Experimental Studies on the Reproductive Biology of the Waterstrider *Gerris buenoi* (Heteroptera: Gerridae).

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Abstract

In a series of enclosure experiments (11 over 3 years) on the waterstrider *Gerris buenoi*, I demonstrated that food resources were limited by both intra- and interspecific competition in the field. Over a 20 fold range of egg production rates in control enclosures, food addition and interspecific competitor exclusion consistently increased egg production. The magnitude of these effects varied up to four fold among dates. Predators consistently reduced gerrid survival; the strength of this effect also varied greatly among experiments. Following a series of tests for enclosure effects, I conclude that both resources and predators limited fitness of adult *G. buenoi* in the wild, and that the strength of these effects varied dramatically among dates.

The effect of reproductive rate on lifetime fecundity, longevity and senescence was investigated. Reproductive rate was an increasing function of food level, and longevity was a decreasing function of reproductive rate. There was no effect of food level on lifetime fecundity. Senescence of females was indicated by a progressive decline in egg quality (developmental stability and hatching success), and increased reproductive rate advanced this decline. Therefore, senescence occurs in *G. buenoi*, and reproductive rate advances its onset.

The mating behaviour of *G. buenoi* was studied with a series of laboratory experiments and field observations. Mating is multiple, females are reluctant, males persistent and mating consists of a period of copulation followed by a guarding phase. Mating in females is shown to conflict with predator avoidance and foraging, but can reduce costly harassment by males. Mating females stop foraging and retreat to refuge. Increased predation risk to mating females results largely from increased capture success by predacious notonectids.

Females control most components of mating (copulation frequency, and male guarding duration), and I demonstrate that mating decisions made by females balance the costs and benefits to her. Mating frequency was significantly less when female foraging needs were increased, and females became more willing to mate when the cost of male harassment was increased. These results demonstrate a strong degree of female control of mating decisions, and support the convenience polyandry hypothesis for superfluous mating.
Table of Contents

Section                                                                 Page
---------------------------------------------------------------------------
Abstract                                                                 ii
Table of Contents                                                          iii
List of Tables                                                            vii
List of Figures                                                           ix
Acknowledgements                                                          xi
Preface                                                                  xii

CHAPTER ONE - The setting and questions.

Introduction                                                               1
  Waterstrider Natural History                                             1
  The Role of Food and Predators                                          2
  Reproductive Costs and Senescence                                      4
  The Economics of Mating Behaviour                                       6
  Conclusion                                                              7

CHAPTER TWO - Food, inter-specific competition, predation and the fitness of Gerris buenoi in the field: temporal variation in the strengths of the interactions.

Summary                                                                  8

Introduction                                                             10

Methods                                                                  12
  Study Area, Species and Food Web                                       12
  Food, Competition and Predation (Experiments 1 - 5)                    13
    Assigning the Responses                                              18
  Seasonal Variation in Egg Production Rate (Experiment 6 - 11)          19
  Tests of Enclosure Estimates                                           20
CHAPTER THREE - Reproductive rate and senescence in Gerris buenoi

Summary .......................................................... 54

Introduction ...................................................... 56

Methods .......................................................... 59
  Diet Restriction and Senescence in the Presence of Males ... 59
  Diet Restriction and Senescence in the Absence of Males ... 61

Results .......................................................... 62
  Reproductive Rate, Longevity and Lifetime Fecundity ..... 62
  Reproductive Rate and Egg Quality .......................... 69
  Regular and Irregular Development of Eggs ................. 77

Discussion ....................................................... 82
  Reproductive Rate, Longevity and Fecundity ................. 82
CHAPTER FOUR - Predation by backswimmers and the costs of mating to male and female *Gerris buenoi*

Summary .......................................................... 89

Introduction ...................................................... 90

Methods ............................................................ 92
  Biology and Study Rational ................................. 92
  Predation Risk to Males and Females ....................... 93
  Habitat Use .................................................... 94
  Movement Rates of Males and Females ....................... 94
  Notonectid Attack Success .................................. 95

Results ............................................................ 96
  Female Mortality and Presence of Males ..................... 96
  Habitat Use .................................................... 99
  Harassment and Movement Rate ............................... 99
  Notonectid Attack Success .................................. 101

Discussion ...................................................... 104
  Predation Risk to Mating Females .......................... 104
  Harassment and Predation Risk to Single Females .......... 105
  A Cost of Mate Choice? ...................................... 107
  Costs of Mating or Costs of Reproduction? ................. 107
  Mating Costs to Males ....................................... 108

CHAPTER FIVE - Convenience polyandry in *Gerris buenoi*: harassment by males, foraging conflicts and female control of mating decisions

Summary .......................................................... 110

Introduction ...................................................... 112

Methods ............................................................ 116
Behaviour in the Field ........................................ 116
Effect of Hunger on Mating Behaviour ....................... 117
Sex Ratio and Mating Behaviour .............................. 118
Harassment and Control of Mating Activity ............... 119

Results ............................................................... 120
  Pre-mating Phase .............................................. 120
  Food and Mating ............................................... 123
  Post-mating Phase ............................................ 124
  Oviposition and Territoriality ............................. 125
  Effect of Hunger on Mating ................................. 125
  Sex Ratio ...................................................... 127
  Harassment and Female Control ........................... 130

Discussion ......................................................... 135
  Convenience Polyandry ...................................... 135
  Food and Mating ............................................... 137
  Components of Mating and Female Control ............ 139
  Comparison with Other Species ............................ 142

CHAPTER SIX - Overview ......................................... 144

Literature Cited .................................................. 149
## List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Table I</td>
<td>Mean egg production rates for the four treatments of the five experiments conducted on Newell Lake</td>
<td>23</td>
</tr>
<tr>
<td>Table II</td>
<td>Results of ANOVA that included egg production for all treatments for all dates of experiments 1 - 5 on Newell Lake</td>
<td>25</td>
</tr>
<tr>
<td>Table III</td>
<td>Mean daily mortality rates for the four treatments of the five experiments conducted on Newell Lake</td>
<td>31</td>
</tr>
<tr>
<td>Table IV</td>
<td>Results of ANOVA that included daily mortality from all treatments for all dates of experiments 1 - 5 on Newell Lake</td>
<td>33</td>
</tr>
<tr>
<td>Table V</td>
<td>Definition of terms for chapter 3</td>
<td>60</td>
</tr>
<tr>
<td>Table VI</td>
<td>The effect of food level on various reproductive variables and longevity</td>
<td>67</td>
</tr>
<tr>
<td>Table VII</td>
<td>ANOVA results of the effect of food level on reproductive period, longevity, hatching period and fertility period</td>
<td>68</td>
</tr>
<tr>
<td>Table VIII</td>
<td>Regression analysis of the effect of reproductive rate and food level on reproductive period, longevity, hatching period and fertility period</td>
<td>72</td>
</tr>
<tr>
<td>Table IX</td>
<td>The effect of sex and presence of the opposite sex on stride rate</td>
<td>100</td>
</tr>
<tr>
<td>Table</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>----------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>X</td>
<td>The effect of the activity of water striders (single, mating, wrestling) on number of attacks and proportion of captures by back swimmers</td>
<td>102</td>
</tr>
<tr>
<td>XI</td>
<td>Effect of hunger on mating behaviour of <em>Gerris buenoi</em></td>
<td>126</td>
</tr>
<tr>
<td>XII</td>
<td>Effect of sex ratio on mating behaviour of <em>Gerris buenoi</em></td>
<td>128</td>
</tr>
<tr>
<td>XIII</td>
<td>Effect of sex ratio on mating behaviour of <em>Gerris buenoi</em></td>
<td>131</td>
</tr>
<tr>
<td>XIV</td>
<td>The effect of sex ratio on the duration of pre- and post-mating struggles</td>
<td>134</td>
</tr>
</tbody>
</table>
# List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Figure 1</td>
<td>The proposed IGP (intra-guild predator) food web showing direct and indirect effects between and among gerrids and notonectids</td>
<td>14</td>
</tr>
<tr>
<td>Figure 2</td>
<td>Variation in responses to food addition and exclusion of competitors</td>
<td>27</td>
</tr>
<tr>
<td>Figure 3</td>
<td>The relationship between the mean change in daily mortality as a result of excluding predators and the mean change in egg production rate as a result of excluding competitors</td>
<td>34</td>
</tr>
<tr>
<td>Figure 4</td>
<td>Proportional change in mortality rate when food is added to enclosures</td>
<td>37</td>
</tr>
<tr>
<td>Figure 5</td>
<td>Mean egg production rate of females in the absence of competition for six consecutive experiments in Box 27</td>
<td>39</td>
</tr>
<tr>
<td>Figure 6</td>
<td>The relationship between daily egg production rates of females observed in enclosures and the number of chorionated eggs in their abdomen following the experiment</td>
<td>42</td>
</tr>
<tr>
<td>Figure 7</td>
<td>The relationship between mean egg production rate in the absence of competition and mean temperature (C) during the experiment</td>
<td>48</td>
</tr>
<tr>
<td>Figure 8</td>
<td>Long-term precipitation records</td>
<td>50</td>
</tr>
</tbody>
</table>
Figure 9  The effects of food level on the temporal pattern of cumulative egg production, reproductive rate and longevity (Experiment 1) ........................................ 63

Figure 10  The effects of food level on the temporal pattern of cumulative egg production, reproductive rate and longevity (Experiment 2) ........................................ 65

Figure 11  The effects of individual reproductive rate observed at each food level on individual oviposition period and longevity ........................................ 70

Figure 12  The effects of food level on the temporal pattern of fertility and hatching success (Experiment 1) .................. 73

Figure 13  The effects of food level on the temporal pattern of fertility and hatching success (Experiment 2) .................. 75

Figure 14  The effects of individual reproductive rate observed on individual fertility period and hatching period .......................... 78

Figure 15  Normal, arrested and overdeveloped eggs ............... 80

Figure 16  Irregular development of eggs ............................... 83

Figure 17  The effect of predator (Notonecta spp.) density on the mortality of males and females in enclosures .................. 97

Figure 18  Path diagram of the mating sequence of Gerris buenoı 121

Figure 19  The effect of male harassment rate on female mating activity, frequency and receptivity .......................... 132

x
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Preface

The work presented in this thesis was conducted by the author, under the supervision of G.G.E. Scudder. Most of Chapter 5 has been published by the author in Rowe (1992). A small portion of the work presented in Chapter 3 has been jointly published with G.G.E. Scudder in Rowe and Scudder (1990). The second author’s role in this publication was that of supervisor. Other publications of the author cited in this thesis (Ludwig and Rowe 1990; Rowe and Ludwig 1991; Schluter, Price and Rowe 1991) were undertaken outside the context of this thesis and play only a minor supportive role in the interpretation of it.
Chapter One

INTRODUCTION

This thesis is about the reproductive biology of the waterstrider *Gerris buenoi* Kirkaldy (Heteroptera: Gerridae). My approach has been to focus on the organism, and to learn about it by direct observation and by experimental methods. The two main goals of the thesis were first, to provide new knowledge about the biology of waterstriders and second, to test some general ideas in evolutionary ecology. In this chapter, I introduce the study organism, identify those gaps in the current knowledge of waterstrider biology that this thesis addresses, and finally introduce the general hypotheses that are tested in this thesis.

Waterstrider Natural History

The Gerridae includes some 388 described species and occurs throughout much of the world. Most gerrids live on fresh water streams, ponds and lakes, although one genus *Halobates* occurs on the oceans (Milne and Milne 1978; Andersen 1982). Gerrids are among a small group of animals (including some spiders, beetles and other semi-aquatic bugs) that live the majority of their lives on the water surface. Specialized tarsi allow gerrids to skate on top of the water surface. *Gerris buenoi* Kirkaldy, the lead character in this thesis, is common on ponds and lakes throughout the mid-latitudes of N. America, and is the most numerous of several gerrids in the two regions of this study: Vancouver in the lower mainland, and the Chilcotin region in the Fraser Plateau (Scudder 1977;
There are five larval instars preceding the adult stage in these hemimetabolous insects. Each instar and the adult live on the water surface, although diapause and dispersive stages of the adult include time spent on land and in flight. Eggs are laid below the water surface on floating debris, or further below the surface on emergent vegetation or other surfaces. Eggs hatch several days after being oviposited, and larvae break through the surface tension to begin life on top of the water. *Gerris buenoi* is partially bivoltine in southern and central B.C. (Spence and Scudder 1980; Spence 1989). In general, adults emerge from overwinter diapause early in the spring, fly to ponds and begin reproduction. Most eggs laid early in the spring mature as wingless breeders. The majority of the eggs of this wingless morph and later eggs of diapaused adults, mature as winged non-breeding adults. In late summer and early fall winged adults leave the pond to overwinter on land in diapause.

The Role of Food and Predators

Early researchers believed that gerrid populations were regulated by cannibalism during periodic food shortages, and further, suggested little role for predators (e.g., Brinkhurst 1966; Maynard 1969; Jarvinen and Vepsalainen 1976). This view was built upon weak foundations. Food inputs to the water surface do vary greatly in time and space (Fox 1975; Spence 1979, 1983), but there was no rigorous evidence for food limitation. Cannibalism does occur in the field and laboratory (e.g., Riley 1922; Maynard 1969; Jamieson 1973), but so does predation (e.g., Jamieson 1973; Spence 1983). Thus, there was little evidence to support the view of food limitation and cannibalism as the major limits on gerrid populations.
Two recent studies by Spence have focused attention away from cannibalism. In a long-term study of the gerrid species assembly on the Fraser Plateau, Spence (1983) found strong evidence for abiotic limits on gerrid abundance and distribution. For example, significant portions of the variation in population persistence were explained by pond vegetation structure, salinity and drying. In a series of field enclosure experiments on *G. buenoi*, Spence (1986) found strong evidence for food and predator limitation of larval growth and survival, and no evidence for a significant role of cannibalism.

The role of food and predator limitation of adult fitness in the wild remains unknown. Despite a lack of supporting evidence, most of the recent work on adult gerrid behaviour and life history has assumed both food and predator limitation (e.g., Kaitala 1987; 1991; Arnqvist 1989b; Sih *et al.* 1990). The general conclusion of these works is that both mating behaviour and reproductive schedules are adapted to periods of food shortage and/or predation risk. Thus, current interpretations of the evolution of adult reproductive biology lack evidence for the very selective forces by which it assumed to be shaped. I view this as one of the critical gaps in our knowledge of gerrid biology. In a series of field enclosure experiments (Chapter 2), I narrow this gap.

Temporal variation in both the biotic and abiotic environment has been a recurrent theme in waterstrider biology and in evolutionary ecology. For example, periodic food shortages for waterstriders are assumed to play a role in population dynamics (Brinkhurst 1966; Spence 1986), and in the evolution of reproductive schedules (Kaitala 1987). However, there is little evidence in support of such variation in either food level or predation risk in waterstriders. Wiens (1977; 1986) has emphasized the role of such environmental variability in evolutionary ecology. He argues that as a result of environmental variability, population densities only rarely reach densities at which competition for resources is intense. For example,
periodic forces of mortality may keep densities below those at which resource
competition is strong. Wiens' view was in direct opposition to that prevailing in
evolutionary ecology; the McArthur-led view of invariant environments with stable
competitive relationships (Wiens 1977, 1986). Nevertheless, evidence for
competition is widespread, and evidence for temporal variability in its intensity is
sparse (Connell 1983; Schoener 1983). In Chapter 2, I discuss my field studies on
temporal variability (within and among seasons) in the intensity of biotic
interactions, including predation, and intra- and inter-specific competition. Eleven
experiments, conducted over 3 years in two locations, are used to directly assay
such environmental variability.

Reproductive Costs and Senescence

Life history theory has been dominated by the idea of "reproductive costs"
since Williams's (1966) influential note to the American Naturalist. Williams argued
that reproductive schedules evolve to maximize the trade-off between the net gain
in fitness of an incremental increase in current reproductive effort, and the fitness
costs (the "cost of reproduction") of that increment that are paid in future
reproductive value. Thus, individuals may invest less than the maximum possible
this year, so that they may preserve themselves for reproduction in the next. In
fact, all coherent discussions of life history evolution prior to (Fisher 1930; Cole
1954), and after (Stearns 1976; Charlesworth 1980) Williams's paper, were built
upon such trade-offs among fitness components. Empirical studies of reproductive
costs have proliferated in the past decade (Reznick 1985; Partridge and Harvey
1988; Lessells 1991). Kaitala (1987, 1991) has conducted a number of experiments
on the relationship between reproductive rate and longevity in waterstriders. In
general, females that are induced to reduce egg production rate (through diet
restriction) live longer than those that reproduce at a greater rate. These data, therefore, suggest that there is a cost of reproduction in some waterstrider species.

Diet restriction is also the main experimental tool for extending longevity, and has thus been extensively used to study the physiology and evolution of senescence (Harrison 1989; Hollliday 1989; Finch 1990). Senescence (aging) is characterized by a progressive decline in age-specific survival and reproductive rate, resulting from physiological deterioration (Finch 1990; Rose 1991). Diet restriction generally results in decreased reproductive rate and increased longevity, suggesting a causal link between reproductive rate and senescence. Kaitala's results suggest that reproductive rate and the rate of senescence are linked in waterstriders. Enesco et al. (1989) and others (see Finch 1990; Bell 1992) have criticized such results in studies of semelparous species. They suggest that these species produce a fixed number of eggs, during which no senescence occurs, and then die after some random interval. This null hypothesis, of no senescence, must be addressed because many studies including those on waterstriders (Kaitala 1987; 1991) and fruitflies (summarized in Rose 1991) are subject to it.

In Chapter 3, I describe similar studies on *G. buenoi* to those conducted by Kaitala (1987, 1991), to address the criticism of Enesco et al. (1989) and others. I measure physiological deterioration, as reflected in egg quality, during the reproductive period, as a function of reproductive rate. Specifically, I test the hypothesis that the rate of decline in egg quality is a function of reproductive rate. In addition, my studies provide new knowledge about *G. buenoi*, and fill gaps in the studies of Kaitala. First, these experiments provide basic life history data for *G. buenoi*, such as reproductive rate, lifetime fecundity, longevity, and the relationship between them. Secondly, I use a design different from Kaitala's, that removes the potentially confounding effect of male aging on female longevity.
The Economics of Mating Behaviour

Mating systems are increasingly viewed as the products of the conflicting interests of both sexes (Walker 1980; Thornhill and Alcock 1983; West-Eberhard et al. 1987). At the root of the conflict, is the observation that male fitness is primarily limited by the number of matings achieved, and female fitness by the quantity of resources acquired. Under this economic view, an understanding of the trade-offs involved in mating decisions is required. Waterstriders are one of the few groups in which variation in mating decisions has been studied in response to conflicting demands (Wilcox 1984; Clark 1988; Sih et al. 1990; Arnqvist 1992a). Chapters 4 and 5 describe a detailed study of mating behaviour in the wild, and a series of experiments designed to assess mating costs, and test economic hypotheses about variation in mating decisions.

In Chapter 4, I focus on predation risk associated with mating behaviour in both sexes (Daly 1978; Gwynne 1989). It is a widely held view that mating increases risk to both sexes. However, evidence for increased risk to females is sparse. Increased risk of predation to mating males and females is also assumed to have influenced the mating behaviour of gerrids (Sih et al. 1990). However, the risk of predation to mating females or males is not known. I test the hypothesis that predation by notonectids is female biased, and then go on to show that this results from mating behaviour. I examine three components of mating behaviour that may increase risk to females (harassment by males, struggles with males and copulation/guarding). I believe that this study, and a concurrent study on gerrids (Fairbairn in press), are the first to study in detail the effect of various components of mating behaviour on predation risk.

In Chapter 5, I describe and quantify mating behaviour of G. buenoi in the wild. It is one of a few comprehensive studies of gerrid mating behaviour in the
wild and the first for *G. buenoi*. These field observations suggested two hypotheses to account for variation in female mating decisions. The first observation was the appearance of a conflict between foraging and mating for females. In both the field and the laboratory, I tested the hypothesis that females with reduced foraging needs are more willing to mate. The second was the appearance of an avoidance by single females of male harassment. I tested the hypothesis that females are more willing to mate when costly harassment by males is experimentally increased. Thornhill and Alcock (1983) have suggested that females may mate multiply to avoid the costs of male harassment, and dubbed such mating systems "Convenience Polyandry". My experiments represent the first test of the hypothesis.

