

THE UNIVERSITY OF CALGARY

FORAGING PATCH SELECTION BY THE LOTIC MAYFLY

Baetis tricaudatus

BY

GARRY J. SCRIMGEOUR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

JULY, 1992

© GARRY J. SCRIMGEOUR 1992



National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file *Votre référence*

Our file *Notre référence*

The author has granted an irrevocable non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of his/her thesis by any means and in any form or format, making this thesis available to interested persons.

L'auteur a accordé une licence irrévocable et non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de sa thèse de quelque manière et sous quelque forme que ce soit pour mettre des exemplaires de cette thèse à la disposition des personnes intéressées.

The author retains ownership of the copyright in his/her thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without his/her permission.

L'auteur conserve la propriété du droit d'auteur qui protège sa thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

ISBN 0-315-79168-3

Canada 

Name SCRIMGEOUR, GARRY J.

Dissertation Abstracts International is arranged by broad, general subject categories. Please select the one subject which most nearly describes the content of your dissertation. Enter the corresponding four-digit code in the spaces provided.

Ecology

SUBJECT TERM

0329

U·M·I

SUBJECT CODE

Subject Categories

THE HUMANITIES AND SOCIAL SCIENCES

COMMUNICATIONS AND THE ARTS

Architecture 0729
 Art History 0377
 Cinema 0900
 Dance 0378
 Fine Arts 0357
 Information Science 0723
 Journalism 0391
 Library Science 0399
 Mass Communications 0708
 Music 0413
 Speech Communication 0459
 Theater 0465

EDUCATION

General 0515
 Administration 0514
 Adult and Continuing 0516
 Agricultural 0517
 Art 0273
 Bilingual and Multicultural 0282
 Business 0688
 Community College 0275
 Curriculum and Instruction 0727
 Early Childhood 0518
 Elementary 0524
 Finance 0277
 Guidance and Counseling 0519
 Health 0680
 Higher 0745
 History of 0520
 Home Economics 0278
 Industrial 0521
 Language and Literature 0279
 Mathematics 0280
 Music 0522
 Philosophy of 0998
 Physical 0523

Psychology 0525
 Reading 0535
 Religious 0527
 Sciences 0714
 Secondary 0533
 Social Sciences 0534
 Sociology of 0340
 Special 0529
 Teacher Training 0530
 Technology 0710
 Tests and Measurements 0288
 Vocational 0747

LANGUAGE, LITERATURE AND LINGUISTICS

Language
 General 0679
 Ancient 0289
 Linguistics 0290
 Modern 0291
 Literature
 General 0401
 Classical 0294
 Comparative 0295
 Medieval 0297
 Modern 0298
 African 0316
 American 0591
 Asian 0305
 Canadian (English) 0352
 Canadian (French) 0355
 English 0593
 Germanic 0311
 Latin American 0312
 Middle Eastern 0315
 Romance 0313
 Slavic and East European 0314

PHILOSOPHY, RELIGION AND THEOLOGY

Philosophy 0422
 Religion
 General 0318
 Biblical Studies 0321
 Clergy 0319
 History of 0320
 Philosophy of 0322
 Theology 0469

SOCIAL SCIENCES

American Studies 0323
 Anthropology
 Archaeology 0324
 Cultural 0326
 Physical 0327
 Business Administration
 General 0310
 Accounting 0272
 Banking 0770
 Management 0454
 Marketing 0338
 Canadian Studies 0385
 Economics
 General 0501
 Agricultural 0503
 Commerce-Business 0505
 Finance 0508
 History 0509
 Labor 0510
 Theory 0511
 Folklore 0358
 Geography 0366
 Gerontology 0351
 History
 General 0578

Ancient 0579
 Medieval 0581
 Modern 0582
 Black 0328
 African 0331
 Asia, Australia and Oceania 0332
 Canadian 0334
 European 0335
 Latin American 0336
 Middle Eastern 0333
 United States 0337
 History of Science 0585
 Law 0398
 Political Science
 General 0615
 International Law and Relations 0616
 Public Administration 0617
 Recreation 0814
 Social Work 0452
 Sociology
 General 0626
 Criminology and Penology 0627
 Demography 0938
 Ethnic and Racial Studies 0631
 Individual and Family Studies 0628
 Industrial and Labor Relations 0629
 Public and Social Welfare 0630
 Social Structure and Development 0700
 Theory and Methods 0344
 Transportation 0709
 Urban and Regional Planning 0999
 Women's Studies 0453

