JJ)
IF(N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1)WRITE(IO,1004)
1ASER,ENC,NK(J,JJ)
1004 FORMAT(2X,2(F10.2,2X),16)
C DETERMINES HANDLING TIME, ETC. FOR THOSE HUNTING AGAIN IN THE HOUR
IF(R.NE.1) F(J)=FF
IF(R.NE.1) NSIZ(JJ)=NIZ
IF(R.NE.1) GO TO 40
C C DETERMINES IF FOOD DESIRED GREATER THAN FOOD OBTAINED
IF(FDES(J).EQ.W(JJ).OR.FDES(J).LT.W(JJ)) GO TO 40
39 NFEED = NK(J,JJ)
C H = POTENTIAL HANDLING TIME
C ENCR = POTENTIAL ENCOUNTER RATE
HT=120.
IF(J.EQ.1) HT = 60.
IF(J.EQ.2) HT = 90.
H = (W(JJ) / ASYM(J)) * HT
IF(H.GT.HT) H = HT
IF(W(JJ).GT.ASYM(J)) W(JJ) = ASYM(J)
ENCR = 60./ NK(J,JJ)
C = (0.5 * ENCR) + (0.5 * ENCR * NFEED)
T(J) = C + H
IF(T(J).GT.60.) GO TO 40
F(J) = F(J) + W(JJ)
NSIZ(JJ) = NSIZ(JJ) - NK(J,JJ)
T(J) = (60. - T(J))
MN = MN * 1
R=0.
GO TO 41
40 CONTINUE
IF(N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1)WRITE(IO,153)
1(NK(J,K),K=1,10)
411 CONTINUE
C DETERMINES ACTUAL PREDATION
DO 53 J = 1,10
IF(NSIZ(J).EQ.0) W(J) = 0.
XNKT = 0.
IF(NSIZ(J).EQ.0) GO TO 370
DO 55 JJ = 1,10
JX=JJ-J
IF(JX.GT.0) GO TO 370
C XNKT = TOTAL NUMBER OBTAINED BY PREDATOR J
NTX=NK(J,JJ)
IF(NTX.GT.NSIZ(J)) NTX=NSIZ(J)
XNKT = XNKT + NTX
55 CONTINUE
370 IF(XNKT.EQ.0.) PROX(J) = 1.
IF (XNKT.EQ.0.) GO TO 53  
PROX(J) = NSIZ(J) / XNKT  
IF (PROX(J).GT.1.) PROX(J) = 1.  
53 CONTINUE  
DO 56 JJ = 1,10  
YNKT = 0.  
IF (NSIZ(JJ).EQ.0) GO TO 371  
DO 57 J = 1,10  
JX=JJ-J  
IF(JX.GT.0) GO TO 371  
C YNKT = TOTAL NUMBER OF PREY JJ KILLED  
YNKT = YNKT * NK(J,JJ)  
57 CONTINUE  
DO 56 JJ = 1,10  
YNKT = 0.  
IF (NSIZ(JJ).EQ.0) GO TO 371  
DO 57 J = 1,10  
JX=JJ-J  
IF(JX.GT.0) GO TO 371  
C PROY = TOTAL NUMBER OF PREY JJ KILLED BY EACH PREY J  
YNKT = YNKT * NK(J,JJ)  
57 CONTINUE  
DO 122 J = 1,10  
NKT(J) = 0  
NWT(J) = 0  
DO 58 JJ = 1,10  
JX=JJ-J  
IF (JX.GT.0) XNK(J,JJ) = 0.  
IF (JX.GT.0) GO TO 372  
XNK(J,JJ) = NK(J,JJ) * PROX(J) * PROY(JJ)  
IF (XNK(J,JJ).GT.0. AND. XNK(J,JJ).LT.1.) XNK(J,JJ) = 1.  
372 IF (XNK(J,JJ).EQ.0.) NK(J,JJ) = 0  
NXNK= XNK(J,JJ) + 0.5  
NKT(J) = NKT(J) + NXNK  
58 NWT(J) = NWT(J) + (NXNK * W(JJ))  
IF (MOD(N,200).EQ.0) WRITE (IO,400) (XNK(J,I),I=1,10)  
IF (MOD(N,1005).EQ.0) WRITE (IO,1005) (NK(J,I),I=1,10)  
1005 FORMAT (2X,10I6)  
IF(NWT(J).EQ.0) MWK(J) = 0  
IF (NWT(J).EQ.0) GO TO 122  
RST=NWT(J)  
MWK(J) = (RST / NKT(J))  
122 CONTINUE  
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,3005) MWK  
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,3005) NWT  
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,405) NKT  
DO 71 JJ = 1,10  
NKT(JJ) = 0  
DO 71 J = 1,10  
NKTST(JJ) = NKST(JJ) + XNK(J,JJ)  
71 NKST(JJ) = NKST(JJ) + XNK(J,JJ)  
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,2002)  
2002 FORMAT (2X,'SIZE CLASS NUMBER KILLED PER ITERATION')  
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,405) NKST  
DO 239 J=1,10  
NKDT(J) = 0  
NKDT(J) = NKDT(J) + NKST(J)  
239 CONTINUE  
C DETERMINES MEAN KILL RATE, HANDLING TIME, FEEDING TIME  
DO 46 J = 1,10
IF (NSIZ (J).EQ.0) GO TO 83
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,405) NKT
IF (NKT (J).EQ.0) GO TO 83