Conclusion

In Chapter 6 I highlight some of the contributions of the thesis, and point to some promising areas of future research.
Chapter Two

FOOD, INTER-SPECIFIC COMPETITION, PREDATION AND THE FITNESS
OF GERRIS BUENOI IN THE FIELD: TEMPORAL VARIATION
IN THE STRENGTHS OF THE INTERACTIONS

Summary

In this chapter, I focus on temporal variation in the intensity of intra- and interspecific competition in determining egg production rate, and predation in determining survival of G. buenoi. In the first part, five replicate enclosure experiments conducted over 3 years to assess temporal variation in biotic interactions. Experiments were in a 2X2 ANOVA design with two levels of food (natural or supplemented), and two levels of competitor/predators (excluded or included). Per capita egg production rates in the controls (natural food, competitors/predators included) varied over 20 fold among experiments. Both food addition, and competitor exclusion, consistently increased egg production rate. Therefore, resources are limited by both by intra- and interspecific competition. The strength of the competitive effect varied over four fold among the five dates. Predators consistently reduced gerrid density, and the strength of this effect varied over three fold among experiments. There was no evidence that reduced egg production rates result from predator avoidance by gerrids. Comparison of the reproductive condition (number of mature eggs in oviducts) of females held inside the enclosures with those captured in the wild, suggested that enclosure studies overestimated resource limitation by 60-100%. Nevertheless, they also suggest that resource limitation does occur in the wild. In a second series of experiments, I compared egg production rates in the absence of competitor/predators. The results
show dramatic seasonal variation in egg production rates, much of which results from seasonal food shortage. Finally, predation rates were measured in two habitat types (open water and 70% vegetation cover) in enclosures. These results show that vegetation reduces predation rates by 62%. In summary, results of this chapter demonstrate that the intensity of resource competition, and predation of adult gerrids, varies greatly between and within years. Both resources and predators limit adult gerrid fitness in the wild.
INTRODUCTION

Invariant environments, leading to stable competitive relationships and equilibrium densities, were key assumptions in early competition theory. These assumptions have been weakened by a growing awareness of environmental variability (Wiens 1977; Caswell 1978; den Boer 1981; Connell and Sousa 1983). Wiens (1977, 1986) has argued that because of environmental variability, populations may only rarely reach densities at which resources are limited and competition for those resources becomes strong. There are two distinct processes through which densities may come to reside below a carrying capacity determined by resource availability. In the first case, forces of mortality, such as predation and disturbance, may shift density below carrying capacity. In the second case, external forces acting directly on resource supply, or indirectly through competitors, can increase the carrying capacity. These forces may act rarely and with little force, in which case periods of relaxed or absent resource competition will be transitory, or they may be frequent and strong, in which case it is the periods of intense resource competition that will be transitory.

There is a need for long term experimental studies to assess the amount of such environmental variability (Wiens 1977, 1986; Schoener 1983; Connell 1983). To date, evidence for competition in the wild is widespread, but evidence for temporal variation in the intensity of competition is sparse (Schoener 1983; Connell 1983). The first purpose of this chapter is to assess temporal variation in both those processes that act to decrease density below carrying capacity, and those that shift carrying capacity in a population of gerrids (Heteroptera, Gerridae).

Little is known of the role of competition and predation in gerrid population dynamics. However, the evidence suggests that both forces may be variable in time. Gerrids feed, develop, and reproduce on the surface of ponds,
lakes, and streams, and are common throughout much of the world (Andersen 1982). Appropriate food on the surface is composed largely of dead or dying insects of terrestrial origin, but may also include emerging or ovipositing insects, and other gerrids (Andersen 1982; Spence 1986; Nummelin and Vepsalainen 1988). Transfer of this resource to the water surface will depend on variable abiotic factors such as wind direction. Indeed, food inputs to the water surface are highly variable in time and space (Fox 1975; Spence 1979; Nummelin and Vepsalainen, 1988).

Predators of gerrids include those attacking from below the surface (eg. backswimmers: Notonectidae, water beetles: Dytiscidae), on the surface (other gerrids and fishing spiders: Psauridae), and above the surface (birds) (Fox 1975; Spence 1983, 1986; Zimmerman and Spence 1989). All of these predators are also potential competitors (defined as intraguild predators or IGP, *sensu* Polis 1981 and Polis *et al.*, 1989). In this study I focus on sub-surface predators, primarily notonectids. Gerrids probably have little effect on notonectid population dynamics. Notonectids feed on a wide variety of sub-surface and surface prey; gerrids probably comprise a small portion of their diet (Giller 1986). Notonectid population dynamics appears to be regulated by cannibalism (Fox 1975; Sih 1981).

In a recent series of experiments, Spence (1986) demonstrated that food limits larval growth, and that predators limit larval survival. There have been no analogous studies of adult gerrids, although food and predator limitation appear to have influenced the evolution of gerrid mating behaviours and reproductive strategies (*e.g.*, Wilcox 1984; Kaitala 1987, 1991; Arnqvist 1989b; Rowe and Scudder 1990; Sih *et al.* 1990; Chapters 4 and 5). In this chapter I report on a series of field enclosure experiments conducted on eleven dates over a three year period. These experiments assess temporal variation in predation risk and food limitation, resulting from both inadequate food inputs to the water surface and from inter-
specific competition for that food. I quantify the effect of these processes on two key fitness components, survival and egg production rate.

My experiments are designed to assess variation in processes acting upon gerrids, not to assess the magnitude of those processes in the wild. For example, an increase in predation rates from 5 to 10% between experiments, demonstrates an increase in predation risk to gerrids. However, because of a myriad of potential enclosure effects, the magnitude of predation rates outside enclosures may differ greatly from those within. Thus, the third purpose of this study is to determine if gerrids are actually food and/or predator limited in the wild. To determine if gerrids outside my enclosures are food limited, I develop an index of egg production rate from females in the enclosures, and then apply the index to gerrids captured in the wild. To determine whether the minimal refuge available in my enclosures results in overestimation of predation rates, I measure the effect of refuge availability on predation rates.

METHODS

Study Area, Species and Food Web

All experiments were conducted in either Newell Lake or Box 27 at Beecher’s Prairie on the Chilcotin Plateau of central British Columbia. Beecher’s Prairie, located just north of Riske Creek, is a 92 km$^2$ grassland containing over 75 lakes and ponds. Limnological and biological characteristics of the water bodies are provided in Topping and Scudder (1977), Spence (1979), and Lancaster and Scudder (1987). Newel Lake and Box 27 are small (1.5 and 2.2 hectares) fresh water ponds, with maximum depths of 2.0m and 0.9m (Boyd and Savard 1987).
Exact locations of these ponds are given in Spence (1979). *Gerris buenoi* is the smallest, and numerically dominant, of five gerrid species at Beecher's Prairie (Spence 1979). The life cycle is partially bivoltine, with seasonal wing polymorphism and winter diapause as adults (Spence and Scudder 1980). The distribution, abundance, and life history of gerrids on Beecher's Prairie have been extensively studied by Spence (Spence 1979, Spence and Scudder 1980, Spence 1983).

My studies concentrate on the interactions between *G. buenoi* and notonectids, one of their IGP predators. This IGP food web under study is shown in Figure 1. Solid arrows leading from gerrids and notonectids to food supply, indicate consumption of surface food. This shared resource results in the potential for food competition between gerrids and notonectids (an indirect negative effect, indicated by the dashed line). Notonectids prey on gerrids, resulting in a direct negative effect of notonectids on gerrids (solid arrow leading to gerrids). Dashed arrows leading to and from gerrids, indicate intraspecific resource competition. My experiments focus on direct (predation) and indirect (interspecific competition) effects of notonectids upon *G. buenoi*, and intraspecific competition among *G. buenoi*. The two response variables were egg production rate and survival. I chose egg production rate because it is easily measured, and responds rapidly to variation in food supply (Kaitala 1987, 1991; Chapter 3).

Food, Competition and Predation (Experiments 1 - 5)

A 2 X 2 replicated factorial experiment was repeated on 5 dates over a three year period to assess temporal variation and covariation in intra- and interspecific competition, reproductive rate and predation on survival of *G. buenoi*. The two factors of the experiment were food level, and presence or absence of
Figure 1. The proposed IGP (intraguild predator) food web showing direct and indirect effects within gerrids and between gerrids and notonectids. Both gerrids and notonectids share the surface food (Resource). Use of the resource is indicated by solid lines leading to it. Sharing the resources leads to the potential for competition within gerrids and notonectids (intraspecific competition) and between them (interspecific competition). These indirect interactions are shown with dashed lines. Notonectids, the IGP, also feed on gerrids (a direct effect), indicated by solid line leading from notonectids to gerrids.
competitors/predators. I describe the four treatments as 1.) Control (CN), where no food is added and interspecific competitors are allowed access to the water surface; 2.) Food Addition (CA), where food is added daily to control enclosures; 3.) Competitor Exclusion (NCN), where interspecific competitors are excluded from control enclosures and; 4.) Food Addition + Competitor exclusion (NCA). Because notonectids are potential predators as well as predators, exclusion of them from enclosures is expected to reduce mortality. Thus, these experiments can also assess the effect of notonectids on survival of gerrids. All four treatments were included in each of the five experiments. The dates of these experiments were 22/6/88 to 2/7/88, 29/6/89 to 12/7/89, 19/7/89 to 26/7/89, 8/7/90 to 20/7/90 and 24/7/90 to 31/7/90.

Field experiments were conducted in aluminum framed enclosures (1.0 x 0.5 x 0.5 m). The sides were sealed with clear polyethylene to enclose a surface area of 0.5m$^2$. Enclosures were secured at the water surface with upright posts driven into the sediment, so that approximately 25 cm of the enclosure was above the water surface. This enclosure design served to prevent entrance of free living gerrids, and the escape of experimental gerrids. It also reduced or prevented access by surface predators (spiders and other gerrids, respectively) to the enclosures. On rare occasions, spiders were found in or on the enclosures and were removed. Enclosures were placed in line parallel to the shore at about 1m depth in the floating vegetation zone. In experiments where winged gerrids were used, I removed 30 - 50% of the wings of each gerrid to prevent flight. Gerrids were marked so that I could distinguish experimental gerrids from those that may have colonized from the air. Colonization was negligible in these experiments. Earlier experiments demonstrate that handling of gerrids during wing removal and marking had no measurable effect on survival.
Food was supplemented in treatments CA and NCA by adding previously frozen fruitflies to the surface of each enclosure daily. Natural food levels consists of dead or living insects that had fallen to the water surface and become trapped. Competitors/predators were either natural (treatments CN and CA) or excluded (treatments NCN and NCA) by sealing the bottom of the enclosures with fibreglass window screening (1mm mesh).

To monitor egg production rates, eight styrofoam strips (approx. 80x30x3mm; henceforth "ovistrips") were placed in each enclosure for oviposition. *G. buenoi* readily use these strips for oviposition (Rowe and Scudder 1990; Chapter 3). Ovistrips were replaced daily, or every second day, and attached eggs were counted under a dissecting microscope. These ovistrips also provided a surface for resting gerrids. To monitor mortality, daily counts were made, and missing gerrids were replaced with gerrids captured in the field. Total mortality per replicate was obtained by accumulating the daily mortality counts over the duration of the experiment.

Egg counts from each enclosure were accumulated over the duration of the experiment. This number was then divided by the total number of female gerrid days to yield the average number of eggs oviposited by each female per day. In enclosures where female mortality occurred, I assumed that this mortality occurred, on average, at the midpoint of the sampling period (12h). Therefore, for each female death I subtracted 0.5 female days from the original number of gerrid days (number of females/enclosure X number of days of the experiment). Thus, in an enclosure containing 6 females in a ten day experiment that produced 120 eggs, and suffered 20 female mortalities, the mean daily egg production rate would be 2.4 (120/6[10]-20[0.5]). This procedure controls for any reduction in intraspecific competition among gerrids that results from predation.
I used densities of 8 gerrids per enclosure (16 adults/m²), at a sex ratio of 1 male to 3 females, for all experiments conducted in 1988 and 1990. I halved the density of males and females, to 4 gerrids per enclosure, for experiments conducted in 1989. These densities are much higher than the average densities of adult *G. buenoi* found on the ponds in Beecher’s Prairie. I used high densities and a female biased sex ratio to minimize variance in egg production rate in each enclosure. However, they are close to the range of total gerrid biomass observed on the ponds. Spence (1979) reports mean biomass of gerrids on 26 surveyed ponds to be about 50mg (wet wt)/m² in mid June, 100 mg/m² in mid July and 90 mg/m² in early August. Spence (1979) estimates mean weights for female *G. buenoi* at 10.33 mg and males at 7.17 mg. At these weights, experiments conducted in 1988 and 1990 had gerrid densities of 152 mg/m² and in 1989, 76.32mg/m². Therefore, densities used in experiments 1988 and 1990 represent about 1.5 to 3 and in 1989 about 0.75 to 1.5 times the average summer gerrid biomass in Beecher’s Prairie. Under the assumption that gerrid food consumption/biomass is about equal between stages and species, food limitation assessed in these enclosures is not unrealistic.

Assigning the Responses

The 2X2 design of these experiments allows for the determination of overall effects of both food addition and competitor/predator exclusion on egg production rates, and competitor/predator exclusion on survival. However, the design also allows for more specific analyses of intra- and interspecific competition, and predation. These are outlined below.

A reduction in egg production between treatments NCN and CN is attributable to the exclusion of sub-surface interspecific competitors. This effect will result largely from competition with notonectids, but a small portion may result
from dytiscids. Notonectids were commonly observed in enclosures feeding at the surface, and dytiscids were rarely and in most experiments, never observed in enclosures. Therefore, the contribution of dytiscids to this effect is expected to be small. Because notonectids are both competitor and predator, reduced egg production when they are excluded may result either from release from exploitation competition or from increased feeding activity of gerrids in the absence of risk from predacious notonectids. The comparison may also underestimate interspecific competition, because excluding competitors may also exclude some food (emerging insects). A comparison between treatments NCN and NCA reveals food limitation in the absence of competition from notonectids, and this effect demonstrates intraspecific competition for food. Finally, the difference in egg production rates between NCA and CN is an estimate of overall resource limitation.

Predation rate on any date is the difference between mortality rates when predators are included and excluded \((CN+CA)/2 - (NCN+NCA)/2\).

Seasonal Variation in Egg Production Rate (Experiments 6-11)

In a second series of experiments on Box 27, I assess seasonal trends in egg production rates in the absence of competition and the effect of food addition. Earlier measurements of food inputs to the water surface at Beecher’s Prairie, and elsewhere, have suggested a mid- to late summer decline in bulk inputs (Fox 1975; Spence 1979, 1983, 1986). The timing of the decrease is coincident with maximal gerrid biomass at Beecher’s prairie (Spence 1979), and thus suggests a period of extreme food limitation. It is not known whether variation in bulk inputs results in analogous variation in food limitation in gerrids, because it is not known what fraction of inputs are used by gerrids, and how this may change over the season.
I conducted a series of experiments in 1990 to test the hypothesis that usable food inputs decline late in the summer. The first component of the design was to measure egg production rates of gerrids held in four enclosures (screened) that excluded predator/competitors, over several periods during the season (treatment 1). On some dates, I had an additional four enclosures with supplemented food (treatment 2). The two treatments are analogous to NCN (predators/competitors excluded with natural food) and NCA (predators/competitors excluded with food added) in the previous series of experiments. Treatment 1 was repeated on June 10-17, June 18-26, July 8-16, July 17-24, July 25-31, August 1-5. Treatment 2 was repeated on the dates beginning on July 8. There were four replicate enclosures for each treatment. In Box 27, the food addition treatment differed from all other experiments reported here, in that supplemental food was two freshly killed damselflies daily, rather than frozen fruitflies. Eight macropterous gerrids were used prior to July 8 and eight apterous (or micropterous) after.

Tests of Enclosure Estimates

To determine whether my estimates of egg production and predation rates from enclosures resemble those in the field, I conducted two studies.

Egg Production Rate (Experiment 12)

Because egg production rates can not be assessed directly in the wild, I developed an index of egg production rate to predict egg production rates in the wild. I hypothesized that the concentration of mature (chorionated) eggs in the oviducts of females would be positively correlated to current egg production rate. To assess this hypothesis, I compared internal egg concentrations of females held
in enclosures with their known egg production rates. I then used the developed relationship to predict egg production rate of females captured in the wild, based upon the number of mature eggs held within their abdomens.

At the end of experiments 1 and 4 in Newell Lake, females were collected from experimental enclosures and preserved in 70% ETOH for determination of the number of mature egg concentrations in their oviducts. Within a few days of each experiment, 12 females were collected from Newell Lake and preserved for comparison with females in enclosures. Females were dissected under a microscope to determine the number of chorionated eggs contained within the oviducts.

Vegetation, Density and Predation Rates (Experiment 13)

My enclosures may overestimate predation rates because they lack floating vegetation, and floating vegetation may serve as a refuge from notonectid predation (Chapter 4). Gerrids spend a significant amount of their time among and on emergent and floating vegetation (Spence 1979; Nummelin et al. 1984; Chapters 4 and 5). For example, my surveys of habitat use by G. buenoi suggest that adults spend 40-80% of their time on top of floating vegetation (Chapters 4 and 5).

I conducted an experiment to test the hypothesis that increased densities of floating vegetation reduce predation rates. The experiment included twelve enclosures divided among three treatments (high vegetation, low vegetation and a control). The high vegetation treatment included approximately 70% cover with floating vegetation gathered nearby and eight ovistrips, and the low vegetation treatment included only eight ovistrips, as in previous experiments. Enclosures used in these two treatments were not screened, and therefore allowed predators access. The control treatment was analogous to the low vegetation treatment, except that predators were excluded by sealing the bottoms of the enclosures. In
these experiments I quantified only mortality. All other details of protocol are the same as the previous experiments in Newell Lake. The experiment was conducted from 1/8/90 - 7/8/90.

Statistics

All statistical analyses in this and following chapters, were carried out with the Systat 5.0. Proportions and percentages were arcsine transformed prior to analysis.

RESULTS

Food, Competition and Predation (Experiments 1 - 5)

Egg Production

Both food addition and exclusion of interspecific competitors/predators had a strong positive effect on egg production rates of females (Tables I, II). The effects were significant, or nearly so, in analysis of each date, and were significant when all experiments were analyzed in a single ANOVA (Tables I, II). Egg production rates observed in the control enclosures varied more than ten fold among dates. This difference is reflected in the highly significant effect of date in the ANOVA of all experiments (Table II). Hence food limitation, resulting from both intra- and interspecific competition, was a potent force across a 10 fold range of egg production in control enclosures.