THE SCIENCES AND ENGINEERING

BIOLOGICAL SCIENCES

Agriculture
 General 0473
 Agronomy 0285
 Animal Culture and Nutrition 0475
 Animal Pathology 0476
 Food Science and Technology 0359
 Forestry and Wildlife 0478
 Plant Culture 0479
 Plant Pathology 0480
 Plant Physiology 0817
 Range Management 0777
 Wood Technology 0746
 Biology
 General 0306
 Anatomy 0287
 Biostatistics 0308
 Botany 0309
 Cell 0379
 Ecology 0329
 Entomology 0353
 Genetics 0369
 Limnology 0793
 Microbiology 0410
 Molecular 0307
 Neuroscience 0317
 Oceanography 0416
 Physiology 0433
 Radiation 0821
 Veterinary Science 0778
 Zoology 0472
 Biophysics
 General 0786
 Medical 0760
 EARTH SCIENCES
 Biogeochemistry 0425
 Geochemistry 0996

Geodesy 0370
 Geology 0372
 Geophysics 0373
 Hydrology 0388
 Mineralogy 0411
 Paleobotany 0345
 Paleocology 0426
 Paleontology 0418
 Paleozoology 0985
 Palynology 0427
 Physical Geography 0368
 Physical Oceanography 0415

HEALTH AND ENVIRONMENTAL SCIENCES

Environmental Sciences 0768
 Health Sciences
 General 0566
 Audiology 0300
 Chemotherapy 0992
 Dentistry 0567
 Education 0350
 Hospital Management 0769
 Human Development 0758
 Immunology 0982
 Medicine and Surgery 0564
 Mental Health 0347
 Nursing 0569
 Nutrition 0570
 Obstetrics and Gynecology 0380
 Occupational Health and Therapy 0354
 Ophthalmology 0381
 Pathology 0571
 Pharmacology 0419
 Pharmacy 0572
 Physical Therapy 0382
 Public Health 0573
 Radiology 0574
 Recreation 0575

Speech Pathology 0460
 Toxicology 0383
 Home Economics 0386

PHYSICAL SCIENCES

Pure Sciences
 Chemistry
 General 0485
 Agricultural 0749
 Analytical 0486
 Biochemistry 0487
 Inorganic 0488
 Nuclear 0738
 Organic 0490
 Pharmaceutical 0491
 Physical 0494
 Polymer 0495
 Radiation 0754
 Mathematics 0405
 Physics
 General 0605
 Acoustics 0986
 Astronomy and Astrophysics 0606
 Atmospheric Science 0608
 Atomic 0748
 Electronics and Electricity 0607
 Elementary Particles and High Energy 0798
 Fluid and Plasma 0759
 Molecular 0609
 Nuclear 0610
 Optics 0752
 Radiation 0756
 Solid State 0611
 Statistics 0463
 Applied Sciences
 Applied Mechanics 0346
 Computer Science 0984

Engineering
 General 0537
 Aerospace 0538
 Agricultural 0539
 Automotive 0540
 Biomedical 0541
 Chemical 0542
 Civil 0543
 Electronics and Electrical 0544
 Heat and Thermodynamics 0348
 Hydraulic 0545
 Industrial 0546
 Marine 0547
 Materials Science 0794
 Mechanical 0548
 Metallurgy 0743
 Mining 0551
 Nuclear 0552
 Packaging 0549
 Petroleum 0765
 Sanitary and Municipal 0554
 System Science 0790
 Geotechnology 0428
 Operations Research 0796
 Plastics Technology 0795
 Textile Technology 0994

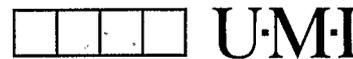
PSYCHOLOGY

General 0621
 Behavioral 0384
 Clinical 0622
 Developmental 0620
 Experimental 0623
 Industrial 0624
 Personality 0625
 Physiological 0989
 Psychobiology 0349
 Psychometrics 0632
 Social 0451



Nom _____

Dissertation Abstracts International est organisé en catégories de sujets. Veuillez s.v.p. choisir le sujet qui décrit le mieux votre thèse et inscrivez le code numérique approprié dans l'espace réservé ci-dessous.