C NM = NUMBER OF PREY PREDATOR HAS EATEN IN ONE HOUR
C H = HANDLING TIME
C ENCR = ENCOUNTER RATE
NM = 0
ENCR = 60. / NKT(J)
NFEED = NKT(J)
IF (NKT(J).GT.NSIZ(J)) NFEED = NSIZ(J)
HT = 120.
IF (J.EQ.1) HT = 60.
IF (J.EQ.2) HT = 90.
IF (FFDES(J) - MWK(J)) 47,48,48

48 H = (MWK(J) / ASYM(J)) * HT
IF (H.GT.HL) H = HT
IF (MWK(J).GT.ASYM(J)) W(J) = ASYM(J)
MISC(J) = 0
WT1(J) = 0.
GO TO 45

47 H = ((ASYM(J) - F(J)) / ASYM(J)) * HT
IF (H.GT.HL) H = HT
MISC(J) = NKT(J)
WT1(J) = MWK(J) - FFDES(J)

45 C = (0.5 * ENCR) + (0.5 * ENCR * NFEED)
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) C
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) H
T(J) = C + H
X = T(J)
NSIZ(J) = NSIZ(J)

70 NSIZ(J) = (NM * NSIZ(J)) + NSIZ(J)
IF (NKT(J).LT.NSIZ(J) .OR. NKT(J).EQ.NSIZ(J)) GO TO 44
NFEED = NKT(J) - NSIZ(J)
NM = NM + 1
GO TO 70

44 T(J) = (NM * T(J)) + T(J)
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) T(J)
NSIZ(J) = NSIZ

C DETERMINES PARAMETERS FOR THOSE HUNTING AND THOSE FEEDING
C AND SUBTRACTS MORTALITY
NSIZ(J) = NSIZ(J) - NKST(J)
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,405) NSIZ
RSI = NSIZ(J)
RAT = RSI / NSIZ0(J)
NFEED = (RAT * NFEED) + 0.5
IF (T(J) - 60.) 49,49,50

50 NJ = 60 / X
IF (X.GT.60.) GO TO 976
F(J) = F(J) + (NJ * MWK(J))
GO TO 977

976 F(J) = F(J)
977 NSIZ1(J) = NFEED
IF (NSIZ1(J).EQ.0) T1(J) = 0.
IF (NSIZ1(J).EQ.0) P1(J) = 0.
IF (NSIZ1(J).EQ.0) GO TO 51
$F1(J) = \frac{((F(J) \times NFEED) + WWT(J) - (NJ \times MWK(J) \times NSIZC(J)) - (WT1(J) \times MISC(J)))}{NSIZ1(J)}$

$T1(J) = 120. - T(J)$

GO TO 51

83 MISC(J) = 0
NSIZ(J) = NSIZ(J) - NKST(J)
WT1(J) = 0.

49 IF (NSIZ(J) .EQ. 0) F(J) = 0.
IF (NSIZ(J).EQ.0) GO TO 373
IF (NKT(J).EQ.0) MWK(J) = 0
IF (NKT(J).EQ.0) WT1(J) = 0
F(J) = F(J) • MWK(J) - WT1(J)