22
Table I. The mean egg production rates for the four treatments of the five experiments conducted on Newell Lake. The treatments (1 through 4) are the control (no food added and competitors present), control + food (food addition), control-competition (competitors excluded) and control+food-competitors (food added and competitors excluded). Each date shows mean egg production rate and the S.E. (in brackets) for each treatment. The two right hand columns show the p values for the main effects of food addition and competitor exclusion, from individual ANOVA's for each experiment.
<table>
<thead>
<tr>
<th>Date</th>
<th>Control</th>
<th>Control + Food</th>
<th>Control - Competition</th>
<th>Control - Competition + Food</th>
<th>Food</th>
<th>Competition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>0.55 (0.09)</td>
<td>2.13 (0.06)</td>
<td>1.64 (0.13)</td>
<td>2.42 (0.25)</td>
<td>&lt;0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>1989a</td>
<td>0.26 (0.04)</td>
<td>1.10 (0.34)</td>
<td>1.03 (0.35)</td>
<td>1.27 (0.20)</td>
<td>0.063</td>
<td>0.101</td>
</tr>
<tr>
<td>1989b</td>
<td>1.33 (0.22)</td>
<td>2.61 (0.51)</td>
<td>2.23 (0.25)</td>
<td>3.27 (0.50)</td>
<td>0.009</td>
<td>0.062</td>
</tr>
<tr>
<td>1990a</td>
<td>2.87 (0.06)</td>
<td>3.35 (0.32)</td>
<td>4.73 (0.44)</td>
<td>5.48 (0.10)</td>
<td>0.049</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>1990b</td>
<td>2.13 (0.50)</td>
<td>2.73 (0.26)</td>
<td>4.89 (0.55)</td>
<td>5.42 (0.46)</td>
<td>0.237</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table II. The results of an ANOVA that included egg production from all treatments for all dates (experiments 1 - 5) on Newell lake. The main effects are the food addition and competitor exclusion treatments, and the date of the experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Mean-Square</th>
<th>F - Ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>4</td>
<td>29.711</td>
<td>69.54</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Food</td>
<td>1</td>
<td>13.22</td>
<td>30.96</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Competition</td>
<td>1</td>
<td>35.41</td>
<td>82.89</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Date X Food</td>
<td>4</td>
<td>0.43</td>
<td>1.01</td>
<td>0.409</td>
</tr>
<tr>
<td>Date X Competition</td>
<td>4</td>
<td>3.82</td>
<td>8.95</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Food X Competition</td>
<td>1</td>
<td>0.41</td>
<td>0.96</td>
<td>0.330</td>
</tr>
<tr>
<td>Date X Food X Competition</td>
<td>4</td>
<td>0.17</td>
<td>0.41</td>
<td>0.794</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>0.42</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Density Effects

Experiments in 1988 and 1990 included 8 gerrids in each enclosure, while those in 1989 included only 4. There is little reason to expect density effects on the strength of either food addition or predator exclusion. Food addition to enclosures was made on a per capita basis; thus, no effect of density is expected. Predators were allowed to move freely in and out of enclosures, and therefore, density dependent processes such as predator satiation are unlikely to play a role in these experiments.

However, both egg production rates in the controls and the response to exclusion of interspecific competitors, are likely to depend upon the number of gerrids in enclosures. If it is assumed that the number of interspecific competitors feeding in enclosures is independent of gerrid density, and that each incremental increase in food results in an equal increment in egg production per gerrid, then I have over-estimated egg production rate in the control enclosures, and the strength of interspecific competition in 1989, relative to 1988 and 1990, by a factor of two. Therefore, for the following comparative analysis, I have adjusted egg production rates in the controls and the effect of competition appropriately. In the figures I highlight data from these years. The effect of this adjustment is to increase the range of egg production in control enclosures from over ten fold to over twenty fold.

Response Strengths

Intra-specific competition was evident on all dates: food additions to enclosures that excluded interspecific competitors increased egg production rates on all dates (Figure 2a). The increase in rates ranged four fold from 0.24 eggs/female/day to 1.04. However, there was no relationship between the magnitude of the response to food addition and egg production rates in the
Figure 2. Variation between response magnitudes of food addition and competitor exclusion, and egg production rates in control enclosures. Each of the five experiments on Newell Lake is represented by one point. Shaded points are those experiments where gerrid density was 8/enclosure and clear points where density was 4/enclosure. Lines are fitted with linear regression. Intraspecific competition effect (panel a): the relationship between the mean increase in egg production rate (eggs/female/day) when food is added to enclosures that exclude interspecific competitors and the mean egg production rate in controls. Interspecific Competition Effect (panel b): the relationship between the mean increase in egg production rate (eggs/female/day) when interspecific competitors are excluded from control enclosures. Food Limitation Effect (panel c): The relationship between the mean increase in egg production rate (eggs/female/day) when food is added and interspecific competitors excluded from control enclosures, and mean egg production rate in controls. Spearman's correlation coefficients are not statistically significant (p>0.05) for any of the three relationships.
FOOD LIMITATION EFFECT

EGG PRODUCTION RATE IN CONTROLS

INTERSP. COMP. EFFECT

INTRASP. COMP. EFFECT
control enclosures (Figure 2a). Interspecific competition was also evident on all
dates, and its effect on egg production rate was greater than the effect of food
addition (Figure 2b). The increase in rates ranged over two fold from 1.04
eggs/female/day to 2.76, and was an increasing, although statistically insignificant,
function of egg production rates in the controls (Spearman's r=0.800, p<0.20). The
combined effect of excluding competitors and adding food (food limitation),
resulted in increased egg production ranging from 1.78 to 3.29 eggs/female/day.
These two values represent increases of over 1300% and 80% over rates in control
enclosures. The magnitude of this increase was an increasing, but non-significant,
function of egg production rates in the controls (Figure 2c; Spearman's r=0.700;
0.50<p>0.20).

Analysis of the percent decrease in egg production rates in response to
either the inclusion of interspecific competitors or the absence of added food,
indicates the change in supportable gerrid density brought on by either effect. This
analysis assumes a linear response to food availability, which appears supportable
within the range of egg production observed here (Chapter 3, Table VI). For
example, if inclusion of interspecific competitors decreases egg production rates
from 4 to 2 eggs/female/day, then interspecific competitors have reduced the
supportable gerrid density by 50%. Hence, to produce the number of eggs in the
presence of interspecific competitors that females did in the absence of interspecific
competitors, gerrid density in the enclosures would have to be reduced by 50%.

The percent reduction in egg production rates in response to the absence of
food addition (intraspecific competition), ranged from 9.8% to 31.7%. The percent
reduction in egg production rates in response to inclusion of interspecific
competitors (interspecific competition), ranged from 39.0% at the highest rates in
the controls to 92.2% at the lowest rates in the control. Finally, the percent
reduction in egg production rates in response to both inclusion of interspecific
competitors and absence of food addition, ranged from 47.8% at the highest rates in the controls to 93.2% at the lowest rates in the controls. Thus, to ameliorate the effects of food limitation observed here, gerrid densities in control enclosures would have to be reduced from 47 to 93%.

Predation

Exclusion of predators consistently increased survival rate (Tables III, IV). This effect was significant on all dates, and was significant when all experiments were analyzed in a single ANOVA (Tables III, IV). There was a great deal of variation in the effect of predation between dates as reflected in the significance of the Date and Predation X Date terms. Predation rate increased with food addition on some dates, and decreased on others, resulting in some significant interaction terms. Nevertheless, predation had a strong and significant effect on survival of gerrids across a wide range of conditions.

Daily predation rates varied from 0.07 to 0.26 among dates. This represents a greater than three fold range. As might be expected with an IGP predator, the strength of the effects of interspecific competition on egg production rate, and predation on mortality, were positively correlated (Spearman's r=0.300). However, the relationship was far from significant (p>0.50; Figure 3).

Given that the interspecific competitor (notonectids) in this system are also predators, increased egg production in these enclosures may have resulted in part from the release of gerrids from interspecific competition for food, and in part from their release from predation risk. Gerrids may have spent more time foraging when predators were absent. Such indirect effect of predators on foraging behaviour are common (Sih 1980, 1987; Lima and Dill 1990). However, there is no evidence that adult gerrids alter foraging behaviour in the presence of notonectids. Nevertheless, predator avoidance behaviour may account for some portion of the
Table III. The mean daily mortality rates for the four treatments of the five experiments conducted on Newell Lake. The treatments are as in Table 1. Each date shows mean egg production rate and the S.E. (in brackets) for each treatment. The two right hand columns show the p values for the main effects of food addition and predator exclusion from individual ANOVA’s for each experiment.
<table>
<thead>
<tr>
<th>Date</th>
<th>Mortality Rate (Proportion Mortality / Day)</th>
<th>Main Effects</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Control + Food</td>
</tr>
<tr>
<td>1988</td>
<td>0.084 (0.021)</td>
<td>0.088 (0.018)</td>
</tr>
<tr>
<td>1989a</td>
<td>0.308 (0.034)</td>
<td>0.274 (0.036)</td>
</tr>
<tr>
<td>1989b</td>
<td>0.161 (0.030)</td>
<td>0.080 (0.009)</td>
</tr>
<tr>
<td>1990a</td>
<td>0.133 (0.022)</td>
<td>0.077 (0.012)</td>
</tr>
<tr>
<td>1990b</td>
<td>0.183 (0.040)</td>
<td>0.293 (0.027)</td>
</tr>
</tbody>
</table>
Table IV. The results of an ANOVA that included daily mortality from all treatments for all dates of experiments 1 - 5 on Newell Lake. The main effects are the food addition and predator exclusion treatments, and the date of the experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>Mean-Square</th>
<th>F - Ratio</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food</td>
<td>1</td>
<td>0.002</td>
<td>0.920</td>
<td>0.341</td>
</tr>
<tr>
<td>Predation</td>
<td>1</td>
<td>0.467</td>
<td>270.147</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Date</td>
<td>4</td>
<td>0.037</td>
<td>22.128</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Food X Predation</td>
<td>1</td>
<td>0.001</td>
<td>0.084</td>
<td>0.773</td>
</tr>
<tr>
<td>Food X Date</td>
<td>4</td>
<td>0.006</td>
<td>3.389</td>
<td>0.014</td>
</tr>
<tr>
<td>Predation X Date</td>
<td>4</td>
<td>0.029</td>
<td>17.117</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Food X Predation X Date</td>
<td>4</td>
<td>0.005</td>
<td>3.234</td>
<td>0.018</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3. The relationship between response strengths of interspecific competitor exclusion and predator exclusion. The interspecific competition effect is the mean increase in egg production rate (eggs/female/day) when interspecific competitors are excluded from control enclosures (as in Figure 2b). The predation effect is the increase in daily mortality rates when predators are excluded from control enclosures.
difference in egg production I have ascribed to interspecific competition.

It is a general conclusion from foraging theory, that food addition to a population that is balancing foraging needs and predator avoidance will result in a decreased predation rate (McNamara and Houston 1987; Ludwig and Rowe 1990). Intuitively, an individual is more likely to take one increment of predation risk to acquire the first item of the day than the tenth. To test this prediction, I calculated the proportional change in predation rate resulting from food addition to enclosures that were open to competitor/predators. This analysis offers little support for the predator avoidance hypothesis: predation rate decreased in three of five cases and increased in two (Figure 4). A second prediction from foraging theory is that individuals in poorer nutritional condition will be less sensitive to predation risk (McNamara and Houston 1986, 1987; Mangel and Clark 1986, 1988; Ludwig and Rowe 1990; Rowe and Ludwig 1991). Therefore, food additions to populations in poor condition are expected to lead to smaller decreases in predation rate than food additions to populations in better condition. Across a 20 fold range in egg production rate (an index of nutritional intake), no such pattern is indicated in the current experiments (Figure 4). In conclusion, I have no evidence that changes in foraging behaviour contributed significantly to the observed increase in egg production in competitor/predator free enclosures. Therefore, I will assign this increase to release from interspecific competition for food.

Seasonal Variation in Egg Production (Experiment 6)

Egg production rates at Box 27, in the absence of competition, varied with date and food addition (Figure 5). In a single factor ANOVA of data from natural food enclosures, Date had a significant effect on egg production rate (F=8.9 DF=5,
Figure 4. The relationship between the proportional change in mortality rate when food is added to control enclosures and egg production rate in control enclosures. The dotted line shows no change in mortality. Points above the line represent experiments where food addition resulted in increased mortality and those below represent those where mortality decreased. Each of the five experiments on Newell Lake is represented by one point. Shaded points are those experiments where gerrid density was 8/enclosure and clear points where density was 4/enclosure.
Figure 5. Mean egg production rate of females in the absence of competition for six consecutive experiments in Box 27 (dotted line). Mean egg production rates of females in the absence of competitors with food added, for the last four of these experiments on Box 27 (solid line). Bars represent standard errors of the mean (N=4). For dates, day 1 equals May 1st.
Egg production rate in natural food enclosures was lowest in early June (1.8 eggs/female/day), reached a peak in early July (4.9), and decreased again late in July. Addition of food increased egg production significantly (p<0.05, independent t-tests) on all dates. A two factor ANOVA for data from those four dates revealed a significant effect of both Date (F=182.2, DF=1, p<0.001), and Food Addition (F=38.8, DF=3, p<0.001) on egg production. The greatest percentage increase resulting from food addition (152%) occurred in late July when egg production was the lowest, and the least (34%) in early July when egg production rate was the highest (Figure 5). This variation in response to food addition is reflected in the significance of the interaction between Date and Food Addition terms in the two factor ANOVA (F=4.2, DF=3, p=0.017).

Egg Production in the Wild

For both experiments 1 and 4, there was a significant relationship between egg production observed in each enclosure and the mean number of mature eggs contained within females in these enclosures (ANCOVA, Effect of egg production, F=13.27, p=0.001; Effect of Experiment, F=43.151, p<0.001; Figure 6). Hence, food limitation results in a reduction of mature eggs held within females. The difference between the relationships from the two experiments may have resulted from the different wing morphs used in each (winged in 1988 and wingless in 1990). Earlier surveys have indicated that wingless morphs retain less eggs in their abdomen than winged morphs (Rowe unpublished data). Nevertheless, each relationship allows estimation of egg production rates in wild caught females from the number of eggs found within their abdomens.

The mean number of eggs held within wild caught winged females in 1988 was 9.75 (SE=0.62, N=12), which indicates an egg production rate of 1.15 eggs per
Figure 6. The relationship between daily egg production rates of females observed in enclosures and the number of chorionated eggs held within their abdomen following the experiment. Each point represents a mean for all females in an enclosure. Circles represent data from Experiment #1 (1988) and squares represent those from Experiment #4 (1990). Lines are fitted with linear regression. Details of the statistical analysis are given in the Results section.
MATURE EGGS IN ABDOMEN

EGG PRODUCTION RATE

1988

1990
female per day (from the 1988 relationship, Figure 6). This rate is twice that observed in the control enclosures, but about half that observed in enclosures with food added and competitors excluded (Table I). Thus, females in the wild appeared to be food limited in 1988. The mean number of eggs held within wild caught wingless females in 1990 was 10.12 (SE=0.88, N=12), which indicates a rate of 4.63 eggs per female per day (from the 1990 relationship, Figure 6). This predicted egg production rate is 61% greater than the mean egg production rate observed in control enclosures, but is about 14% less than that observed in enclosures with food added and competitors excluded (Table I). Thus, the evidence for food limitation of females in the wild 1990 is weak. Overall, these results suggest that control enclosures overestimate food limitation by about 60-100%.

Vegetation and Predation Rates

The introduction of floating vegetation to enclosures reduced predation rates by 62%. Daily mortality rate was 0.103 (SE=0.005, N=4) in enclosures containing 70% vegetation cover, 0.273 (SE=0.031, N=4) in enclosures containing no vegetation, and 0.018 (SE=0.007, N=4) in enclosures that excluded predators. There is a significant difference in all pair-wise comparisons (Tukey test, p<0.03). These results suggest that all estimates of predation rates in my previous enclosure experiments are exaggerated. The degree to which they are over estimated is not known, because I do not know the average density of vegetation cover in gerrid habitat. Furthermore, this average will change through the breeding season (early in the season, pond vegetation is poorly developed). However, because 70% cover is at the upper end of the spectrum in ponds, I expect that estimates are somewhat less than 62% too high.
DISCUSSION

Environmental Variation

These experiments provide strong evidence for temporal instability in the intensity of competition. The data support Wiens' (1977, 1986) non-equilibrium view that environmental variation leads to temporal variability in the intensity of competition. My experiments were designed to assess this environmental variation directly. Across a twenty fold range in egg production rate in controls, egg production increased in all cases when food was added or interspecific competitors were excluded. These results demonstrate that intra- and interspecific competition were potent forces in limiting egg production rates on all dates. Nevertheless, increases in rates resulting from these treatments varied up to four fold, and this effect was independent of gerrid density in enclosures (controlled for in the design). In addition to resource limitation, predation was a significant force of mortality on all dates, and varied over three fold in intensity among dates. Therefore, both environmental processes that act to determine resource availability and those that decrease density, independently of resource availability, varied dramatically among dates.

Earlier studies of this gerrid community have similarly suggested such non-equilibrium processes, and have demonstrated strong spatial (pond to pond) variation in population success and community composition (Spence 1983). Population persistence, measured by the number of populations that completed one generation, was remarkably low. Of 219 populations of G. buenoi, only about 75% completed a generation. Populations of three closely related species fared even worse. Spence argued that population success was determined, in part, by density independent abiotic factors such as temperature and particularly pond
drying. Both of these processes are likely to vary among years. Nevertheless, not all variance in population success could be accounted for by abiotic processes, and therefore, variable biotic interactions such as competition and predation were implicated (Spence 1983). The current study demonstrates that both resource limitation and predation, play significant roles in adult reproductive success.

I have not measured adult density variation in this study. It is conceivable that adult density actually tracked the variation in resource availability that these data suggest. However, this seems highly improbable for several reasons. First, strong and temporally variable predation acts to bring density below any equilibrium that may be tracked. Second, resource availability itself is varying independently from predation. For example, in 1989 predation rates and resource limitation were high in late June (Experiment 2), but by mid July (Experiment 3) both resource limitation and predation had decreased in intensity. In contrast, both predation rates and food limitation increased in intensity late in the summer of 1990. Third, it is unlikely that new recruits from the pond could consistently make up the difference in adult populations. Recruitment is limited by food and predators by the same processes that limit adults (Spence 1986; this study). It is possible, that adult colonization from nearby ponds could make up those population numbers lost to predation. However, it is unlikely that such colonization could track the environmental variation documented here. Indeed, my comparison of the reproductive condition of females in 1988 and 1990 suggests that resource limitation of females in the wild was strong in 1988, but not in 1990.
Climatic Effects

Climatic variation within and among seasons may account for some portion of the variation observed in egg production rate, either directly through physiological limitation, or indirectly by affecting abundance and behaviour of prey, competitors and predators. Spence (1979) has shown that egg production rate of *G. bueno* in the laboratory decreases as temperature decreases below 23 C, and ceases at 10 C. I used temperature records from Environment Canada’s station at nearby Alexis Creek to compare with egg production rates. I chose to use data from treatment 3 (competitor/predator exclusion) enclosures, because this is the only treatment that was represented in all eleven egg production experiments. Analysis of covariance, with "lake" as one effect, and mean daily temperature as the other, indicates no significant effect of either on egg production rate, although the effect of temperature was nearly so (for lake, F=0.001, p=0.974; for temperature, F=4.7, p=0.062; Figure 7). It is probable that low temperature during some experiments constrained egg production to some degree. However, the variation unaccounted for by temperature is great (Figure 7).

Both the abiotic and biotic environments were clearly different in the 1989-90 reproductive seasons from those in 1988. Egg production rates in 1990 were over twice those in 1988-89 in both control enclosures, and in enclosures with supplemented food and competitors excluded. I suspect that this was related to precipitation and pond level. 1988 and 1999 were at the tail end of a several year dry period, and the 1990 season followed a year with rainfall 25% greater than the average since 1976 (Figure 8). The littoral vegetated zone of ponds was largely absent in 1988-9, but in 1990 the littoral zone had been restored with increased water levels (personal observation). It appeared that invertebrate productivity increased dramatically in 1990. The water surface was littered with food, and
Figure 7. The relationship between egg production rate in enclosures that excluded interspecific competitors and mean temperature (C) during the experiment. Each point represents the mean from an experiment. Open squares represent the five experiments on Newell Lake and solid squares represent the six experiments on Box 27. The line is fitted with linear regression. Details of the statistical analysis are given in the Results section.
Figure 8. Long-term precipitation records. Solid line indicates total yearly precipitation. Dotted line is the average precipitation for this period. Solid dots mark yearly precipitation totals for 1988-1990.
gerrid and notonectid densities appeared much higher. For example, notonectid densities observed in enclosures were typically zero or a few in 1988-9, and were typically several or more in 1990. It is interesting to note that one of the few other long term studies of competition suggests a similar pattern (Dunham 1980; Smith 1981). Dunham and Smith report strong year to year variation in competition among insectivorous lizards. In dry years, insect abundance decreased dramatically and competition increased. The current study suggests similar patterns for gerrid populations on Beecher's Prairie.

Food and Predator Limitation in the Wild

This series of experiments provide the first evidence of food and predator limitation of adult gerrid fitness. Both forces have long been assumed to be a force in the evolution of gerrid life histories and mating behaviour (e.g., Wilcox 1984; Kaitala 1987, 1991; Arnqvist 1989b; Rowe and Scudder 1990; Sih et al. 1990; Rowe 1992). My experimental protocol probably overestimated the magnitudes of both food limitation and predation rate. Gerrid biomass used in these experiments were up to 300% greater than the mean in surrounding ponds (Spence 1979). The comparison of the reproductive condition of gerrids in the enclosures, and in the wild, suggests that I have overestimated food limitation, but the same results also suggest that gerrids in the wild are food limited in at least some years. Furthermore, increases in egg production of 80 to 1300%, resulting from competitor exclusion and food addition, would seem to overwhelm the effect of higher than average biomass in enclosures.