SUJET

CODE DE SUJET

Catégories par sujets

HUMANITÉS ET SCIENCES SOCIALES

COMMUNICATIONS ET LES ARTS

Architecture 0729
 Beaux-arts 0357
 Bibliothéconomie 0399
 Cinéma 0900
 Communication verbale 0459
 Communications 0708
 Danse 0378
 Histoire de l'art 0377
 Journalisme 0391
 Musique 0413
 Sciences de l'informatique 0723
 Théâtre 0465

ÉDUCATION

Généralités 515
 Administration 0514
 Art 0273
 Collèges communautaires 0275
 Commerce 0688
 Économie domestique 0278
 Éducation permanente 0516
 Éducation préscolaire 0518
 Éducation sanitaire 0680
 Enseignement agricole 0517
 Enseignement bilingue et multiculturel 0282
 Enseignement industriel 0521
 Enseignement primaire 0524
 Enseignement professionnel 0747
 Enseignement religieux 0527
 Enseignement secondaire 0533
 Enseignement spécial 0529
 Enseignement supérieur 0745
 Évaluation 0288
 Finances 0277
 Formation des enseignants 0530
 Histoire de l'éducation 0520
 Langues et littérature 0279

Lecture 0535
 Mathématiques 0280
 Musique 0522
 Orientation et consultation 0519
 Philosophie de l'éducation 0998
 Physique 0523
 Programmes d'études et enseignement 0727
 Psychologie 0525
 Sciences 0714
 Sciences sociales 0534
 Sociologie de l'éducation 0340
 Technologie 0710

LANGUE, LITTÉRATURE ET LINGUISTIQUE

Langues
 Généralités 0679
 Anciennes 0289
 Linguistique 0290
 Modernes 0291
 Littérature
 Généralités 0401
 Anciennes 0294
 Comparée 0295
 Médiévale 0297
 Moderne 0298
 Africaine 0316
 Américaine 0591
 Anglaise 0593
 Asiatique 0305
 Canadienne (Anglaise) 0352
 Canadienne (Française) 0355
 Germanique 0311
 Latino-américaine 0312
 Moyen-orientale 0315
 Romane 0313
 Slave et est-européenne 0314

PHILOSOPHIE, RELIGION ET THEOLOGIE

Philosophie 0422
 Religion
 Généralités 0318
 Clergé 0319
 Études bibliques 0321
 Histoire des religions 0320
 Philosophie de la religion 0322
 Théologie 0469

SCIENCES SOCIALES

Anthropologie
 Archéologie 0324
 Culturelle 0326
 Physique 0327
 Droit 0398
 Économie
 Généralités 0501
 Commerce-Affaires 0505
 Économie agricole 0503
 Économie du travail 0510
 Finances 0508
 Histoire 0509
 Théorie 0511
 Études américaines 0323
 Études canadiennes 0385
 Études féministes 0453
 Folklore 0358
 Géographie 0366
 Gérontologie 0351
 Gestion des affaires
 Généralités 0310
 Administration 0454
 Banques 0770
 Comptabilité 0272
 Marketing 0338
 Histoire
 Histoire générale 0578

Ancienne 0579
 Médiévale 0581
 Moderne 0582
 Histoire des noirs 0328
 Africaine 0331
 Canadienne 0334
 États-Unis 0337
 Européenne 0335
 Moyen-orientale 0333
 Latino-américaine 0336
 Asie, Australie et Océanie 0332
 Histoire des sciences 0585
 Loisirs 0814
 Planification urbaine et régionale 0999
 Science politique
 Généralités 0615
 Administration publique 0617
 Droit et relations internationales 0616
 Sociologie
 Généralités 0626
 Aide et bien-être social 0630
 Criminologie et établissements pénitentiaires 0627
 Démographie 0938
 Études de l'individu et de la famille 0628
 Études des relations interethniques et des relations raciales 0631
 Structure et développement social 0700
 Théorie et méthodes 0344
 Travail et relations industrielles 0629
 Transports 0709
 Travail social 0452