373 NSIZ1(J) = 0
F(J) = 0.
T1(J) = 0.
T(J) = 60.

C DETERMINES FOOD LOST OWING TO DIGESTION AND SUBTRACTS THIS
IF (NSIZ(J).EQ.0) GO TO 46

51 MMJ=1
IF (J.EQ.8.OR.J.EQ.10) MMJ=2
A = 0.9 • ASYM(J)
IF (F(J).GT.A) F(J) = A
HS = (ALOG (ASYM(J) / (ASYM(J) - F(J)))) / AD(MMJ)
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) F(J)
HS = HS - (1. * TTH(J))
IF (HS.LT.0.) HS = 0.
F(J) = ASYM(J) * (1. - EXP(-AD(MMJ) * HS))
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) F(J)
IF (F1(J).EQ.0.) GO TO 46
IF (F1(J).GT.A) F1(J) = A
HS1 = (ALOG (ASYM(J) / (ASYM(J) - F1(J)))) / AD(MMJ)
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) F1(J)
HS1 = HS1 - (1. * TTH(J))
IF (HS1.LT.0.) HS1 = 0.
F1(J) = ASYM(J) * (1. - EXP(-AD(MMJ) * HS1))
IF (N.EQ.160.AND.MOD(N,1).EQ.0.AND.MJ.EQ.1) WRITE (IO,1006) F1(J)

46 CONTINUE

52 CONTINUE

C DETERMINES NEW DAILY NUMBERS AFTER DAY'S PREDATION
IF (N.EQ.160.AND.MOD(N,1).EQ.0) WRITE (IO,2000) NSIOO

2000 FORMAT (2X,'NSIOO',2X,10(I5,2X))
IF (N.EQ.160.AND.MOD(N,1).EQ.0) WRITE (IO,2001) NKDT

2001 FORMAT (2X,'NKDT *',2X,10(I5,2X))
DO 75 J = 1,10
RSIO=NSIOO(J)
IF (RSIO.EQ.0) RATT(J) = 0.
IF (RSIO.EQ.0) GO TO 75
RATT(J) = NSIZ(J) / RSIO

75 CONTINUE
DO 888 J=1,5
NR=NINS(J,8)
K=NOSIZ(J,7)
NOR=RATT(K)*NR
NRB(J)=NR-NOR

888 CONTINUE
DO 76 J = 1, 5
DO 77 JJ = 2, 8
JJ = JJ + 1
JJJ = JJ - 1
DO 78 K = 1, N
 IF (NIDA(J,K) - NDDM(J,JJ)) 78, 78, 79
79 IF (NIDA(J,K) - NDDM(J,JJJ)) 123, 123, 78
123 KK = NOSIZ(J,JJJ)
 IF (NINA(J,K) .EQ. 0) GO TO 78
NINA(J,K) = (NINA(J,K) * RATT(KK)) + 0.5
CONTINUE
77 CONTINUE
76 CONTINUE
IF (N .NE. 160 .OR. MOD(N, 1).NE. 0) GO TO 413
WRITE(IO, 111)
WRITE(IO, 107)
107 FORMAT(2X, 'DEGREE DAYS'/)
WRITE(IO, 103) (NIDA(1, J), J=1, N)
103 FORMAT(10(I8, 2X))
WRITE(IO, 111)
111 FORMAT(/)
WRITE(IO, 108)
108 FORMAT(2X, 'SPECIES NUMBER AT END OF DAY'/)
DO 99 J = 1, 5
WRITE(IO, 153) (NINA(J,K), K=1, N)
153 FORMAT(10(I8, 2X))
WRITE(IO, 111)
99 CONTINUE
WRITE(IO, 109)
109 FORMAT(2X, 'SPECIES INSTAR NUMBERS AT BEGINNING OF DAY'/)
WRITE(IO, 104) ((NINS(J, KK), KK=1, 8), J=1, 5)
104 FORMAT(8(I8, 4X))
WRITE(IO, 111)
110 FORMAT(2X, 'SIZE CLASS NUMBERS AT END OF DAY'/)
WRITE(IO, 116) NSIZ
116 FORMAT(8(I8, 4X))
WRITE(IO, 111)
413 IF (N - NTWET) 10, 201, 201
201 WRITE(IO, 3540)
3540 FORMAT(/, 4X, 'NUMBER OF GERRIDS ENTERING DIAPAUSE')
WRITE(IO, 2223)
DO 2225 J = 1, N
2225 WRITE(IO, 2224) J, (NDP(K, J), K=1, 5)
WRITE(IO, 2228)
2228 FORMAT(/, 4X, 'NUMBER OF ADULTS MATURING TO BREED')
WRITE(IO, 2223)
DO 2229 J = 1, N
2229 WRITE(IO, 2224) J, (NAFB(K, J), K=1, 5)
2226 FORMAT(/, 4X, 'NUMBER OF FIRST INSTARS')
WRITE(IO, 2226)
WRITE(IO, 2223)
DO 2227 J = 1, N
2227 WRITE(IO, 2224) J, (NGER(K, 2, J), K=1, 5)
CALL EXIT
## Appendix 2

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