Predation rates observed in these experiments (1-5) are probably overestimates of those in the wild. Gerris buenoi appear to use vegetation and other floating debris as a refuge from notonectid predation (Chapters 4 and 5),
and there was little floating debris in my enclosures. Predation rates by notonectids on gerrids decreased by 62% when vegetation to a cover of 70% was added to enclosures. Even with the inflation of predation rates taken into account, daily mortality rates measured in some of the Newell Lake experiments seem very high. However, past studies by Spence (1983) on penultimate larval stages of gerrids, reveal similar mortality rates in a nearby lake. Casual observation of gerrid-notonectid interaction in the wild, also suggest that notonectids can reduce abundant gerrid populations to near extinction within a few days (Spence and Rowe, personal observation). Therefore, despite overestimation of food and predator limitation in enclosures, these experiments demonstrate that gerrid fitness in the wild is limited by food and predators.
Chapter Three

REPRODUCTIVE RATE AND SENESCENCE IN
GERRIS BUENOI

Summary

In this series of laboratory studies, I investigate the effect of reproductive rate on lifetime fecundity, longevity, and senescence. The purposes of these experiments were first, to determine maximum reproductive rates, lifetime fecundity, and longevity of *G. buenoi*; second, to determine if longevity was a decreasing function of reproductive rate as predicted by life history theory (a "cost of reproduction"); and third, to determine if the rate of senescence (physiological deterioration) was an increasing function of reproductive rate. In the first experiment, pairs collected from the field early in the reproductive season were held at three food levels throughout their remaining life. Reproductive rate (daily egg production) was an increasing function of food level, and longevity was a decreasing function of reproductive rate. There was no effect of food level on lifetime fecundity. I repeated the first experiment, but with two main differences in protocol. First, I used females that had overwintered in the laboratory and therefore had produced no eggs prior to the experiment. This was done to ensure that total lifetime fecundity could be estimated. Second, females were only intermittently exposed to males (to maintain fertility) that were drawn randomly from a single laboratory population held with abundant food. This was done to remove any effect of the food level treatment on males that could be transmitted to the female. The results of this experiment matched those of the first. To determine if senescence was accelerated by reproductive rate, I recorded indices of
egg quality throughout the prior experiments. Egg quality (hatching success and
developmental stability) declined midway through life at all food levels. Increased
reproductive rate advanced this decline. Therefore, senescence occurs in *G. buenoi*
and reproductive rate advances the onset of senescence.
INTRODUCTION

Senescence, or aging, is characterized by a progressive decline in age-specific survival and reproductive rate resulting from physiological deterioration (Comfort 1979; Finch 1990; Rose 1991). Senescence has proximate causes at all levels of organization, ranging from molecular to whole organism levels, and the causes are multiple, including DNA damage, cell death, and mechanical damage of organs. Proximate causes and symptoms have been the field of physiologists (Finch 1990), and evolutionary biologists have focused on ultimate evolutionary explanations (Rose 1991). Life history theory attempts to predict age-specific probabilities of survival and rates of reproduction, and is thus intimately related to research on aging. Both theoretical and empirical research on life histories is dominated by the concept of trade-offs among life history components (Cole 1954; Stearns 1976; Partridge and Harvey 1988). Costs of reproduction are trade-offs between current reproductive rate or investment and other fitness components, such as future survival or fecundity (Williams 1966; Reznick 1985; Schluter et al. 1991). Reproductive costs achieve their closest link to senescence when current reproduction contributes to the physiological deterioration of senescence. Other reproductive costs, such as increased predation risk associated with male mating rate, are not closely related to senescence, because mortality is externally imposed rather than the result of physiological deterioration (eg. Chapter 4).

Diet restriction is one of the most common means of experimentally varying longevity (Harrison 1989; Holliday 1989). These studies have played a central role in physiological research on senescence. Diets that restrict bulk intake, while maintaining essential nutrients, typically increase life span, and delay declines in function and vitality (Comfort 1979; Finch 1990). Diet manipulation is also of increasing interest to the study of costs of reproduction. Diet restriction of
reproductive females typically reduces reproductive rate, and increases longevity, as would be predicted by cost of reproduction arguments (e.g., Kaitala 1987; Partridge et al. 1987; Rowe and Scudder 1990; Ernsting and Isaaks 1991). In a series of diet manipulation studies, Kaitala (1991) has investigated relationships between reproductive rate and other fitness components (longevity and flight capacity). In general, her results support the hypothesis that there are costs of reproduction. They are an important contribution, because they represent one of the few thorough studies of a group other than drosophilids and rotifers.

However, the contribution of such phenotypic manipulations (e.g. diet restriction) to our understanding of reproductive costs have been the focus of considerable debate (e.g. Reznick 1985, 1992a,b; Bell and Koufopanou 1986; Schluter et al. 1991; Partridge 1992). One criticism that is particularly relevant to the food manipulation has been raised by Enesco et al. (1989) and Bell (1992; personal communication). They suggest that a negative correlation between reproductive rate and longevity components may arise in the absence of a meaningful direct effect of one on the other. They propose that individuals begin with a fixed number of eggs, oviposit until the eggs are used up and then die. Death is cued, by some unknown process, by the termination of the reproductive period. Such a case would be suggested if the probability of survival were constant during the reproductive period, and then declined rapidly only after reproduction ceased. Therefore, they propose that mortality (the usual indicator of senescence) may be causally linked to the time at which reproduction ceases. Rapid reproductive rate would advance senescence, but only because it advanced the time when reproduction ceased. Thus, no causal relationship between reproductive rate and senescence is implied.

Gerrids, rotifers and other semelparous species may exemplify such a pattern. Diet restriction often results in their reduced reproductive rate and
increased longevity (reviews in Comfort 1979; Kaitala 1991). However, in some species of both groups mortality occurs only after reproduction has ceased (Meadow and Barrows 1971; Enesco et al. 1989; Rowe and Scudder 1990). Nevertheless, a direct role of reproductive rate in the timing of senescence is not excluded simply because mortality occurs after reproduction has ceased. For example, several measures of egg quality of rotifers begin a decline long before the end of the reproductive period (Jennings and Lynch 1928). If the onset of senescence in eggs is advanced at high reproductive rates, then a direct causal link between reproductive rate and the timing of senescence is implied.

In the present study, I investigate the effect of reproductive rate on both longevity and senescence of reproductive function. I have previously demonstrated a negative correlation between reproductive rate and longevity in the gerrid, *Gerris buenoi*, when food level is manipulated (Rowe and Scudder 1990). Food level appears to have little direct effect on longevity of gerrids; there was no effect of food level on male survival in *G. buenoi* (Rowe and Scudder 1990), or in *G. thoracicus* (Kaitala 1987). Mortality of *G. buenoi* females typically occurred after the reproductive period has ceased. In other species of gerrids, the timing of mortality relative to the reproductive period has not been reported (Kaitala 1987, 1991). To determine whether senescence begins prior to the end of the reproductive period, and is a function of reproductive rate, I analyze previously unreported data on the temporal pattern of senescence in three reproductive functions (reproductive rate, fertility and egg quality) from the earlier experiment (Rowe and Scudder 1990). This study is then repeated in such a way that any confounding contribution of males to reproductive senescence in females can be excluded.
METHODS

Diet Restriction and Senescence in the Presence of Males

In the first experiment, I assessed the effect of food level on reproductive rate, reproductive period, longevity, fertility and hatching success (see Table V for definitions). Gerrids were collected from the University of British Columbia Botanical Gardens early in the reproductive season of 1988 (April 7), and held in the laboratory at 10-12 C for five days. Gerrids were observed over the five day period to be sure that they were intact, mating and producing eggs. Beginning on April 13, 15 pairs of males and females were placed in polyethylene pails (20 cm diameter) at 3 food levels; high (15 flies/pair/day), medium (6 flies), and low (3 flies). I have assumed that the sexes divide these food resources equally. However, it is more likely that females consume more than males because of their requirements for egg production.

Pails were filled to 5 cm depth with dechlorinated water. Within each pail was a styrofoam strip (ovistrip) of approximately 6 cm² that was marked with the date, the treatment and individual identification. Ovistrips provided a floating surface for oviposition, and a dry resting position. Pails were held in an environmental chamber at 22 C under a light dark cycle of 18:6 h. On each day of the experiment, oviposition strips were collected and replaced, old food was replaced with new, and about 20-30% of the water was replaced. Every 3-4 days gerrids were transferred to clean pails with new water. All ovistrips collected on a day were placed in a single pail (30 cm diameter), filled to a depth of 5 cm with water, and monitored for fertility and hatching success. Three to 5 days after collection, these eggs were counted, and scored as fertile (tan mottled surface), or infertile. Ovistrips were then returned to their pail and held until hatching was
Table V. Definition of terms.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
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</thead>
<tbody>
<tr>
<td>Fecundity</td>
<td>Total number of eggs produced: Lifetime reproductive success.</td>
</tr>
<tr>
<td>Reproductive Rate</td>
<td>Total number of eggs produced, divided by the oviposition period.</td>
</tr>
<tr>
<td>Reproductive Period</td>
<td>Number of days from the start of the experiment to the last day that a female will oviposit.</td>
</tr>
<tr>
<td>Longevity</td>
<td>Number of days from the start of the experiment to mortality.</td>
</tr>
<tr>
<td>Fertility</td>
<td>Proportion of eggs oviposited that are fertile.</td>
</tr>
<tr>
<td>Hatching Success</td>
<td>Proportion of eggs oviposited that hatch.</td>
</tr>
<tr>
<td>Hatching Period</td>
<td>Period over which females produce eggs that successfully hatch</td>
</tr>
<tr>
<td>Fertility Period</td>
<td>Period over which females produce eggs that are fertile.</td>
</tr>
</tbody>
</table>
completed (15 days; eggs typically hatch in 8-10 days). Irregular checks of the egg containers allowed me to determine the proportion of fertile eggs that had hatched.

Diet Restriction and Senescence in the Absence of Males

In a second experiment, I removed any confounding effects of the presence of males on female senescence by repeating the previous experiment, but with only brief exposures to males of uniform histories. This experiment used gerrids that had not reproduced in the field prior to the experiment, whereas those used in the previous experiment had probably produced some portion of their eggs in the field prior to the experiment. Differences between this experiment and the previous experiment are as follows. Virgin adults, destined to diapause, were collected early in September 1988 and held in mass culture at 10-12 C for 10 days with abundant food. Collection of gerrids prior to winter ensured that no oviposition had occurred prior to the experiment (Spence 1989). Gerrids were put into diapause by placing them in moist moss, in darkness at 2-6°C. On March 15 1989, gerrids were transferred to a mass culture for five days, prior to commencing the experiment, at room temperature with abundant food. A 5 day period after diapause was chosen because 5 days is the mean time to first oviposition for G. buenoi diapaused in this fashion (Spence 1989). A total of 24 males and 16 females that appeared gravid (swelling abdomen) were chosen from this culture for the experiment. The 16 females were randomly assigned to one of two treatments: low food (2 flies/day) and high food (6 flies).

In this experiment, females were held in pails without males. Every 4-6 days a single male was added to pails containing females for 6-12 h. Males were chosen at random from the culture containing 24 males with abundant food. This
treatment kept exposure to males at a minimum while maintaining sperm stores in females. Ovistrips were collected and replaced every 3-4 days. All other conditions were the same as those in the previous experiment. Eggs were monitored for fertility throughout the experiment and hatching success for the first 31 days.

RESULTS

Reproductive Rate, Longevity and Lifetime Fecundity

Temporal patterns of egg production, and survival at the different food levels are shown in figures 9 (Experiment 1) and 10 (Experiment 2). At all food levels, egg production is relatively stable early in the experiment, and then rapidly declines to zero. Both the rate and the time of decline are a function of food level. At higher food levels, the initial reproductive rate is higher, and declines earlier than at lower food levels (figures 9b and 10b). Mortality typically occurred shortly after production ceased. The probability of survival is 1 for all treatments during the period of stable egg production rates, and then declines rapidly to zero. Females differ in the rate that they accumulate lifetime fecundity, but differ little in lifetime fecundity (figures 9a and 10a).

To analyze these patterns, the following summary statistics were calculated for each female: reproductive rate, reproductive period, longevity, and fecundity (see Table V for definitions). Data from both experiments were analyzed first in a single ANOVA, with treatment (food level) and "experiment" (1 or 2) entered as a categorical variables. There was no effect of experiment on any of the variables. Therefore, experiment was dropped from the analysis.

Reproductive rate, reproductive period, and longevity differed strongly among food levels (p<0.001 for all variables; Tables VI and VII). The positive effect
Figure 9. The effects of food level (Experiment 1) on the temporal pattern of cumulative egg production (panel a), reproductive rate (panel b) and longevity (panel c). Solid line = 7.5 flies/female/day; dashed line = 3.0 flies/female/day; dotted line = 1.5 flies/female/day. Lines are 3 day running average of daily means.
Figure 10. The effects of food level (Experiment 2) on the temporal pattern of cumulative egg production (panel a), reproductive rate (panel b) and longevity (panel c). Solid line = 6 flies/female/day; dotted line = 2 flies/female/day. Lines are a 3 day running average of daily means.
Table VI. The effect of food level on various reproductive variables and longevity. Variables are defined in Table V. Food levels of 2 and 6 flies are from experiment 2, the rest are from experiment 1. The first row is the mean and the second the standard error. An asterisk beside the variables indicates a significant effect of food level. See Table VII for details of ANOVA.

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<td>9.04</td>
<td>20.45</td>
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<td>36.71</td>
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<td>3.97</td>
<td>1.75</td>
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</table>
of food on reproductive rate, and was balanced by a negative effect of food on reproductive period, such that lifetime fecundity was unaffected by food level (Table VI and VII). Reproductive rate at the highest food level (6.6 eggs/female/day) was nearly double that at the lowest food level (3.4 eggs/female/day), and reproductive period was reduced from 68.2 days to 38.7 days (Table VI). However, mean fecundity differed by only 3% from the highest (222 eggs) to lowest food level (229 eggs; Table VI). The greatest fecundity (249 eggs) occurred at the middle food level (3 flies/day; Table VI).

I tested for an independent effect of reproductive rate on reproductive period and longevity by using regression analyses with both food and reproductive rates entered as continuous effects, and experiment as a categorical variable. There is a clear negative relationship between reproductive rate and reproductive period (Figure 11a), and a similar effect is apparent between reproductive rate and longevity (Figure 11b). Even when the effect of food level is controlled for, reproductive rate had a significant (p<0.05) negative effect on both reproductive period and longevity (Table VIII).

Reproductive Rate and Egg Quality

The temporal pattern of fertility and hatching success was similar to that of longevity (Figures 12 and 13). Both fertility and hatching success was high (about 95%), and independent of treatment early in the experiment, and then decline rapidly. The time of decline was a function of food level, with the decline advanced at higher food levels. Hatching success declines prior to the decline in fertility.

To analyze these data, the mean duration of the production of fertile eggs was calculated (fertility period; Table V), and the duration of production of
Figure 11. The effects of individual reproductive rate observed at each food level on individual oviposition period (panel a) and longevity (panel b). A least squares regression has been drawn for all individuals. Open squares = 1.5 flies/female/day; open circle = 2 flies/female/day; thatched squares = 3 flies/female/day; solid circles = 6 flies/female/day; solid squares = 7.5 flies/female/day. All squares are from experiment 1 and all circles from experiment 2.
REPRODUCTIVE RATE

a.

b.

REPRODUCTIVE PERIOD

REPRODUCTIVE RATE

LONGEVITY

REPRODUCTIVE RATE
Table VIII. Regression analysis of the effect of reproductive rate (RR) and food level on reproductive period, longevity, hatching period and fertility period (see Table V for definition of terms). In these analyses, both food and reproductive rate are assumed to be continuous effects. Experiments 1 and 2 are analyzed together except in the case of hatching period where data were available for experiment 2. The block effects account for any effect of differing protocols between the two experiments. Data are shown in Figures 12 and 15.

<table>
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<th>Dependent Variable</th>
<th>Source</th>
<th>d.f.</th>
<th>Mean-Square</th>
<th>F - Ratio</th>
<th>P</th>
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<td>29</td>
<td>0.775</td>
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Figure 12. The effects of food level (Experiment 1) on the temporal pattern of fertility (panel a) and hatching success (panel b). Solid line = 7.5 flies/female/day; dashed line = 3.0 flies/female/day; dotted line = 1.5 flies/female/day. Lines are a 3 day running average of daily means.
Figure 13. The effects of food level (Experiment 2) on the temporal pattern of fertility (panel b) and hatching success (panel b). Solid line = 6 flies/female/day; dotted line = 2 flies/female/day. Lines are a 3 day running average of daily means.
successfully hatching eggs (hatching period; Table V). I analyzed fertility data from both experiments in a single ANOVA, with experiment entered as a categorical effect. Data for hatching success late in life were not available for experiment 2. Females at higher food levels had significantly (p<0.001) shorter periods of hatching and fertility (Table VI and VII).

I tested for an independent effect of reproductive rate on hatching and fertility periods by using regression analyses, with both food and reproductive rates entered as continuous effects, and experiment as a categorical variable (Figure 14). Only food level had a significant (p = 0.017) effect on fertility period. However, both reproductive rate (p = 0.1) and experiment effects (p = 0.094) approached significance (Table VIII). In the analysis of hatching period, reproductive rate was significant (p = 0.035), and food level was not (p = 0.56).

Regular and Irregular Development of Eggs

Eggs from early in a female’s reproductive period undergo a stable sequence of development prior to hatch. This "normal" developmental sequence is pictured in figure 15a. All oviposited eggs are initially opaque and white or yellow in color. Infertile eggs remain this way. Fertile eggs develop a mottled brown surface over a period of 1 to three days. Over the next several days, red eye spots appear followed by other body parts that are visible through the egg capsule. Hatch occurs after 8 to 10 days of development.

Later in the reproductive period, at the time of declining hatching success, several developmental abnormalities characterize unsuccessfully hatched eggs. First, in a proportion of hatched eggs, the instars were unable to completely free themselves from the egg capsule and died (Figure 15b). Second, some unhatched eggs appeared to have undergone some normal development, but never hatched.
Figure 14. The effects of individual reproductive rate observed at each food level on individual oviposition period (panel a) and longevity (panel b). A least squares regression has been drawn for individuals. Open squares = 1.5 flies/female/day; open circle = 2 flies/female/day; thatched squares = 3 flies/female/day; solid circles = 6 flies/female/day; solid squares = 7.5 flies/female/day. All squares are from Experiment 1 and all circles from experiment 2. Data for hatching period was not available for Experiment 2.
Figure 15. Normal, arrested and over-developed eggs. a.) The normal sequence of egg development. At oviposition, all eggs are white/yellow and opaque (top left). After a few days, the surface of fertilized eggs becomes mottled and red eyespots begin to appear (moving toward the top right in panel a.). Development continues until hatch (bottom row of panel a.). An egg that will hatch within a few hours is shown second from the right in the bottom row. The remaining egg capsule is shown at the bottom right. b.) Arrested and "over" developed eggs. Top row shows eggs whose development has arrested at various stages. The two middle eggs in the bottom row appear to have continued to develop beyond their normal hatching period (indicated by dark pigmentation). A hatched egg in which the larva has failed to completely free itself from the capsule is shown at the far right in the bottom row.
In these eggs, development had arrested at various points prior to completion (Figure 15b). A portion of eggs that appeared infertile may actually have been fertile, but had arrested in development prior to the egg capsule darkening. Third, many eggs appeared "over" developed. These eggs contained completely developed larvae that had undergone some of the pigmentation that occurred after hatching in healthy eggs (Figure 15b). Fourth, in some eggs development occurred only at one end of the egg (Figure 16a). In such cases, eyespots often formed in the middle of the egg instead of at one end. Fifth, some eggs had varying degrees of development scattered throughout the egg capsule (Figure 16b).