SCIENCES ET INGÉNIERIE

SCIENCES BIOLOGIQUES

Agriculture
 Généralités 0473
 Agronomie 0285
 Alimentation et technologie alimentaire 0359
 Culture 0479
 Élevage et alimentation 0475
 Exploitation des péturages 0777
 Pathologie animale 0476
 Pathologie végétale 0480
 Physiologie végétale 0817
 Sylviculture et faune 0478
 Technologie du bois 0746
 Biologie
 Généralités 0306
 Anatomie 0287
 Biologie (Statistiques) 0308
 Biologie moléculaire 0307
 Botanique 0309
 Cellule 0379
 Écologie 0329
 Entomologie 0353
 Génétique 0369
 Limnologie 0793
 Microbiologie 0410
 Neurologie 0317
 Océanographie 0416
 Physiologie 0433
 Radiation 0821
 Science vétérinaire 0778
 Zoologie 0472
 Biophysique
 Généralités 0786
 Médicale 0760

Géologie 0372
 Géophysique 0373
 Hydrologie 0388
 Minéralogie 0411
 Océanographie physique 0415
 Paléobotanique 0345
 Paléocologie 0426
 Paléontologie 0418
 Paléozoologie 0985
 Palynologie 0427

SCIENCES DE LA SANTÉ ET DE L'ENVIRONNEMENT

Économie domestique 0386
 Sciences de l'environnement 0768
 Sciences de la santé
 Généralités 0566
 Administration des hôpitaux 0769
 Alimentation et nutrition 0570
 Audiologie 0300
 Chimiothérapie 0992
 Dentisterie 0567
 Développement humain 0758
 Enseignement 0350
 Immunologie 0982
 Loisirs 0575
 Médecine du travail et thérapie 0354
 Médecine et chirurgie 0564
 Obstétrique et gynécologie 0380
 Ophtalmologie 0381
 Orthophonie 0460
 Pathologie 0571
 Pharmacie 0572
 Pharmacologie 0419
 Physiothérapie 0382
 Radiologie 0574
 Santé mentale 0347
 Santé publique 0573
 Soins infirmiers 0569
 Toxicologie 0383

SCIENCES DE LA TERRE

Biogéochimie 0425
 Géochimie 0996
 Géodésie 0370
 Géographie physique 0368

SCIENCES PHYSIQUES

Sciences Pures
 Chimie
 Généralités 0485
 Biochimie 487
 Chimie agricole 0749
 Chimie analytique 0486
 Chimie minérale 0488
 Chimie nucléaire 0738
 Chimie organique 0490
 Chimie pharmaceutique 0491
 Physique 0494
 Polymères 0495
 Radiation 0754
 Mathématiques 0405
 Physique
 Généralités 0605
 Acoustique 0986
 Astronomie et astrophysique 0606
 Électronique et électricité 0607
 Fluides et plasma 0759
 Météorologie 0608
 Optique 0752
 Particules (Physique nucléaire) 0798
 Physique atomique 0748
 Physique de l'état solide 0611
 Physique moléculaire 0609
 Physique nucléaire 0610
 Radiation 0756
 Statistiques 0463

Biomédicale 0541
 Chaleur et thermodynamique 0348
 Conditionnement (Emballage) 0549
 Génie aérospatial 0538
 Génie chimique 0542
 Génie civil 0543
 Génie électronique et électrique 0544
 Génie industriel 0546
 Génie mécanique 0548
 Génie nucléaire 0552
 Ingénierie des systèmes 0790
 Mécanique navale 0547
 Métallurgie 0743
 Science des matériaux 0794
 Technique du pétrole 0765
 Technique minière 0551
 Techniques sanitaires et municipales 0554
 Technologie hydraulique 0545
 Mécanique appliquée 0346
 Géotechnologie 0428
 Matières plastiques (Technologie) 0795
 Recherche opérationnelle 0796
 Textiles et tissus (Technologie) 0794