**DISCUSSION**

Three main conclusions can be drawn from these experiments. First, they show that longevity is a decreasing function of reproductive rate in *G. buenoi*: diet restriction consistently reduced reproductive rate and increased longevity. Second, they show that reproductive senescence precedes death: developmental stability and hatching success of eggs, declines gradually prior to death. Third, like its effect on longevity, diet restriction delays the onset of senescence.

**Reproductive Rate, Longevity and Fecundity**

The decrease in reproductive rate, and increase in longevity following diet restriction shown here, has been previously demonstrated in a European gerrid, *G. thoracicus* (Kaitala 1987), and in several other species (*e.g.* fruitflies, Partridge *et al.* 1987; Chippendale *et al.* in press: rotifers, Meadow and Barrows 1971; Enesco *et al.* 1989; beetles, Ernsting and Isaaks 1991). However, diet restriction in some populations of *G. thoracicus*, and in other gerrid species, results in both reduced
Figure 16. Irregular development of eggs. a.) Partially developed eggs. Note that the mottled surface, that characterizes normal eggs, has proceeded only part way along the egg capsule. In some of these eggs, eye spots appear at the leading edge of the pigmentation and this is often in the middle of the egg. b.) Scattered development. Note patches of pigmentation scattered about the eggs and eye spots appearing at mid-points in the eggs. The two eggs at the bottom right are particularly small.
reproductive rate and longevity, and in decreased fecundity (Kaitala 1991). These previous results with gerrids are difficult to compare with mine. First, in contrast to my studies, all of Kaitala's diet manipulations simultaneously altered food quality as well as quantity, and thus her results may be confounded. In rotifers, diet quality is known to effect reproductive rate, longevity, and lifetime fecundity (Enesco et al. 1989). Secondly, gerrids used in Kaitala's experiments were captured during the breeding season, and thus had probably produced a significant proportion of their eggs prior to the experiment. It is not known how this may affect the results. It is possible that gerrids respond differently to diet restrictions at different times in the breeding season. My results are not confounded by either of these problems.

Values for lifetime fecundity at all food levels reported here correspond closely to those reported recently by Spence (1989) for *G. buenoi* under *ad libitum* food level. He reported a mean fecundity of 281 eggs per female compared to a range of 222 - 299 reported here. However, his estimates of reproductive rate and longevity under *ad libitum* food, more closely correspond to my estimates at lower food levels. He reports a reproductive rate of 4.5 eggs/female/day and a longevity of 77 days. This resembles my estimates, at the second lowest food level, of 4.1 eggs/female/day and a longevity of 75 days. There are two potential reasons for this discrepancy. First, his *ad libitum* treatment may have been less than *ad libitum*. More likely, warmer temperatures used in my experiments offer a reasonable explanation for the differences. I held gerrids at 22 C and he at 18 C, and egg production of *G. buenoi* is known to increase with temperature up to 22 C (Spence 1979). Given the negative relationship between reproductive rate and longevity shown here, increased reproductive rate and consequentially decreased longevity are expected.
Reproductive Costs and Senescence

My results are the first direct evidence of senescence in gerrids. There is a progressive decline in egg quality with age in G. buenoi. As females age, reproductive rate declines, hatching success declines, and several signs of abnormal embryological development increase in frequency. Prior to death hatching success reaches zero, and finally, egg production ceases. Analogous components of reproductive senescence have been demonstrated in other taxa (Parsons 1964; Comfort 1979; Finch 1990; Mousseau and Dingle 1991). For example, Jennings and Lynch (1928) reported, decreased hatching success, increased variation in egg length, and oddly shaped eggs in old rotifers. Parsons (1962) reported decreased egg production rate, decreased hatching success, and increased variation in egg length in eggs of old Drosophila melanogaster, and increased morphological asymmetry in adults reared from these eggs.

Parsons (1962, 1964) refers to the poor and variable quality of eggs from old females as indicators of developmental instabilities. The name aptly describes the appearance of these eggs. However, the mechanism underlying abnormal development is not known. Accumulated damage to both physiological and genetic systems have been implicated (Parsons 1964; Comfort 1979; Finch 1990). Two potential genetic mechanisms underlying developmental instabilities in old G. buenoi can be rejected. First, the effect was maternal in origin with little or no contribution of males (e.g. genetic quality of sperm). In my second experiment, females in both high and low food level treatments had access to the same group of males. Therefore, the treatment effect on the timing of reproductive senescence can not be attributed to any property of ageing males. Second, it is unlikely that the effect resulted from accumulated genetic defects in the nurse cells that provision eggs or in the oocytes themselves. Unlike Drosophila spp., oocytes and
nurse cells in gerrids and other hemipterans, are not generated *de novo* and sequentially from stem cells in the adult (Wick and Bonhag 1955; Eschenberg and Dunlap 1966). In gerrids, germaria proliferate during the early instars, and the final division of germaria into oocytes and nurse cells appears to occur simultaneously in a late larval stage (Wick and Bonhag 1955; Eschenberg and Dunlap 1966). Thus accumulated genetic damage in stem cells, leading to genetic errors in oocytes and nurse cells, can be ruled out.

Data presented in this chapter provide strong evidence for a cost of reproduction in *G. buenoi*. Negative correlations between reproductive rate and longevity, resulting from either phenotypic manipulation of reproductive rate or selection on reproductive rate, are commonly cited as evidence for the existence of a cost of reproduction (e.g. Kaitala 1987; 1991; Partridge *et al.* 1987; Rowe and Scudder 1990; Lessels 1991). Enesco *et al.* (1989) and Bell (1992) have suggested that such results may occur despite the lack of a cost of reproduction. In their scenario, mortality occurs for some unknown reason when a constrained number of eggs have all been produced: manipulation of reproductive rate merely manipulates the time at which all eggs have been laid. My results show that not only was mortality delayed when reproductive rate was experimentally reduced, but so was reproductive senescence. Reproductive senescence began long before mortality; it was cumulative, and an increasing function of reproductive rate. Therefore, the onset of senescence was not causally linked to the end of the reproductive period, but to the rate at which eggs were being produced.

Females lived for a short period after reproduction ceased. However, death itself is of little evolutionary consequence, because females stopped producing eggs that could contribute to fitness long before death. I do not believe that death was causally linked to the end of the reproductive period, as suggested by Enesco *et al.* (1989). Late in life, but during the reproductive period, females became sluggish.
and unresponsive to prodding. Near the end of life they even had trouble keeping their abdomen above the water surface. It makes sense that females in this condition would stop producing energetically costly eggs prior to actually dying. It would be relatively easy to test the hypothesis that somatic function of females progressively declines as a function of reproductive rate, and like reproductive function, prior to the end of the reproductive period.
Chapter Four

PREDATION BY BACKSWIMMERS AND THE COSTS OF MATING TO MALE AND FEMALE GERRIS BUENOI

Summary

In this chapter, I describe a series of field and laboratory experiments designed to assess the predation risk associated with a variety of the components of mating in both sexes of G. bueno. Predation rate by notonectids was shown to be female biased. A field survey revealed greater use of risky habitat by males than females. Therefore, the observed higher predation on females was not the result of greater exposure to notonectids. Notonectids are attracted to gerrid activity. In the laboratory, males are more active than females. Therefore, males are expected to attract more attacks than females. Activity of both sexes increases when held in the presence of the opposite sex, because of harassment of females by males. Therefore, harassment is expected to increase attacks on both sexes. There was no difference between sexes, when single, in the success of notonectid attacks. Capture of mating and struggling pairs of gerrids by notonectids was increased dramatically, compared to capture of single gerrids. When gerrids were mating or struggling, it was usually the female of mating pairs that was captured. Therefore, mating increases predation risk to females, and pre- and post-mating struggles increase risk to both sexes.
INTRODUCTION

It is a commonly held view that mating is costly to both sexes (Daly 1978; Walker 1980; Bell and Koufopanou 1985; Gwynne 1989). These costs may be associated with various components of mating behaviour, including searching for mates, courtship, choosing mates, intra-sexual combat, and copulation. Currencies may include energy, time, parasite transfer and predation risk, and they may be paid by both sexes. Males should be more willing to pay costs than females, because mating frequency is more likely to limit reproductive success in males than females. Recent reviews suggest that mating costs, particularly predation risk, are more prevalent in males than females (Gwynne 1989; Magnhagen 1991). Yet, mating costs to females may play an important role in structuring mating systems, although evidence so far is scarce (Wing 1988; Aronqvist 1989b; Gwynne, 1989; Fairbairn in press). In this chapter I investigate elevated predation risk resulting from mating behaviour in both sexes of *Gerris buenoi*.

Distinguishing the components of mating behaviour that increase risk to females is informative for the evolution of mating systems, life histories, and secondary sexual traits (eg. Partridge and Endler 1987; West-Eberhard *et al.* 1987; Curtsinger 1991). For example, discriminating among mates of various quality may increase predation risk. This information demonstrates a cost to mate choice, which is critical to models of sexual selection (Kirkpatrick and Ryan 1991). Sexual harassment of females by males may expose females to predation risk. Under these conditions, females are expected to be more willing to accept superfluous mating than otherwise (Chapter 5). Finally, copulation itself may increase risk. Here, females are expected to be more reluctant to accept superfluous mating than the former case (Aronqvist 1989b; Sih *et al.* 1990), and may prefer male traits that minimize this risk (Partridge and Endler 1987).
Several recent studies have suggested a role for predation risk in the ecology and evolution of mating behaviour of gerrids. Mating *Gerris buenoi* females retreat to refuge (Chapter 5), mating activity of *Aquarius remigis* is reduced in the presence of predacious fish (Sih *et al.* 1990), and two studies present evidence for increased predation risk to females when mating (Arnqvist 1989b; Fairbairn in press). As part of an economic analysis of the mating system of *G. odontogaster*, Arnqvist (1989b) demonstrated that predation by backswimmers (Heteroptera: Notonectidae) on females in the laboratory increased in the presence of males. Fairbairn (in press) found that predation by frogs on copulating pairs of *A. remigis* was higher than on single gerrids. Mating behaviour of these and related species includes repeated harassment of females by males, pre- and post mating struggles, copulation, and guarding (Wilcox 1984; Arnqvist 1989b; Rowe 1992), any one of which could contribute to elevated predation risk to both sexes. Arnqvist’s (1989b) study does not address how the presence of males increases risk to females. Fairbairn’s (in press) study focuses only on copulation, but is one of only two studies that demonstrate an increased risk of predation to mating females (see also Wing 1988).

In the present study I investigate the mating behaviour of male and female *Gerris buenoi* Kirkaldy, and the predatory behaviour of notonectids, in an attempt to associate specific components of mating behaviour with elevated predation risk. I focus on the major components of mating behaviour in the species: harassment of females by males, pre- and post-mating struggles, and mating (copulation/guarding; Chapter 5). I test the following hypotheses: 1) predation on *G. buenoi* by notonectids is female biased; 2) male harassment (mating attempts), including pre- and post mating struggles of single females, exposes both sexes to predation risk; and 3) mating pairs are at greater risk to predation than either single males or females.
METHODS

Biology and Study Rationale

I used macropterous, overwintered gerrids in experiments reported here. These adults emerge from diapause in the early spring to mate and reproduce for the remainder of their adult life (a few weeks to months). Females mate frequently, and oviposit approximately daily during this period (Chapters 3 and 5). Like other gerrids (Arnqvist 1988; Rubenstein 1989), females store sperm for about 10 days, and therefore most matings appear superfluous to females (unpublished data). The mating system of *G. buenoi* is described in Chapter 5. Males frequently attempt to mate females (harassment) that often lead to vigorous pre-mating struggles initiated by females that are reluctant to mate. Few struggles lead to copulation. Males ride on the backs of females during copulation, and subsequently during guarding of the females. I will refer to the combination of copulation and guarding periods as the mating period. Mating is terminated by a struggle initiated by females. Each component of mating (harassment, struggle and mating) may increase predation risk to males or females.

In a series of field enclosure studies, I have often found predation on *G. buenoi* to be female biased (Chapter 2). The predator or predators that cause this bias are not known, although previous field studies suggest notonectids are a major predator of adult *G. buenoi* in the field (Spence 1983; Chapter 2). In an initial field enclosure experiment in this chapter, I demonstrate that predation by notonectids is biased toward female gerrids. This bias may result from differences in behaviour or morphology of the sexes that increase susceptibility to predation, and is independent of sexual behaviour. Specifically, females may spend more time in habitats associated with notonectid attacks, female behaviour may attract
predacious notonectids, notonectids may simply prefer to attack females, or notonectid attack success may be greater on females than males. Alternatively, some aspect of mating behaviour may result in an increased number or success rate of notonectid attacks on females (a cost of mating). I address each of these hypotheses in a series of field and lab tests.

Predation Risk to Males and Females

To test for a sex bias in predation by notonectids, I compared mortality of mixed sex groups over a range of enclosed notonectid densities. Experiments were conducted at Newell Lake in the Fraser Plateau of British Columbia. Enclosures were constructed of aluminum frame (1 X 0.5 X 0.5 m), wrapped on the outer sides with polyethylene sheeting. Each enclosure enclosed an area of 0.5 m\(^2\) and protruded about 0.25 m above the water surface. Enclosures were sealed on their bottom surface with fibreglass window screen (pore size of about 1mm). The portion of the plastic walls above the water surface served to contain the gerrids, and the portion below the surface as well as the screening served to contain the notonectids. Floating debris was cleared from enclosures and 6 polystyrene strips (80 X 35 X 2 mm) which served as resting and oviposition sites were added to each. Enclosures were placed in a row, parallel to the shore, in the nearshore habitat that is frequented by gerrids.

On June 4 1989, I placed 8 gerrids in each of eight enclosures at a sex ratio of 1:1. These individuals had their wings clipped so that they could not leave and were marked so that I could distinguish them from any immigrants. In each enclosure, I also added one of four levels of adult notonectids as predators (0, 4, 8 or 16) for two replicates at each level. Notonectids were a random mixture of Notonecta undulata and N. kirkii. It was not possible to clip the wings of
notonectids without harming them. On each day of the four day experiment, I recorded the number and sex of dead or missing gerrids and replaced these with others collected nearby. I also searched each enclosure to estimate notonectid density and density was adjusted to the original treatment level.

Habitat Use

Both male and female *G. buenoi* spend a significant portion of time on top of floating debris (grooming, feeding, resting, etc; Chapter 5) and floating debris appears to serve as a refuge from predation by notonectids, which attack from below (Chapter 2). Sexes may vary in the use of refuge, and thus in the duration of time that they are exposed to predatory attacks by notonectids. To determine whether use of refuge varied between the sexes, I documented the proportion of observed individuals of each sex that occurred on either open water or on floating debris (refuge). Three surveys, at Shallow Pond in the University of British Columbia Botanical Gardens, on June 27, 29 and July 1, were conducted from the shore with a pair of binoculars. On each date, I surveyed the same patch of pond surface (approx. 1 X 3 m) that contained a dense concentration of single and mating gerrids.

Movement Rates of Males and Females

Notonectids are attracted to movement on the water surface, and are even able to discriminate movements of prey (including skating gerrids) from non prey items (Lang 1980). Thus, movement of gerrids on the water surface is expected to increase attack rates. I, therefore, compared the movement rates of males and females in the laboratory when held with their own sex or with the opposite sex,
to determine if sexes differ in their movement rate and if sexual behaviour independently increases movement rate.

Gerrids used in these laboratory experiments were collected from Shallow Pond and held for 24-48 h prior to the experiment in large plastic wading pools in the laboratory with abundant food (fruitflies). For the experiment, I placed 6 marked individuals in a single experimental pool for a 15 min acclimation period followed by a 10 min period of observation. Experimental pools were constructed of plexiglass, and had a surface area 0.5 m$^2$ and depth of 3 cm. I chose an individual at random, and counted the number of movements (strides) made over the 5 min period. Occasionally, focal individuals would skate into a corner and repeatedly run into the plexiglass. When this disturbing behaviour occurred, I switched to a new focal individual. I compared three treatments: 1.) 6 females (5 replicates), 2.) 6 males (5 replicates) and 3.) 3 males + 3 females (10 replicates). Replication of the latter treatment is doubled because in any replicate I followed either a male or female. Therefore, the experiment included five replicates each of a focal male among males, female among females, male among both sexes and female among both sexes. Treatments were alternated over a two day period.

Notonectid Attack Success

I compared the attack success of notonectids on single males and females, and males and females engaged in struggles (pre- or post-mating) and mating (copulation or guarding). A difference between attack success on single males and females reveals variation in the predatory ability of notonectids that is based on sex of the gerrid, and an increase in attack success on either males or females engaged in mating behaviour reveals variation in predatory ability based on sexual behaviour of the gerrids. The latter is conclusive evidence for a cost of mating and

95
the former is not.

This experiment was conducted in the laboratory pools with gerrids collected and maintained as in the previous experiment: 10 males and 5 females, marked according to sex, were placed in pools containing 4 adult *N. kirkii*. Notonectids were starved for 24 - 48 h prior to the experiment. Over a 1 h period, I recorded all attacks by notonectids on single males and females, mating or guarding pairs, and pairs engaged in pre- or post-mating struggles. Captured gerrids were removed and replaced as soon as the success of the attack was determined. The experiment was repeated 4 times over a 2 day period, with new gerrids and notonectids in each replicate. I defined 1.) attack, as a lunge toward and attempt to grasp a gerrid or gerrids, 2.) capture, as those attacks by notonectids that resulted in the gerrid or gerrids being pulled under water, 3.) attack success, as the ratio of captures to attacks and, 4.) predation, as an immobilization of the captured gerrid.

RESULTS

Female Mortality and the Presence of Males

Total mortality of gerrids in mixed sex enclosures was an increasing function of notonectid density and was biased toward females at higher notonectid densities (Figure 17). Both male and female mortality rates were increasing functions of notonectid density, but females were preyed upon about 2.7 times as often as males. The regression of female mortality on notonectid density was highly significant \( p < 0.002, r = 0.932, F = 39.39, \text{DF} = 1,6 \). The corresponding regression for males was also significant \( p < 0.02, r = 0.829, F = 12.01, \text{DF} = 1,6 \) .
Figure 17. The effect of predator (*Notonecta spp.*) density on the total mortality (accumulated over the 4 day experiment) of males (open squares) and females (shaded squares) in enclosures. The lines are fitted with linear regression. Details of the statistical analysis are given in the Results section.
Habitat Use

On all three survey dates a higher proportion of females than males was found on the refuge of floating vegetation. The proportion of individuals on floating vegetation was 0.63 (n=40), 0.73 (n=55) and 0.81 (n=37) for females, and 0.47 (n=36), 0.32 (n=47) and 0.46 (n=37) for males. The pooled chi square (30.23) indicates a significant difference (p<0.001, DF=1). Therefore, the bias in notonectid predation rate toward females in the presence of males cannot be explained by a female association with risky habitats. In the field, females use refuges more than males.

Harassment and Movement Rate

In the laboratory experiment males moved more frequently than females when grouped with their own sex or the opposite sex, and the presence of males increased the movement rate of females (Table IX). Movement rate of individual gerrids was significantly affected by both sex and grouping, and there was no significant interaction between the factors (ANOVA: sex; p<0.001, F=28.4, DF=1: group; p=0.03, F=5.7, DF=1: sex X group p=0.439, F=0.6, df=1). Males actively harassed (chased and attempted to mount) both males and females during these experiments. Movement rate of males was 49% greater than that of females in single sex pools, and was 9% greater in pools containing both sexes. Females rarely chased other females or males, but were frequently chased by males, which resulted in a 25% increase in movement rate of females grouped with males compared to those grouped with females.
Table IX. The effect of sex and presence of the opposite sex on stride rate. Top row shows mean (n=4) and bottom row shows standard error of the mean. Left columns show stride rates of each sex held in same sex groups and the two right columns show stride rates of each sex held in mixed sex groups.