Sciences Appliqués Et Technologie

Informatique 0984
 Ingénierie
 Généralités 0537
 Agricole 0539
 Automobile 0540

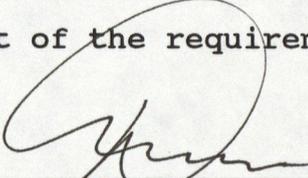
PSYCHOLOGIE

Généralités 0621
 Personnalité 0625
 Psychobiologie 0349
 Psychologie clinique 0622
 Psychologie du comportement 0384
 Psychologie du développement 0620
 Psychologie expérimentale 0623
 Psychologie industrielle 0624
 Psychologie physiologique 0989
 Psychologie sociale 0451
 Psychométrie 0632

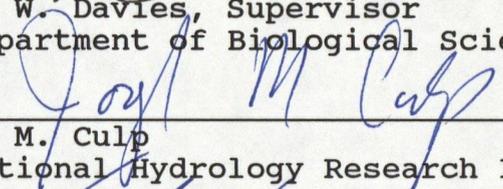


THE UNIVERSITY OF CALGARY
FACULTY OF GRADUATE STUDIES

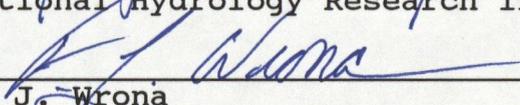
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "FORAGING PATCH SELECTION BY THE LOTIC MAYFLY Baetis tricaudatus", submitted by Garry J. Scrimgeour in partial fulfillment of the requirements for the degree of Doctor of Philosophy.



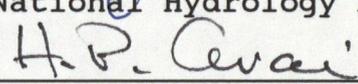
R. W. Davies, Supervisor
Department of Biological Sciences



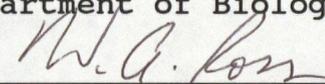
J. M. Culp
National Hydrology Research Institute



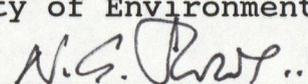
F. J. Wrona
National Hydrology Research Institute



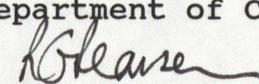
H. P. Arai
Department of Biological Sciences



W. A. Ross
Faculty of Environmental Design



N. G. Shrive,
Department of Civil Engineering



Dr. R. Pearson,
James Cook University
External Examiner

Date

92-07-17

ABSTRACT

A set of behavioural trade-off models was used to describe the effects of predation risk and food reward on foraging patch selection by the lotic mayfly Baetis tricaudatus. Field estimates of predation risk on B. tricaudatus by the longnose dace, Rhinichthys cataractae, and the stonefly, Claassenia sabulosa, indicated that mortality risk imposed on small B. tricaudatus exceeded that on large larvae. Additionally, predation on B. tricaudatus by R. cataractae was twice that from C. sabulosa. These observations were used to test the hypotheses that the behavioural trade-off between predation risk and food reward was not significantly affected by: (1) forager size (i.e., B. tricaudatus) and (2) predator species (i.e., when risky patches contained R. cataractae and/or C. sabulosa).

The first set of short-term laboratory experiments investigated the effects of forager size of the behavioural trade-off between predation risk and food reward. Results from these experiments indicated that small and large B. tricaudatus displayed a risk-adjusting trade-off when risky patches contained R. cataractae. Thus, time spent in safe patches exceeded that spent in risky patches; and the reduction in the use of risky patches was independent of food reward. While small and large B. tricaudatus displayed the same qualitative trade-off, large larvae spent more time feeding in risky patches when they contained high food

reward. Small larvae spent a low and constant amount of time in risky patches. Increased time allocation in risky patches by large larvae was associated with a reduction in the distance at which they displayed a drift response.

A second set of short-term experiments were performed to test the hypothesis that the trade-off displayed by a forager was dependent on whether risky treatments contained one R. cataractae and/or one C. sabulosa. Results from this experiment indicated that large B. tricaudatus displayed a risk-adjusting trade-off irrespective of predator species. Differences in time allocation patterns in foraging patches by large B. tricaudatus were minimal irrespective of whether risky patches contained a R. cataractae and/or C. sabulosa.

A final set of experiments was performed to determine whether short-term time allocation patterns among foraging patches differing in food reward and predation risk affect an individual's fitness. Larval growth trajectories, time to adult, adult body mass, fecundity and egg size were significantly affected by food reward and disturbance by a model R. cataractae. Moreover, fitness effects were consistent with those predicted if the risk-adjusting trade-off was the optimal trade-off by B. tricaudatus when patches vary in predation risk and food reward. The combination of short-term experiments with longer-term experiments will be a useful tool to investigate behavioural trade-offs.

ACKNOWLEDGMENTS

I am grateful to Drs. R. W. Davies, J. M. Culp and F. J. Wrona for supervising my thesis research. Thanks to Drs H. P. Arai, W. A. Ross, N. G. Shrive, and R. Pearson for serving on my supervisory committee and for their numerous constructive comments.

Many fruitful discussions with Joseph Culp, Fred Wrona, Malcolm M^cKee, Kevin Cash and members of the Behavioural Ecology Lunchtime Critique Hour (BELCH) improved the clarity of my understanding of ecology and emphasized the importance of a strong conceptual framework. Lawrence Harder, Fred Wrona, Kevin Cash and Dave Prescott assisted with statistical analyses.

Fieldwork and laboratory experiments in this thesis required intensive work, over long periods, which often resulted in sleep deprivation. The assistance of Joseph Culp, Chris Beers, Greg Townsend, Robert Kershaw, Malcolm M^cKee, Allan Woo, Sandra Bitner, Robert Verbisky, David Petrovich, Shelley Pruss and Nancy Glozier are greatly appreciated.

Financial support for this research was provided by NSERC operating grants to J. M. Culp and F. J. Wrona, and from teaching and research scholarships and equipment grants from the University of Calgary.

Support from the Departmental Office Staff is greatly appreciated. Josie Cleland faxed, typed, and copied large amounts of material and continued to smile.

On a personal level, I am greatly indebted to Joseph and Fred for their guidance and friendship. Above all other people, I thank Shelley Pruss for her continued love, support, encouragement and perseverance.

TABLE OF CONTENTS

	PAGE
APPROVAL PAGE	ii
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
TABLE OF CONTENTS	vii
LIST OF TABLES	x
LIST OF FIGURES	xiii
CHAPTER 1: GENERAL INTRODUCTION	1
PREY PATCH SELECTION	1
CONFLICTING DEMAND SCENARIOS	4
THE ALGAL - MAYFLY - PREDATOR FOOD WEB	10
GENERAL OBJECTIVES	15
CHAPTER 2: ESTABLISHING DIEL FEEDING PERIODICITY OF <u>Baetis tricaudatus</u> , <u>Claassenia sabulosa</u> AND FIELD ESTIMATES OF MORTALITY RISK	17
INTRODUCTION	17
METHODS	19
RESULTS	23
DISCUSSION	34

CHAPTER 3: ESTABLISHING THE CONFLICTING DEMAND SCENARIO: FIELD AND LABORATORY ESTIMATES OF FOOD REWARD LEVELS	38
INTRODUCTION	38
METHODS	43
RESULTS	48
DISCUSSION	58
CHAPTER 4: EFFECTS OF PREDATION RISK AND FOOD REWARD ON FORAGING PATCH SELECTION BY THE LOTIC MAYFLY <u>Baetis tricaudatus</u> : EVIDENCE FOR A RISK-ADJUSTING TRADE-OFF	66
INTRODUCTION	66
METHODS	70
RESULTS	79
DISCUSSION	98
CHAPTER 5: EFFECTS OF PREDATOR TYPE ON THE BEHAVIOURAL TRADE-OFF BY THE LOTIC MAYFLY <u>Baetis tricaudatus</u>	105
INTRODUCTION	105
METHODS	110
RESULTS	115
DISCUSSION	134

CHAPTER 6: FITNESS CONSEQUENCES OF PREDATION RISK AND FOOD REWARD FOR <u>Baetis tricaudatus</u> LARVAE	141
INTRODUCTION	141
METHODS	145
RESULTS	150
DISCUSSION	172
CHAPTER 7: SUMMARY	179
LITERATURE CITED	186