<table>
<thead>
<tr>
<th>Number of Strides</th>
<th>Single Sex Groups</th>
<th>Mixed Sex Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td></td>
<td>126.8</td>
<td>85.2</td>
</tr>
<tr>
<td></td>
<td>(7.4)</td>
<td>(3.7)</td>
</tr>
</tbody>
</table>
Notonectid Attack Success

Attack success of notonectids was higher on mating and wrestling pairs than on single gerrids, and females were more likely to be preyed upon than males when notonectids captured pairs (Table X). Notonectid attacks on single females resulted in 10.2% (S.E. = 1.0%) and on single males there was a 10.5% (S.E. = 1.7%) capture success. No significant difference was detected between the sexes when they were single. I first analyzed the effect of state (single, mating or struggling) on capture success independently of which sex was captured (Table X, row 2), and then repeated it for each sex. There was a significant effect of state on total capture success (ANOVA, F=28.8, DF=2, p<0.001). One member was captured in 29.7% (SE=4.7) of attacks on mating pairs, and in 49.8% (SE=6.7) of attacks on struggling pairs. These two values are significantly different from the mean capture success on single gerrids (10.4% (SE 1.3); p<0.02, p<0.001 respectively; Tukey multiple comparison; Table X). There was a significant effect of state on capture success of males (ANOVA, F=7.6, DF=2, p<0.012). The male was captured in only 3.8% (SE=2.3) of attacks on mating pairs, and in 21.5% (SE=4.8) of attacks on struggling pairs. However, these two values are not significantly different from the mean capture success on single males (10.5% (SE 1.7); p=0.367, p=0.088; Table X, row 3). There was a significant effect of state on capture success of females (ANOVA, F=13.6, DF=2, p<0.002). Females were captured in 25.8% (SE=5.9) of attacks on mating pairs, and in 28.3% (SE=2.8) of attacks on struggling pairs. These two values are significantly different from the mean capture success on single females (10.2% (SE 1.0); p=0.007, p=0.002; Table X, row 4).

Capture of single gerrids always resulted in predation. Capture of mating or wrestling pairs usually resulted in predation of the female rather than the male, and never resulted in predation of both. Females suffered predation in 87% of
Table X. The effect of the activity of gerrids (single, mating, wrestling) on number of attacks and proportion of captures by notonectids. The first row shows mean number of notonectid attacks on gerrids in different activities. In the single column attacks are shown for both male (left) and female (right). Second row shows the proportion of attacks that resulted in capture for bugs in either sex. Capture rates are divided by sex in the third and forth row. The top number of each row is the mean and the bottom number, in brackets, is the standard error of the mean. Asterisks in the first column indicate overall significant effect of activity (ANOVA) and in the remaining columns asterisks indicate significant difference between adjacent mean and the value for single gerrids in that row (* p<0.05; ** p<0.01; *** p<0.001).

<table>
<thead>
<tr>
<th></th>
<th>Single</th>
<th>Mating</th>
<th>Wrestling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Attacks</td>
<td>47.0 / 22.0</td>
<td>10.0</td>
<td>5.5</td>
</tr>
<tr>
<td></td>
<td>(1.8) / (2.7)</td>
<td>(1.9)</td>
<td>(1.3)</td>
</tr>
<tr>
<td>% Capture (Total)</td>
<td>10.4</td>
<td>29.7**</td>
<td>49.8***</td>
</tr>
<tr>
<td></td>
<td>(1.3)</td>
<td>(4.7)</td>
<td>(6.7)</td>
</tr>
<tr>
<td>% Capture (Male)</td>
<td>10.5</td>
<td>3.8</td>
<td>21.5</td>
</tr>
<tr>
<td></td>
<td>(1.7)</td>
<td>(2.3)</td>
<td>(4.8)</td>
</tr>
<tr>
<td>% Capture (Female)</td>
<td>10.2</td>
<td>25.8**</td>
<td>28.3**</td>
</tr>
<tr>
<td></td>
<td>(1.0)</td>
<td>(5.9)</td>
<td>(2.8)</td>
</tr>
</tbody>
</table>
captures of mating pairs, and in 57% of captures of struggling pairs. This bias toward females in captures of mating pairs was clearly a positioning effect: notonectids attack from below and male gerrids ride on top females when mating. In those cases where the male was guarding the female, males would often release the female at the instant of capture by the notonectid, and therefore escape. In contrast, captures of copulating pairs always resulted in both male and female being dragged under the water by the notonectid. This is because males in copula cannot instantly withdraw their genitalia, and thus are attached to females for a few seconds. When mating pairs were captured, the male would usually soon float to the surface and escape. Capture of wrestling pairs rarely resulted in both individuals being pulled under water. Because wrestling pairs somersault and roll, the male would often be grasped by the notonectid. In these cases it was the female that often escaped at the surface, or soon floated to the surface.

I was not able to determine the proportion of time that gerrids were single, mating or wrestling. Therefore, I was unable to calculate the rate at which each class suffered attacks. However, observations suggest that attack rate was highest on wrestling pairs, and lowest on mating pairs. It was clear that notonectids were attracted to movement on the water surface. Wrestling is vigorous, thus disturbance at the water surface was high. On the other hand, mating pairs appeared to reduce movement. There was no indication that attacks were biased toward either sex: the proportion of females in the pools was 0.33, and the mean proportion of attacks on single gerrids that were directed toward females was 0.32. Therefore, there is no evidence that females are selected for attack by notonectids.

Total mortality in these experiments was biased toward females, despite an available sex ratio biased toward males. Females represented 51.8% (SE=2.8) of the total mortality in these experiments. Given a sex ratio of 2:1, the risk of predation to females was 2.08 (S.E. = 0.21) times the risk to males. These results are
comparable to those in the field enclosure experiment (Figure 17).

**DISCUSSION**

These experiments demonstrate that mating behaviour in *Gerris buenoi* is costly to females. Both in field enclosures and in laboratory pools, predation by notonectids was female biased (Figure 17, Table X). There was no evidence that female biased predation resulted from a greater exposure of females to predation than males. Males spend less time on the refuge of floating vegetation, and there was no evidence that notonectids were more likely to attack single females than males (Table X). However, mating females and females struggling with males are more likely to be captured in notonectid attacks than single females (Table X). These support earlier results of Arnqvist (1989b), who showed that predation of female *G. odontogaster* increased in the presence of males. All of the major components of mating behaviour appear to increase predation risk to female *G. buenoi* to some degree. These components include 1.) harassment by males; 2.) premating struggles where females attempt to repel male mating attempts, and postmating struggles, where females attempt to dislodge guarding males; and 3.) mating which includes copulation and guarding. This study represents one of the few studies to demonstrate an increased predation risk to females as a result of mating activity (Wing 1988; Arnqvist 1989b; Gwynne 1989; Fairbairn in press).

**Predation Risk to Mating Females**

Notonectids are more efficient predators on mating females than on single females. The proportion of notonectid attacks that resulted in capture of females
was more than doubled when females were in mating compared to attacks on single females. Attack success increased from 10.2% on single females to 25.8% (Tables X). The increased susceptibility of females to predation results from their reduced speed and agility when burdened with a male. The response of gerrids to notonectid attack is to leap off the water surface, and/or skate rapidly from the scene. Leaping from the surface is undoubtedly more difficult with the additional weight of a male. In addition, Arnqvist (1989b) has shown that female escape speeds are reduced when in mating.

Females appear to adjust their behaviour when mating in such a way that predation rates are probably less than those expected from the attack success of notonectids alone. In the experiment on notonectid attack success, notonectids oriented to disturbance of the water surface. Perhaps in response to their abilities, female gerrids appeared to reduce their skating rate in the presence of notonectids. Sih et al. (1990) have likewise shown that female A. remigis reduce their rate of movement in the presence of sunfish predators. In the field, mating females further reduce exposure to predation by moving to the refuge of floating vegetation (Rowe 1992).

Harassment and Predation Risk to Single Females

I have shown that the rate of harassment may be as high as 47 mating attempts per hour (Chapter 5). Females typically respond to these attempts by skating rapidly from the scene. Harassment of females by males increases the risk of predation to females through three mechanisms. First, increased movement alone appears to attract notonectids, by increasing the disturbance of the watersurface (see above and Lang 1980). It is not possible to determine under natural conditions the degree to which female movement was increased as a result
of male harassment, since males were always present. Nevertheless, movement of females is no doubt increased to some degree. In the laboratory, female movement was increased about 25% as a result of harassment by males (Table IX).

Second, escape from males will often require females to move from the refuge of floating vegetation to risky open water. I have not quantified this behaviour, but it is almost certainly significant given the frequency of harassment by males. Females in the wild were found to spend less time in the open water than males. However, in the absence of male harassment they are expected to spend even less time on the open water. Thirdly, a portion of male mating attempts lead to a vigorous struggle between males and females (Chapter 5). These struggles increase predation risk to females. Notonectid attack success increased from 10.2% on single females to 57% on wrestling females (Table X). Attack success alone probably underestimates the risk to wrestling females. Wrestling is vigorous, including somersaulting (Chapter 5), and such disturbance probably attracted notonectids.

Females must balance predation risk associated with remaining unmated (further harassment by males) with risk associated with mating. A direct test of the sensitivity of females to predation risk requires the monitoring of mating dynamics following the manipulation of predation risk. In the presence of predatory sunfish, *A. remigis* mates less frequently, and for a shorter duration than in their absence (Sih *et al.* 1990). Qualitative predictions about the effect of predation risk on mating behaviour of *G. buenoi* can not be made *a priori*, because these predators increase predation risk associated with both mating and repelling males. Nevertheless, *G. buenoi* do respond to variation in the costs of mating. In *G. buenoi*, mating also conflicts with foraging, and thus there is an additional cost of mating. Hungry females reduce mating activity and females are more willing to mate, and to mate for longer when the rate of harassment by males is
experimentally increased (Chapter 5).

A Cost of Mate Choice?

Most pre-mating struggles result in the escape of the female, and these struggles are significantly longer than those that result in mating (Rowe 1992). If pre-mating struggles function as either active or passive mate choice then mate choice is costly, because struggling with males increases predation risk (Figure 17). Arnqvist (1992a) has argued that pre-mating struggles in *G. odontogaster* are motivated by a general reluctance to mate rather than a means of mate choice, because much of the variation in female reluctance can be explained by variation in factors (eg. density) other than male phenotype. However, the possibility of mate choice remains: there is evidence for assortative mating, and there has been no test of the dependence of female reluctance on male phenotype. Similarly, there is no evidence of active mate choice in *G. buenoi*. However, there is some evidence for size assortative mating (Fairbairn 1988; Rowe unpublished data), and females are able to control the success of mating attempts by males (Chapter 5). Taken together, these data suggest that assortative mating comes at a cost to females. However, whether females vary the duration of these struggles as a means of mate choice remains unresolved.

Costs of Mating or Costs of Reproduction?

Magnahagen (1991) has recently emphasized the relationship between mating costs and reproductive costs. Reproductive costs describe negative effects of reproductive effort (eg. rate) on other fitness components (eg. longevity; Williams 1966). It is arguably the case that most mating costs to males are reproductive
costs. This results from a close positive association between mating success and reproductive success in males: there is little doubt that mating frequency is positively correlated to male reproductive success in many species. However, there is no a priori reason to expect that the mating rate of females, beyond that required to maintain fertility, is related to their reproductive success. The major causes of variance in female reproductive success are typically reproductive rate (the rate of egg production) and longevity. In G. buenoi and other gerrids, longevity is a negative function of reproductive rate (Kaitala 1987, 1991; Chapter 3). This may be interpreted as a reproductive cost that is distinct from the mating costs shown here. Only in those species where reproductive rate is a positive function of mating rate, should mating costs be considered a cost of reproduction. Such a relationship probably is limited to those species where males contribute resources to females.

Mating Costs to Males

Although I have thus far focused on the costs of mating only to females, the data reported here clearly suggest mating costs to male G. buenoi. Males spend a large proportion of their time searching for females and harassing them (Chapter 5), and I have shown that as a result, movement rate is increased in the presence of females. These activities occur on open water, and thus increase exposures to predators. Consider that males could alternatively retreat to refuge for the amount of time that they were pursuing females. Finally, pre-mating struggles with females are rarely successful and increase the risk of male capture by striking notonectids, and also probably attract predators. It is interesting to note that mating males appear to be at lower risk to predation than single males. Attack success of notonectids is more than halved, although not significantly, on
mating males relative to single males. Exposure of mating males to predators is further reduced, because most mating occurs in refuge.
Chapter Five

CONVENIENCE POLYANDRY IN GERRIS BUENOI:
HARASSMENT BY MALES, FORAGING CONFLICTS
AND FEMALE CONTROL OF MATING DECISIONS

Summary

In this chapter, the mating behaviour of *G. buenoi* is investigated in the field and laboratory. The conflict between foraging demands and mating was examined, and the convenience polyandry hypothesis for superfluous mating was tested directly. Mating is multiple, females are reluctant, males are persistent, and mating consists of a period of copulation followed by a guarding phase in which the male and female remain in tandem without genital contact. Males make frequent attempts to mate females that often lead to vigorous struggles initiated by females. All matings were terminated with a struggle initiated by the female, which continued until the male was dislodged. Field data support the hypothesis that mating conflicts with foraging. Females occupied with prey offered little resistance to male suitors, and guarding durations were significantly longer when females were currently consuming prey or had fed recently. To test the hypothesis that females were more willing to mate when foraging demands were reduced, mating behaviour of bugs under different feeding regimes were compared. Female hunger reduced mating frequency in the laboratory, and male hunger had no effect. These data demonstrate that mating conflicts with foraging by females, and females appear to vary mating behaviour according to this conflicting demand. The convenience polyandry hypothesis predicts that females will accept superfluous copulations when costs of repelling male mating attempts (remaining
are greater than the costs of mating. To test this hypothesis, mating behaviour was compared under two sex ratios (1:1 and 3:1), where harassment of females, and thus the cost of repelling males, was expected to be higher in the male biased treatment. Female mating activity, frequency and duration all increased significantly under a sex ratio of 3:1. In the male biased treatment, harassment of females by males increased significantly, and both mating activity and frequency were a positive function of harassment rate. Increased mating frequency resulted from an increase in the proportion of mating attempts that led to copulation. Pre-mating struggles that led to mating were about one quarter the duration of those that did not. Therefore, increased mating frequency under high harassment rate resulted from a decrease in female reluctance to mate. There was no treatment effect on the duration of post-mating struggles, indicating that increased guarding duration observed under the male biased sex ratio resulted from a female decision to postpone dislodging the male. These results demonstrate a strong degree of female control over most components of mating, and support the convenience polyandry hypothesis for superfluous mating.
INTRODUCTION

The economics of multiple mating has attracted considerable interest (Daly 1978; Walker 1980; Thornhill and Alcock 1983). The costs of mating to females can be divided into two classes: costs of mating itself, and the costs associated with repelling males. Costs of both classes may include risk of predation, and loss of time and energy (devoted to or lost to either activity). Thus, mating may conflict with other activities, such as foraging and predator avoidance, and females therefore, face trade-offs when deciding to repel suitors or accept them. Few studies have examined mating in light of such conflicting demands.

Multiple mating by males can have a direct positive effect on male fitness: reproductive success of a male is often limited by the number of ova he can fertilize. On the other hand, reproductive success of females is unlikely to be limited by sperm and thus additional mating is less likely to have a direct positive effect on their fitness. Nevertheless, there are several potential indirect benefits of mating for females. These include parental investment by males (e.g., nuptial feeding and nutritional resources passed with sperm), reduced predation risk, and increased genetic diversity of offspring (see reviews in Walker 1980; Thornhill and Alcock 1983; Smith 1984; Gwynne 1989). Here multiple mating is viewed as advantageous to females if benefits of mating are greater than costs. If females can control mating, then they should mate at a rate that maximizes the net benefits.

Alternatively, females may accept superfluous mating to reduce costs of harassment by male suitors (e.g. Walker 1980; Parker 1984; Wilcox 1984): females may accept additional mating if the cost of repelling amorous males is greater than the cost of accepting them. Thornhill and Alcock (1983) refer to such mating systems as 'convenience polyandry'. Although it is intuitively clear that females will mate when the costs of repelling males becomes high, to my knowledge there
have been no attempts to test the hypothesis of convenience polyandry. Furthermore, a suite of testable predictions arising from this idea have not been formulated.

In their discussion of convenience polyandry, Thornhill and Alcock (1983) focus on the proposition that males can make it so costly (direct costs) for females to repel their mating attempts that females will mate out of convenience. For example, the act of preventing copulation may have a direct energetic cost. As costs are elevated, it will become adaptive for females to accept the male. Testing this hypothesis seems difficult, because a simple method of manipulating direct costs of male mating attempts is not apparent. Alternatively, repelling males may have some indirect cost, such as increasing predation risk, and females may accept superfluous copulations when risk is elevated. However, interpretation of such a test would be confounded if mating and repelling males both increased predation risk to females. Females might then be more or less likely to mate when predation risk is increased.

A second set of indirect costs of repelling males are those incurred after the physical interaction with the male. One consequence of successfully repelling a male is exposure of single females to further costly harassment. Therefore, the costs of successfully repelling males should be a positive function of harassment rate. Manipulation of harassment rates is relatively easy, and will not be confounded in cases where costs of repelling males and mating are analogous. Simple methods include (1) removing refuges for females from males, and (2) increasing density and thus encounter rates between the sexes, or (3) biasing the sex ratio towards males and thus the encounter rate of females with males. The overall prediction is a positive relationship between harassment rate and mating activity of individual females. However, such a relationship may result without any response of females to the manipulation. Mating activity may increase without
increased female receptivity, because an increased rate of male mating attempts alone could produce such a result. Therefore, a demonstration that females mate for convenience should include a positive relationship between harassment rate and female receptivity to mating.

Gerrids are one of the few groups where variation in mating behaviour has been studied in response to variation in conflicting demands. Gerrids mate multiply, despite probable energetic costs and predation risks to females (e.g., Andersen 1982; Wilcox 1984; Arnqvist 1989b). Sperm is stored, last male sperm precedence occurs, and sperm is transferred rapidly relative to total mating durations (Andersen 1982; Arnqvist 1988; Rubenstein 1989). Therefore, most mating may be considered superfluous to the female. Males ride on the back of females during copulation, and may remain in tandem, guarding the females after copulation has ceased (Andersen 1982; Wilcox 1984; Arnqvist 1988). Rubenstein (1984) and Wilcox (1984) hypothesized that females of the lotic gerrid *Aquarius remigis*, may actually benefit from long matings despite a probable cost of carrying males. Females in tandem are harassed less by other males, and are therefore able to spend more time foraging and foraging success is nearly tripled (Rubenstein 1984; Wilcox 1984).

In one laboratory study of *A. remigis*, female hunger level had no effect on mating duration, but duration was extended when sex ratio was male biased (Clark 1988). Clark concluded that sperm competition, not Wilcox's enhanced foraging hypothesis, accounted for variation in mating duration. However, in a similar study, Sih *et al.* (1990) found that mating duration of *A. remigis* was reduced when males and females were simultaneously deprived of food. The latter authors concluded that mating duration was reduced because mating conflicted with feeding by males; males in contrast to females do not feed in tandem. Interpretations offered by Clark (1988) and Sih *et al.* (1990) imply that males
control mating duration, despite a lack of information on control of either mating frequency or mating duration in gerrids. Therefore, the role of food in the mating behaviour of *A. remigis* remains ambiguous.

In contrast to lotic gerrids, foraging by females of lentic (still water) species is less likely to be enhanced by males in tandem: food in lentic habitats is not concentrated in patches (e.g., Vepsalainen and Nummelin 1985b; Spence and Wilcox 1986). Thus, in pond species, foraging in tandem is probably less efficient, and may increase the risk of predation (Vepsalainen and Nummelin 1985b; Arnqvist 1989b). Therefore, mating is predicted to conflict with foraging. However, the role of food in mating behaviour of lentic gerrids has not been addressed.