LIST OF TABLES

TABLE	TITLE	PAGE
1.	Field estimates of predation risk of small and large <u>Baetis tricaudatus</u> by <u>Rhinichthys cataractae</u> and <u>Claassenia sabulosa</u>	33
2.	Attack coefficients (mg/h) (a) and handling times (mg/h) (T_h) ($\bar{X} \pm 95\%$ confidence intervals) of small and large <u>Baetis tricaudatus</u> grazing diatoms in laboratory streams	56
3.	Low and high food reward levels predicted from examination of functional response curves of small and large <u>Baetis tricaudatus</u> feeding on the diatom <u>Navicula</u>	57
4.	Summary of food reward levels based on examination of the functional response of small and large <u>Baetis tricaudatus</u> grazing on the diatom prey, <u>Navicula</u>	74
5.	Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on time allocation in simultaneously available foraging patches by small and large <u>Baetis tricaudatus</u>	84
6.	Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high), and the interaction of these factors on food consumption rates of large <u>Baetis cataractae</u> in simultaneously available foraging patches	89
7.	Results of ANCOVA determining the effects of <u>Baetis tricaudatus</u> size (small, large), predation risk (safe, risky), and the interaction of these factors on \log_{10} drift rate (covariate)	94

TABLE	TITLE	PAGE
8.	Results of two-factor ANOVA determining the effects of <u>Baetis tricaudatus</u> size (small, large), food reward (low, high), and the interaction of these factors on mean distance initiating a flight response to <u>Rhinichthys cataractae</u>	95
9.	Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on time allocation in simultaneously available foraging patches by large <u>Baetis tricaudatus</u> when risky patches contained <u>Rhinichthys cataractae</u> and/or <u>Claassenia sabulosa</u>	119
10.	Two factor ANOVA showing the effects of predator species (<u>Rhinichthys cataractae</u> and/or <u>Claassenia sabulosa</u>), food reward (low, high) and the interaction of these factors on mean per capita attack rate on <u>Baetis tricaudatus</u> during patch choice trials	124
11.	Mean number ($\bar{x} \pm se$) of times <u>Baetis tricaudatus</u> were attacked when risky patches contained only <u>Rhinichthys cataractae</u> and/or <u>Claassenia sabulosa</u>	125
12.	Results of (A) repeated measures, single factor ANOVA determining the effects of predation risk (control, <u>Claassenia sabulosa</u> , and/or <u>Rhinichthys cataractae</u>) on mean drift rates and (B) comparison of treatment means using Tukeys Studentized Range test	128
13.	Results of two-factor ANOVA determining the effects of food reward (low, high), and predation risk (<u>Rhinichthys cataractae</u> , and/or <u>Claassenia sabulosa</u>) and the interaction of these factors on mean distance initiating a flight response by large <u>Baetis tricaudatus</u>	131

TABLE	TITLE	PAGE
14.	Results of (A) ANCOVA determining the effects of predation risk (safe, risky) and food reward (low, high) on \log_{10} growth rates of <u>Baetis tricaudatus</u> reared in laboratory streams and (B) comparison of growth curve slopes	153
15.	Results of two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on mean time to adult for (A) male and (B) female <u>Baetis tricaudatus</u>	157
16.	Results of two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on mean mass of adult (A) male and (B) female <u>Baetis tricaudatus</u>	161
17.	Results of two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on mean fecundity of adult <u>Baetis tricaudatus</u>	164
18.	Results of two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on mean egg size of <u>Baetis tricaudatus</u>	169