In the present study, I examine mating behaviour of the lentic gerrid *G. buenoii* in light of conflicting demands, and directly test the convenience polyandry hypothesis. Field and laboratory studies are used to determine the effect of variation in both costs of mating and repelling males (e.g., not mating; remaining single) on mating behaviour. First, I describe mating behaviour in the field with reference to foraging. The mating behaviour of this species has not yet been described. Second, I test the following hypotheses (1) mating conflicts with foraging and variation in mating behaviour reflects variation in foraging demands of females; (2) mating activity (frequency x duration) is a positive function of the rate of harassment by males; (3) females play a significant role in determining mating frequency and duration; and (4) female receptivity to mating is a positive function of harassment rates.
METHODS

Behaviour in the Field

In the first part of the study, I describe the behaviour of *G. buenoi*. All data, in this and subsequent sections, are taken from observations of macropterous, overwintered gerrids. Field observations were conducted at Shallow Pond in the University of British Columbia Botanical Gardens, during June and July of 1990. Shallow Pond is a small (12 X 8 m) permanent pond that is surrounded by gardens, and lacks shading from trees. Therefore, the entire surface of the pond can be surveyed from the shore. During the study period, about 25-50% of the pond surface was littered with floating and emergent vegetation. *Gerris buenoi* is the numerically dominant gerrid throughout the season in this pond. *Gerris incognitus*, *G. incurvatus* and *Limnoporus notabilis* were also present. Sex ratio in this and nearby ponds varies from male to female biased (Rowe unpublished data).

I used several methods to quantify behaviour. I made observations from the shoreline with binoculars, between 1100 and 1700 hours. During a five day period, focal animal observations were made on 27 females. Single females were observed continuously for a total of 10 min or until lost from sight. If mating occurred during the sampling period, observation continued until mating terminated. An assistant recorded the number of lunges by males at females (attempts), the female's reaction and the durations of any ensuing pre-mating struggle, copulation and guarding, and the number of attempts by males to copulate or interrupt these pairs. Five matings were observed during the focal animal study. By searching the pond for struggling pairs I was able to estimate the duration of an additional 28 matings. In five of these cases I came across pairs during copulation and four cases during guarding. In these cases I assumed that
my observation started half way through the phase in question. On several occasions, I surveyed the pond to determine whether tandem pairs were in the open water or on floating debris. In a final survey, I scanned the pond to determine the ratio of feeding to non-feeding males, females and pairs. In summary, location only was determined for 170 pairs, location and feeding was determined for an additional 73 pairs and, location, feeding and foraging for prey was determined for an additional 33 pairs. Throughout the study, I recorded information on foraging, feeding and oviposition behaviour. I will refer to consuming prey as 'feeding' and searching and capturing prey as 'foraging'.

Effect of Hunger on Mating Behaviour

I determined the effect of hunger on both sexes by comparing mean mating activity, frequency and duration of matings in replicate experimental containers. Plexiglass pools had a water surface area of 0.5 m² and depth of 3 cm. Gerrids collected from J.K. Henry Pond in the University of British Columbia Botanical Gardens, were held for 72 h in large plastic wading pools in the laboratory until 24 h prior to the experiment, when sexes were separated and gerrids were individually marked with acrylic paints. Food (frozen fruit flies) was provided *ad libitum* until 6 h prior to the experiment. At that point, gerrids were further divided into fed and unfed males and females. Unfed gerrids were deprived of food for the remaining 6 h period, while fed gerrids continued with abundant food.

I assigned six males and six females to each of nine pools (three replicates for each of three treatments). Treatments were the 'control' (both sexes fed), 'male hunger' (males unfed, females fed) and 'female hunger' (males fed, females unfed). At 10 min intervals each pool was visited, and the activity of each individual was
recorded as either mating or non-mating. The experiment continued for 4.5 h. At that point, the first mating of any female had been terminated, although some females had not mated once, and others had mated more than once. Duration of a mating was estimated from the number of consecutive visits that a pair was seen in tandem.

Each pool was treated as a replicate for statistical analyses. Mating activity was the proportion of time females were mating, and was calculated as the sum of the number of mating pairs on each of 27 visits divided by the potential number of matings (number of females x 27 visits). Mating frequency was the total number of matings that occurred in each replicate divided by the number of females present. Mating duration was calculated as the mean duration of matings that had occurred in each replicate. Only matings in which neither individual had mated previously during the experiment were used for analysis of mating duration ("independent matings" as in Clark 1988). Nevertheless, results were similar if all matings were included.

Sex Ratio and Mating Behaviour

In a second experiment I determined the effect of sex ratio on mean mating activity, mating frequency, and durations of copulation and guarding in replicate experimental pools. I set up four replicate pools containing 12 gerrids for each of two treatments; the two treatments were male:female sex ratios of 1:1 and 3:1. Details of this experiment and analyses are as in the previous experiment, except that I determined whether pairs were copulating (genital contact) or guarding (no genital contact) on each visit.
In a third experiment, I determined the effect of sex ratio on several dependent variables chosen to indicate which sex controls mating frequency and duration. This experiment focused on detailed components of mating behaviour that could not be addressed in the first experiment. Dependent variables were frequency of attempted matings by males on females, proportion of attempts resulting in pre-mating struggles, duration of these struggles, proportion of struggles resulting in matings, mating activity, and duration of post-mating struggle. Because of the high density of gerrids in these pools it was difficult to distinguish lunges of males at females, as I had in the field. Therefore, I defined a mating attempt as a deliberate lunge at females by males that resulted in contact. Hence harassment rate is underestimated in the laboratory relative to the field. I similarly recorded the number of male attempts on other males and on mating pairs.

Observations on single pools were made continuously for 45 min. Each pool contained 12 gerrids at sex ratios of 1:1 or 3:1. Males were marked with acrylic paint to aid in identification of the sexes. Events were recorded by type and time. Pre- and post-mating struggles were recorded to the second except in cases where struggles were less than 3 s, in which case all were given values of 1.5 s. The experiment was repeated four times on 12 June, and four times on 13 June, with alternation of treatments. Untested gerrids were used in each replicate. Sexes were separated in holding pools 16-24 h prior to experiments. Remaining experimental conditions were as in the previous experiments.

All comparisons of means were made on log transformed data, except for proportions which were arcsine transformed. Unless otherwise stated, I used t-tests to test for significance of differences between means.
RESULTS

There are four phases to mating behaviour in *G. buenoi*: pre-mating, copulation, guarding, and post-mating (Figure 18). The pre-mating phase is initiated by males lunging at the female. Males that successfully contact females attempt to grasp the female's thorax with their forelegs, and insert their genitalia. Females respond by rearing up on their mid-legs, and somersaulting in an attempt to dislodge males from their back. Females use their forelegs to break the male's grasp of their abdomen. The copulation phase begins when males successfully insert their genitalia, and struggling ends. After several minutes of copulation, a guarding phase is initiated when the male withdraws his genitalia, but remains on top of the female. I refer to the combination of copulation and guarding phases as mating. The post-mating phase consists of a struggle initiated by females, similar to struggles in the pre-mating phase, that terminates mating. A second male would often attempt to copulate or perhaps interrupt mating pairs (mean in the field was 2.2 attempts per mating, S.E. 0.51, n=20). However, these attempts are usually short lived: males mount the pair, occasionally probing with their genitalia and then quickly dismount. Attempts by second males usually elicited little response from mating pairs, and never resulted in take-over or interruption.

Pre-mating Phase

Females spend much of their time avoiding harassment by males. In the field, a given female was lunged at by males about 47 times per hour. Most of the 147 attempts recorded were unsuccessful (97%), usually contact was not made (females leap vertically and/or skate off), and few attempts resulted in pre-mating struggles (15%). Mean duration of pre-mating struggles was 7.3 s, and only 22% of
Figure 18. Path diagram of the mating sequence of *G. Buenoi*. Proportions accompanying arrows are estimated from field observation and reset to 1.00 after each outcome. Left column indicates which sex initiates the action described to the right. Further details are given in the methods and results section.
**Female**

- Mating attempt → Female escapes
  - Male dislodged

**Male**

- Pre-mating struggle → Male dislodged
  - Copulation
    - Guarding → Oviposition
      - Post-mating struggle
        - Male dislodged
struggles resulted in a mating (Figure 18). Although my sample size is small, there was no evidence that the probability of a male copulating resulted from that particular male’s ability to withstand struggles. The longest pre-mating struggle observed in the field was 63 s, and did not lead to a copulation. All others were less than 15 s.

Food and Mating

Foraging males and females skate about searching for living and dead insects trapped on the water surface. Prey location appears to be both visual and tactile. Gerrids often approach inanimate (often non-food) items and probe them with their mouthparts, but are particularly attracted to prey items struggling to escape the water surface. Gerrids pick up smaller prey items (e.g., midges) and skate off to floating debris to feed. Larger prey (e.g., damselflies), that can not be transported, are fed upon where they were found. Large prey are often fed upon by several individuals, but are rare in the diet. Females appear to spend more time feeding than males. In the pond survey, single females were found feeding almost twice as often as males (16.3%, n=92 and 9.4%, n=85 respectively), but this difference was not significant (0.25 > p > 0.10, contingency table test).

Mating conflicts with foraging of both males and females. Upon commencement of copulation, females skate to or remain on floating debris, and become inactive: 89% of 276 mating pairs, located throughout my field study, were inactive on floating debris. Some mating females did dart out from a resting spot to capture prey items struggling on the water surface nearby. However, this was observed in only 3 of the 33 pairs where behaviour during mating was observed. Although females often feed while mating, they are consuming prey captured prior to initiation of mating (see below). I never observed a male feeding while
Females are more willing to mate while feeding than while undertaking other tasks such as foraging for prey, grooming or resting. Of 5 matings recorded in the focal individual observations, 3 occurred after females had captured and were feeding on a prey item. Of the 33 complete matings observed, 36% of these females had prey items in their grasp at some time during the mating. This is probably an underestimate, since very small prey items may have been missed in these observations. In the feeding survey, 29% (n=73) of mating females were feeding, while only 16% (n=92) of single females were feeding, and this difference approaches significance (0.1 > p > 0.05, contingency table test). On several occasions, I placed a freshly killed damselfly on the water surface and observed gerrid behaviour around it. Within a few minutes, both males and females could be seen feeding upon it. Often males approaching the carcass would mount feeding females, and females offered little or no resistance.

Variation in mating duration in the field was high, ranging from 4.0 - 61.5 min. Most of this variation reflected variation in duration of guarding (range 0 - 54.4 min.), not copulation (range 4.0 - 14.0 min). Females that fed during copulation were guarded significantly longer than those that had not fed (p < 0.01). Mean guarding duration was 16.4 min (S.E. = 1.50) in cases in which females had fed, and 0.5 min (S.E. = 0.04) in those that had not. However, copulation duration did not differ between females that had fed and those that had not (p > 0.1). Mean copulation duration was 7.1 min (S.E. = 0.33) for females that had fed, and 7.7 for those that had not (S.E. = 0.16).

Post-mating Phase
In all cases matings were terminated during the guarding phase, after the female had initiated a post-mating struggle. Males never simply dismounted. Post-mating struggles, once initiated, continued until the male was dislodged. I did not time these struggles. However, they appeared to be about the same duration as pre-mating struggles. Often the switch from copulatory to guarding phase occurred just after the female had dipped the tip of her abdomen under the water surface.

Oviposition and Territoriality

Oviposition in this species is difficult to observe. Females dip their abdomen under the water, and oviposit one or several eggs on floating debris, such as algal mats, leaves and other floating vegetation. They rarely oviposit while mating; only 1 of 33 females that I monitored during mating oviposited, and only 2 of the 25 ovipositions I observed throughout the study occurred with males in tandem. Furthermore in the remaining 23 events, there was no evidence of males non-contact guarding nearby. I saw no evidence of territoriality by males or females. Both males and females roamed over much of the pond, and I never observed fighting or other aggression between females. Although males often attempted to mount one another, they did not fight on contact or chase one another. Males commonly attempted to mate other males, conspecific males and females, and even inanimate objects.

Effect of Hunger on Mating

Results of the laboratory test on the effect of hunger on mating behaviour showed that female hunger had a strong effect on mating behaviour, and male hunger had no effect (Table XI). Hungry females spent 55% less time mating than
Table XI. Effect of hunger on mating behaviour of *G. buenoi*. Mating activity is the mean proportion of time females mate; mating frequency is the mean number of matings per female throughout the experiment and mating duration is the duration (min) of the average mating and comprises both copulation and guarding phases. Last row shows results of ANOVA for treatment effect in comparison of means between rows; ** = P<0.01, * = P<0.05, ns = p>0.05; n=4 for all means; means are followed by (SE).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Activity</th>
<th>Frequency</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females Fed &amp; Males Fed</td>
<td>0.42</td>
<td>1.71</td>
<td>55.33</td>
</tr>
<tr>
<td></td>
<td>(0.10)</td>
<td>(0.45)</td>
<td>(6.49)</td>
</tr>
<tr>
<td>Females Fed &amp; Males Unfed</td>
<td>0.45</td>
<td>2.23</td>
<td>61.67</td>
</tr>
<tr>
<td></td>
<td>(0.05)</td>
<td>(0.53)</td>
<td>(7.92)</td>
</tr>
<tr>
<td>Females Unfed &amp; Males Fed</td>
<td>0.20</td>
<td>0.85</td>
<td>57.67</td>
</tr>
<tr>
<td></td>
<td>(0.03)</td>
<td>(0.18)</td>
<td>(6.36)</td>
</tr>
</tbody>
</table>

* ns = p>0.05, * = P<0.05, ** = P<0.01.
recently fed females. This was largely owing to a significant 53% decrease in mating frequency. I compared treatments with an analysis of variance, and where significant treatment effects were detected, I partitioned the treatment sum of squares to compare the effects of female hunger and male hunger (Snedecor and Cochran 1967, pp 308-310). There was a significant overall treatment effect on mating activity and frequency, but not duration (Table XI). A comparison of the female hunger treatment to the remaining two treatments revealed a significant effect of female hunger on both mating activity (p < 0.05), and frequency (p < 0.01). The combined effect of control and male hunger treatments on mating activity and frequency was not significant (p > 0.50). Variation in duration of the 87 observed individual mating events was high (10 - 140 min).

Sex Ratio

Sex ratio had a strong effect on most measured aspects of mating behaviour in the laboratory (Table XII). Mating activity increased 64%, and mean mating duration increased about three fold, from 34.2 to 100.7 min., when the sex ratio was increased from 1:1 to 3:1. Most of this increase in mating duration was due to an increase in guarding duration (60.5 min), although copulation duration also increased (6.0 min) (Table XII). The 97 individual mating events ranged from 10 - 240 min in duration.

Mating frequency decreased significantly from 4.6 to 3.5 matings per female when sex ratio was male biased (Table XII). This was an unexpected effect that may result solely from the increase in mating duration, since some matings continued over much (up to 89%) of the duration of the experiment. To disentangle mating frequency from duration, I compared the proportion of females that had commenced mating within the first 30 minutes of the experiment. Viewed
Table XII. Effect of sex ratio on mating behaviour of G. buenoi. Early frequency refers to the mean proportion of females mating within the first 30 min of the experiment. Other terms are as in table I. Last row shows results of t-test for sex ratio effect in comparison of means between rows; ** = P<0.01, * = P<0.05, ns = p>0.05; n=4 for all means; means are followed by (SE).
<table>
<thead>
<tr>
<th>Sex Ratio</th>
<th>Mating Activity</th>
<th>Mating Frequency</th>
<th>Early Frequency</th>
<th>Duration (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Mating</td>
</tr>
<tr>
<td>1:1</td>
<td>0.51 (0.04)</td>
<td>4.65 (0.49)</td>
<td>0.54 (0.08)</td>
<td>34.25 (6.58)</td>
</tr>
<tr>
<td>3:1</td>
<td>0.85 (0.05)</td>
<td>3.50 (0.32)</td>
<td>0.92 (0.08)</td>
<td>100.75 (20.26)</td>
</tr>
</tbody>
</table>

* ns **
in this manner, mating frequency increased when sex ratio was male biased from 54 to 92% of females mating within the first 30 minutes of the experiment (Table XII).

Harassment and Female Control

As expected, increasing sex ratio from 1:1 to 3:1 resulted in a significant increase in the rate at which males harassed females in the laboratory. Single females were exposed on average to 11.75 mating attempts per hour at 1:1, and 29.25 at 3:1 (Table XIII). Related to this increase in harassment rate was a significant increase in mating activity and frequency (Table XIII, Figure 19a,b). Increased mating activity and frequency was not due solely to an increased harassment rate. The proportion of attempts by males that resulted in copulation was more than doubled under a male biased sex ratio (Table XIII), and success rate (the number of attempts/single female/hour) was an increasing function of the rate of male attempts on females (Figure 19c). Differences in success rate of males does not appear to result from some difference in effort by males in pre-mating struggles in response to sex ratio. Successful struggles were less than one third the duration of unsuccessful struggles in both treatments (Table XIV), and successful and non-successful pre-mating struggles were actually slightly shorter in the male biased treatment (Table XIV). Thus, increases in the bias of sex ratio towards males leads to increases in harassment rate, and in turn to a decrease in female reluctance.

Males do not appear to give up in attempts to gain or retain a mating. All observed terminations of matings (n = 17) were initiated by females attempting to dislodge the male, and these always occurred after the male had withdrawn his genitalia. Once an attempt to dislodge the male was initiated, the struggle was
Table XIII. Effect of sex ratio on mating behaviour of *G. buenoi*. Harassment rate is the number of male attempts to copulate females per single female hour (see methods). Success rate is the proportion of mating attempts that resulted in copulation. Other terms are as in table I. Last row shows results of t-test for sex ratio effect in comparison of means between rows; ** = P<0.01, * = P<0.05, ns = p>0.05; n=4 for all means; means are followed by (SE).

<table>
<thead>
<tr>
<th>Sex Ratio</th>
<th>Mating Activity</th>
<th>Mating Frequency</th>
<th>Harassment Rate</th>
<th>Success Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:1</td>
<td>0.19</td>
<td>0.66</td>
<td>11.75</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>(0.04)</td>
<td>(0.18)</td>
<td>(1.26)</td>
<td>(0.02)</td>
</tr>
<tr>
<td>3:1</td>
<td>0.66</td>
<td>1.25</td>
<td>29.25</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>(0.10)</td>
<td>(0.09)</td>
<td>(4.00)</td>
<td>(0.04)</td>
</tr>
</tbody>
</table>

**  *  **  *
Figure 19. The effect of male harassment rate on female (a) mating activity, (b) mating frequency and (c) receptivity. Harassment rate is the number of male mating attempts per single female hour; female receptivity is the proportion of male mating attempts per female that resulted in mating. Open circles indicate a sex ratio of 1:1 and shaded circles indicate a sex ratio of 3:1 (male:female). Pearson’s correlation coefficients for the relationships between harassment rate and mating activity (r=0.97), mating frequency (r=0.72) and success rate (r=0.92) are all significant (p<0.01; N=8).
Table XIV. The effect of sex ratio on the duration of pre- and post- mating struggles. Successful struggles led to mating, unsuccessful struggles did not. Other terms are as in table I. Last row shows results of t-test for sex ratio effect in comparison of means between rows; ns = p>0.05; n=4 for all means; means are followed by (SE).

<table>
<thead>
<tr>
<th>Sex Ratio</th>
<th>Pre-Mating</th>
<th>Post-Mating</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Successful</td>
<td>Unsuccessful</td>
</tr>
<tr>
<td>1:1</td>
<td>8.8</td>
<td>34.4</td>
</tr>
<tr>
<td></td>
<td>(0.7)</td>
<td>(1.8)</td>
</tr>
<tr>
<td>3:1</td>
<td>7.5</td>
<td>31.3</td>
</tr>
<tr>
<td></td>
<td>(1.0)</td>
<td>(5.0)</td>
</tr>
<tr>
<td></td>
<td>ns</td>
<td>ns</td>
</tr>
</tbody>
</table>
continued until the male was dislodged. There is no evidence that males put more effort into frustrating the female’s attempts at dislodgement when sex ratio was biased toward males. Post-mating struggles were longer than pre-mating struggles, and there was no difference in post-mating struggles between treatments (Table XIV). Therefore, longer guarding durations in the male biased sex ratio in the prior experiment appear to result not from increased efforts by males, but from a lack of attempts to terminate mating by females. The longer duration of post-mating struggles relative to pre-mating struggles is probably due to males having gained a secure grasp of the female in the former case, rather than any increased effort on their part.

**DISCUSSION**

Convenience Polyandry

Several authors have suggested that females accept superfluous matings because of the high costs of harassment imposed by male suitors ('convenience polyandry' *sensu* Thornhill and Alcock 1983; see also Walker 1980; Parker 1984). To my knowledge, my results with *Gerris buenoi* represent the first experimental evidence of convenience polyandry. The cost of repelling a male mating attempt, which is analogous to increasing the costs of being single, was manipulated by increasing the frequency at which single females were harassed. Female mating activity more than tripled when the cost of repelling males was increased: females became more receptive to mating when harassment rate by males was increased.

As expected, under a male biased sex ratio, harassment rate increased and mating frequency increased (Tables XIII, XIV and Figure 19a). Increased mating frequency did not increase because of more frequent encounters with amorous
males; rather, the proportion of male attempts to mate that resulted in copulation was a positive function of harassment rate (Figure 19c). Furthermore, increased success of mating attempts was not because of an increased vigour on the part of males attempting to mate, but because of an increase in female receptivity. Premating struggles resulting in copulation were significantly shorter than those that did not, and there was no effect of treatment on the duration of successful and unsuccessful mating attempts. Therefore, the observed increased mating frequency resulted from a higher proportion of short (successful) pre-mating struggles when harassment rate was increased. In summary, females are more receptive to mating when harassment rate, and thus the costs of not mating are increased.

Wilcox (1984) suggested that female gerrids would accept longer mating durations if male harassment rates were high. My results support his hypothesis. Mating durations (copulation + guarding) were about three fold higher at a sex ratio of 3:1 than 1:1 (Table XIII), and increased mating durations are correlated with increased harassment rates at 3:1 (Table XIII, XIV). Similarly, mating durations of A. remigis were increased at a sex ratio of 3:1 relative to 1:3 (Clark 1988). Although Clark (1988) did not measure male harassment rate, it is expected to be higher (per female) when sex ratio is male biased.

Several studies have reported increased copulation or guarding durations when sex ratio is male biased (McLain 1980, 1989; Sillen-Tullberg 1981; Clark 1988; Telford and Dangerfield 1990). Results of these studies were interpreted as male responses to increased male competition (but see Moore 1989). When sex ratio becomes male biased, sperm competition is intensified, and pay offs to guarding males should increase. However, my experiments reveal that females, not males, control guarding duration. Termination of all matings followed a post-mating struggle initiated by the female during the guarding phase. Males appear to have little control over the outcome of female attempts to dislodge them. Post-mating
struggles, once initiated, continue until males are dislodged. There was no evidence of males struggling more vigorously to remain on top of the female.

Food and Mating

In contrast to earlier studies of lotic gerrids (Rubenstein 1984; Wilcox 1984; Vepsalainen and Nummelin 1985a), my results indicate that mating conflicts with foraging by females in this lentic gerrid. Upon commencement of mating females typically skate to floating debris and then become inactive. There are several potential reasons for females to cease foraging for prey when mating. Carrying about a male is presumably energetically costly for female gerrids, and skating speed is reduced in *G. odontogaster* (Arnqvist 1989b). Furthermore, predation risk to females may be increased when in tandem. When male *G. odontogaster* are introduced to experimental pools containing predacious backswimmers (*Notonecta* sp.), predation of females increased (Arnqvist 1989b). Backswimmers are a major predator of *G. buenoi* (Spence 1983, 1986). My studies of predation by backswimmers, show that capture success of female gerrids is doubled when *G. buenoi* are in tandem (Chapter 4). Backswimmers strike from below, and floating debris represents a refuge for gerrids from predation. Female *A. remigis* become inactive and often attempt to crawl off the water surface when predation risk is experimentally increased (Sih *et al.* 1990). In summary, female *G. buenoi* probably retire to floating debris when mating to reduce energetic costs of skating in tandem and to reduce predation rates. Males do not feed while mating.

Experimental manipulation of female hunger supported the hypothesis that mating activity is influenced by the conflicting demand of foraging by females. Hungry females mated half as often as recently fed females and thus reduced time lost to mating by half (Table XI). These results mirror preliminary experiments I
undertook with *G. buenoi* and *G. incognitus* in which females were deprived of food for 18 h, rather than 6 h, and mating frequency was reduced 80-90%. Although mating also conflicts with foraging by males, male hunger had no effect on mating activity, duration or frequency. These results provide another line of evidence for female control of mating frequency in *G. buenoi*. It is perhaps not surprising that females and not males respond to hunger. Food requirements and hence the value of foraging are probably much lower for males. Males appeared to forage less often in the field (this study), are smaller than females (Fairbairn 1990), and egg production rate by females is strongly limited by food in *G. buenoi* (Rowe and Scudder 1990), and other gerrids (Kaitala 1987). Nevertheless, males may alter mating behaviour after extended food deprivation.

Clark (1988) found no effect of food deprivation of female *A. remigis* on mating duration, and did not report mating frequency. In contrast, Sih *et al.* (1990) showed that mating activity of *A. remigis* was reduced when both males and females were deprived of food, and this was largely because of reduced mating duration. Sih *et al.*'s (1990) treatment was much more severe than mine: 24 h food deprivation versus 6 h. In addition, mean mating duration in control gerrids was greater than 3.5 h for Sih *et al.*'s (1990) study, compared to about 1 h for Clark's (1988) and the current study (Table XIII). Therefore, each mating in the former study represents a much higher cost in lost foraging time than those in the latter studies. Sih *et al.* (1990) reported a 15%, but statistically insignificant, decrease in mating frequency in hungry gerrids. Interpretation of their frequency results may be confounded by the decrease in mating duration of hungry gerrids. Such a decrease would lead to an increase in availability of single females relative to the fed treatments. Under equal availability of single females the effect on mating frequency may become significant. Perhaps the most significant difference between the studies of Clark (1988) and Sih *et al.* (1990) is that the former was carried out
in running water and the latter in still water. In streams, females maintain territories, and thus may accept mating to retain these territories independent of hunger (see below). In pools, *A. remigis* may behave more like *G. buenoi*, since maintaining a territory is unlikely to be profitable in still water.

Guarding duration in my study was much greater when females were consuming prey. There are probably two reasons for this. Any attempt to dislodge the male may lead to the loss of that prey item. Prey items are grasped with the forelegs during feeding which are therefore unavailable to break the grasp of males. Furthermore, feeding females have no need to forage, and hence the costs of mating to them are reduced. Guarding duration is also positively associated with the rate of male harassment (mating attempts) of females. This effect may explain greater mating durations in the laboratory experiment relative to field matings. Density of gerrids and hence harassment rate was much greater in the laboratory than in the field (personal observation).

Components of Mating and Female Control

Aspects of mating behaviour in *G. buenoi* are common to most gerrids. They mate multiply, females are reluctant, males are persistent and ride on top of females during copulation and subsequent guarding (Andersen 1982). In *G. buenoi*, copulation is initiated by male attempts to mount the female followed by female attempts to dislodge them. Although common in gerrids, the function of pre-mating struggles is unclear. They may be a form of mate selection or simply represent a general reluctance of females to mate. Male *G. odontogaster* which have longer abdominal grasping apparatus are better able to withstand attempts by females to dislodge them, and enjoy higher mating success (Arnqvist 1989a). These data lend support to the mate selection hypothesis in *G. odontogaster*. Nevertheless,
much of the variation in mating duration and frequency in *G. odontogaster* can be explained by a general reluctance of females to mate (Arnqvist 1992a). *G. buenoi* males do not possess an abdominal grasping apparatus, and I found no evidence suggesting that success of mating attempts is related to a male’s ability to withstand struggles to dislodge them.

Successful mating attempts appear to result from a lack of female resistance. Females currently occupied with a prey item offered little or no resistance. In the laboratory studies, struggles leading to mating were significantly shorter than those that did not. Therefore, pre-mating struggles in *G. buenoi* appear to represent a general reluctance to mate, and duration of these struggles is related to the degree of female reluctance. Nevertheless, mate selection may also motivate struggles to some degree. There is some evidence for homogamy in *G. buenoi* (Fairbairn 1988; Rowe unpublished data); perhaps females also adjust their level of reluctance according to their assessment of individual males.

Males do control copulation duration and vary it according to sex ratio (Table XV). Copulation is terminated by males withdrawing their aedeagus, thus variation in copulation duration reflects a male decision. It is not entirely clear why males prolong copulation when sex ratio is male biased. Males may be responding to increased competition from other males. In several insect species, including gerrids, sperm precedence increases with copulation duration (Thornhill and Alcock 1983; Parker 1984; Rubenstein 1989). Alternatively, males may increase copulation duration as a means of guarding. Females wait until males have terminated copulation before dislodging them. Perhaps dislodging males is too difficult when they have two points of attachment to the female (forelegs grasping the thorax and genitalia inserted). In the field, females often dipped their abdomen as if to oviposit. Perhaps as a response, males then often withdrew their genitalia as if to facilitate oviposition. Therefore, males face a trade-off in deciding whether
to withdraw their genitalia: withdrawal of genitalia allows females to oviposit, but also allows females to dislodge them. This behaviour remains intriguing and requires further study.

Termination of mating in gerrids is also poorly understood. In *G. buenoi* all matings were terminated with a struggle initiated by the female. Similar results have been reported for *G. lateralis* and *G. odontogaster* in Sweden (Arnqvist 1988; 1989a). It is unknown how mating is terminated in *A. remigis*, although both female and male initiation of mating termination have been proposed or implied (Wilcox 1984; Clark 1988; Sih *et al.* 1990). If males simply dismount females then male control is clear. However, if termination of mating is initiated by female struggles, then at least partial female control is suggested. My results suggest that female *G. buenoi* control mating duration. In both the laboratory and field, all matings were terminated with a struggle initiated by females. Most mating in the field is relatively short, and I quantified terminations occurring only in my second sex ratio experiment. Therefore, longer matings may be terminated by the male. Nevertheless, in casual observation I have seen many long matings (>1h) terminated by females, and I have never seen males simply dismount. Therefore, I conclude that the extension of the guarding phase when females are feeding results from a female decision to allow males to remain mounted.

Although, mate guarding duration in *G. buenoi* is determined by females, guarding may still be viewed as a male strategy to reduce sperm competition. Males continue guarding as long as females tolerate it. Males insure that their sperm is not displaced while guarding. Furthermore, in the field the guarding period of some portion of these males (albeit small) will continue over a bout of oviposition. Nevertheless, males may play some unseen role in determining guarding duration. For example, females may base part of their decision to terminate mating on male quality. In the current experiments males were
randomly assigned among treatments, and therefore male quality cannot explain the observed variation between treatments.

Comparison with Other Species

Mating and foraging behaviour in *G. buenoi* is less structured than it is in better studied gerrid species. Behaviour of lotic species, such as *A. remigis* and *A. najas*, are characterized by food territoriality (Wilcox and Ruckdeschel 1982; Vepsalainen and Nummelin 1985a; Blankenhorn 1991a, 1991b). In streams food is localized by current, and territoriality is profitable. Maintenance of territories by females conflicts with repelling male suitors (Wilcox 1984). Thus, superfluous mating in this group may be a consequence, in part, of a female's need to maintain a food territory. Territoriality also occurs in one group of lentic species, represented by *Limnopus* spp. (Hayashi 1985; Vepsalainen and Nummelin 1985b; Spence and Wilcox 1986). However, in this group territories are centred on oviposition sites and are maintained by males. Thus, females may mate to gain access to these oviposition sites. These two groups diverge in other life history traits (reviewed in Fairbairn 1990). The first are sexually dimorphic, primarily micropterous, and common to permanent habitats. The second are generally large bodied, less dimorphic, macropterous, univoltine and common to temporary habitats. *G. buenoi* shows neither food nor oviposition site territoriality. *G. buenoi* belongs to a third group of gerrids that contains members of the subgenus *Gerris*. They are small bodied, highly dimorphic, partially micropterous, and partially bivoltine. Mating behaviour of *G. buenoi* may be representative of this group.

*G. odontogaster* appears to be morphologically and ecologically similar to *G. buenoi* (Arnqvist 1989a). In a recent study of mating behaviour in this species, Arnqvist (1992a,b) found that mating frequency and duration both increased, and
female reluctance to mate decreased, when sex ratio was biased toward males and when density was increased. These results suggest that the mating system of *G. odontogaster* is also similar to *G. buenoi*. Although Arnqvist did not measure harassment rate, it is expected to increase with both sex ratio and density, and thus provide the thread that ties his results with *G. odontogaster* to my results with *G. buenoi*.

The role of harassment rate will vary with the degree to which females benefit from mating. In cases where females benefit from mating, females should be less reluctant to mate, and therefore harassment by males becomes less important. Although there is no evidence of direct benefits of mating to female gerrids (e.g. nutritional, Andersen 1982; Arnqvist 1989b), females of some species may gain an indirect benefit (see above). However, there are a large number of lentic species, such as *G. buenoi*, where neither males nor females appear territorial (e.g. the sub genus *Gerris*, Arnqvist 1989a; Fairbairn 1990; this study). Females in these species probably gain little or nothing by mating, and therefore harassment of females by amorous males is predicted to play a larger role in their mating systems.
Chapter Six

OVERVIEW

In this chapter, I highlight some of the main contributions of the thesis, and point to some future areas of research that I believe will be profitable.

Chapter 2 is the first field study of the biotic limits to adult gerrid fitness. The experiments make a strong case for intense resource competition among gerrids and other surface feeders. Both limitation of food inputs to the water surface and competition from other surface feeders, constrains reproductive output of female *G. buenoi*. Longevity of both males and females is limited by subsurface predators. These results are important contributions to our knowledge of waterstrider biology. Both food and predator limitation are assumed or suggested to have shaped the evolution of waterstrider reproductive and behavioural strategies, and of sexual size dimorphism (e.g., Kaitala 1987, 1989; Fairbairn 1990; Sih *et al.* 1990). These data confirm that such selective forces actually occur in the wild.

The field studies described in Chapter 2 also demonstrate that resource availability fluctuates greatly in time. Both within and among season variation in resource availability results from variation in both food inputs and interspecific competition for that food. The strength of predation risk to gerrids also varies greatly in time and space. Therefore, the intensity of competition for resources among gerrids varies over time for two reasons. First, resource availability varies with time and second, gerrid densities will be intermittently reduced as a result of predation. These results confirm Wiens' (1977, 1986) view that populations are only rarely in equilibrium with their resources. Nevertheless, they also suggest that competition occurs over a vary wide range of resource availabilities: food addition
and removal of interspecific competitors consistently increased egg production rates over a 20 fold range in rates. Therefore, non-equilibrium dynamics need not mean that competition only rarely occurs (Grant 1986).

Two promising areas of research in population and community ecology, that these results point toward, are spatial variation and meta-population dynamics. Spence (1979, 1983) and Spence and Scudder (1980) have argued that habitat (aquatic vegetation) variation plays an important role in community composition and gerrid species coexistence. Spence has shown that different species of gerrids choose specific habitats, and that their reproductive success is habitat specific. Hence, habitat characteristics explain much of the variation in gerrid community composition on the Fraser Plateau. The mechanisms underlying these observations remain unclear. One possibility is that both food availability (or quality) and predation risk depend on both habitat type and on gerrid species. My experiment on predation rates in different habitats (Chapter 2) demonstrates that predation risk to G. buenoi is habitat dependent. Spence (1983) has found habitat dependent variation in food quality and quantity to be habitat specific. More work on such habitat variability, and in species specific responses to it, may identify the underlying mechanisms for gerrid community patterns.

The Fraser Plateau is speckled with dozens of ponds that vary in size, depth, salinity, and vegetation characteristics. Movements of gerrids among the ponds during the breeding season is remarkably high (Spence personal communication). Many ponds that are colonized by given gerrid species are later abandoned (Spence 1983, personal communication). These results suggest that the community can be described as meta-population composed of productive (source) and unproductive (sink) populations (e.g., Pulliam 1988). Gerrids may move by flight among them, escaping declining resources or increasing predation risk. Moreover, notonectids that are partially responsible for deteriorating conditions are
also mobile, and may move among ponds (Scudder, unpublished). Dynamics of metapopulations are poorly understood, and the waterstrider community on the Fraser Plateau appears to be an excellent place to learn about these dynamics.

Chapter 3 presents clear evidence that longevity of *G. buenoi* is a decreasing function of reproductive rate: there is a cost of reproduction. Moreover, senescence occurs prior to death, and the onset of senescence is advanced at higher reproductive rates. The hypothesis of Enesco *et al.* (1989) and Bell (1992), that senescence does not occur in semelparous organisms, can be rejected in this case. I have recently shown that these results are not the artifact of poor quality diet in the laboratory or some other laboratory effect. Gerrids brought into the laboratory, late in the breeding season, senesce faster in the laboratory than gerrids of the same cohort brought in earlier. The difference between the two groups show that the onset of senescence was advanced in late gerrids simply by the rigors of living for longer in the wild. Therefore, senescence occurs in the wild.

The pathway between senescence of the somatic function (longevity) and reproductive function (egg quality) requires more attention. Experiments in Chapter 3 show that increased "work" in the reproductive component decreases longevity as well as increasing the rate of decline of egg quality. We do not know if the path is bi-directional: does non-reproductive "work" increase the rate of reproductive senescence. Field data suggest that it does. Same-aged females that have spent more of their lives in the wild, suffer reproductive senescence at an earlier age than those that have spent less time in the field and have reproduced at the maximum rate (unpublished). Females in the laboratory do not have to forage or avoid predators, and to some degree, harassment by males. These data suggest that increased non-reproductive activity in the field advance reproductive senescence. Laboratory tests of the hypothesis are possible. Female gerrids with weights glued to their backs have reduced longevity (unpublished data) although
egg quality of these females is not known. Similar experiments in the future should include monitoring of egg quality. If there is a direct pathway between non-reproductive work and reproductive senescence, then weighted females are expected to have advanced declines in egg quality.

The data in Chapter 2 suggest that notonectids are both major competitors for food and major predators. Thus, we can expect an evolutionary response of gerrids to these selective forces imposed by notonectids. Some of these are discussed in Chapters 4 and 5. Predation risk from notonectids is elevated by mating behaviour (Chapter 3), and these results clarify those of Arnqvist (1989b). He found that predation by notonectids on females increased when males were present, and suggested that this was the result of mating behaviour. My experiments demonstrate that predation risk to females is elevated by mating behaviour, and that this is the result of several components of mating behaviour. Predation risk to males is also elevated by mating behaviour. Thus, predation risk imposes a cost of mating to both sexes. These results provide one of few confirmations of the widely held view that mating behaviour increases predation risk to females (Wing 1988; Gwynne 1989; Fairbairn in press).

In Chapter 5, I provide that first quantitative description of mating behaviour of a species in the large group of waterstriders characterized by their small body size and lentic habitat use (subgenus Gerris). There appear to be no direct benefits to females of multiple mating. Furthermore, I show that mating by females conflicts with foraging (Chapter 5), and avoidance of predators (Chapter 4). Therefore it is difficult to see why females mate so often. I argue that females mate to avoid costly harassment by males (convenience polyandry). Experiments presented in Chapter 5 support this hypothesis, and thus provide the first experimental evidence for convenience polyandry. Females accept additional mating when the costs of mating are reduced or when the costs of remaining
single are increased.

The study is unusual in that I have focused on the interests of females, and on their ability to control mating decisions (Walker 1980; Knowlton and Greenwald 1984; Eberhard 1985). This approach has led to new insights. For example, mate guarding of females by males is usually viewed as a male strategy to reduce sperm competition (Thornhill and Alcock 1983). Thus variation in guarding duration is usually interpreted as an adaptive response by males to changing competitive conditions (e.g., McClain 1980; Clark 1988; Telford and Dangerfield 1990). In contrast, my study shows that guarding duration is limited by female decisions, and variation in guarding duration reflects variation in female interests.

It will be of interest to determine if female mating decisions depend upon male phenotype. We now know a lot about the ecological costs of mating decisions by females. This knowledge is largely absent from current studies of female choice (West-Eberhard et al. 1987). The existence and form of natural selection on female choice is critical to disentangling the various models for the evolution of preferred male traits (Kirkpatrick and Ryan 1991). In field surveys, I have found that large males have a mating advantage, and that among mating males, mating is assortative for size (unpublished). In addition, fecundity appears to be an increasing function of female body size (unpublished). Thus, there is selection for large male body size. The mating advantage of large males may come about by female choice. Large males may be better able to withstand female reluctance (passive choice), or females may reduce their reluctance to large males (active choice). Alternatively, large males may simply have the vigour required to make more mating attempts. All of these hypotheses are testable in the laboratory.
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