LIST OF FIGURES

FIGURE	TITLE	PAGE
1.	The four predation risk-food reward trade-offs described by Fraser and Huntingford (1986) when foragers are provided with spatial variation in predation risk and food reward	5
2.	The algal - mayfly - predator food web: a paradigm to investigate behavioural trade-off strategies	11
3.	Diel changes in mean ($\bar{x} \pm se$) density (No./m ²) of (A) small and (B) large <u>Baetis tricaudatus</u> on upper stone surfaces in the Bow River	25
4.	Diel changes in mean percent ($\bar{x} \pm se$) gut mass of (A) small and (B) large <u>Baetis tricaudatus</u> collected from the Bow River and Jumpingpound Creek, 1989	27
5.	Diel changes in mean number of fresh prey items ($\bar{x} \pm se$) in the foregut of <u>Claassenia sabulosa</u> from Jumpingpound Creek	30
6.	Type I, II, III functional response curves of food intake rate versus food abundance	41
7.	Mean ingestion rates ($\bar{x} \pm se$) of small (\blacktriangle) and large (\blacksquare) <u>Baetis tricaudatus</u> when grazing on natural algal mats representing 25%, median, and 75% quartiles of algal biomasses observed in the Bow River in May ...	50
8.	Functional response curves (mean ingestion rate $\pm se$) of small (\blacktriangle) and large (\blacksquare) <u>Baetis tricaudatus</u> when grazing on patches of the diatom prey, <u>Navicula</u>	54
9.	Risk-balancing and risk-adjusting trade-offs when foragers experience spatial variation in both food reward and predation risk	64

FIGURE	TITLE	PAGE
10.	Design of circular stream (4L, planar area = 470 cm ²) used to determine the effects of predation risk and food reward on time allocation among four simultaneously available patches (quadrants)	72
11.	Effect of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) percent time allocation in patches by (A) small and (B) large <u>Baetis tricaudatus</u>	82
12.	Mean percent reduction ($\bar{x} \pm se$) in time allocation in risky patches compared to equal food in safe patches for small (●) and large (■) <u>Baetis tricaudatus</u>	85
13.	Effect of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) food ingestion rates of large <u>Baetis tricaudatus</u> .	90
14.	Log ₁₀ mean drift rates ($\bar{x} \pm se$) of (A) small and (B) large <u>Baetis tricaudatus</u> in streams containing predators (●) to streams without predators (■)	92
15.	Effect of food reward (low, high) on mean distance ($\bar{x} \pm se$) initiating a flight response by small (●) and large (■) <u>Baetis tricaudatus</u> to <u>Rhinichthys cataractae</u>	96
16.	Effects of predation risk (safe, risky) and food reward (low, high) on mean time allocation ($\bar{x} \pm se$) in patches by <u>Baetis tricaudatus</u> when risky patches contained (A) a single (<u>Claassenia</u> and/or a single <u>Claassenia sabulosa</u>)	117
17.	Effect of predator species and food reward on mean ($\bar{x} \pm se$) per-capita attack rate on <u>Baetis tricaudatus</u> when risky patches contained (A) a single ■ <u>Rhinichthys cataractae</u> , (B) a single ● <u>Claassenia sabulosa</u> , or (C) or both predators at the same time ▼ <u>Rhinichthys cataractae</u> and <u>Claassenia sabulosa</u>)	122

FIGURE	TITLE	PAGE
18.	Comparison of mean drift rate ($\bar{x} \pm se$) of large <u>Baetis tricaudatus</u> larvae in streams without predators to those containing <u>Rhinichthys cataractae</u> (■), <u>Claassenia sabulosa</u> (●) or both predators at the same time (▼)	126
19.	Effect of food reward (low, high) and predator type (■ <u>Rhinichthys cataractae</u> , ● <u>Claassenia sabulosa</u> , ▼ both predators present) on mean flight initiation distance ($\bar{x} \pm se$) by <u>Baetis tricaudatus</u>	129
20.	Linear regressions of flight initiation distances versus number of <u>Baetis tricaudatus</u> in (A) low food patches and (B) high food patches	132
21.	Effects of predation risk (safe, risky) and food reward (low, high) on mean larval growth rates ($\bar{x} \pm se$) of <u>Baetis tricaudatus</u>	151
22.	Effects of predation risk (safe, risky) and food reward (low, high) on mean time to adult ($\bar{x} \pm se$) of (A) male and (B) female <u>Baetis tricaudatus</u>	155
23.	Effects of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) body mass (dry weight) of (A) male and (B) female adult <u>Baetis tricaudatus</u>	159
24.	Effects of predation risk (safe, risky) and food reward (low, high) on mean fecundity ($\bar{x} \pm se$) of <u>Baetis tricaudatus</u>	162
25.	Relationship between body mass and fecundity for <u>Baetis tricaudatus</u> reared in laboratory streams under different regimes of predation risk (safe, risky) and food reward (low, high)	165
26.	Effects of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) egg mass of adult <u>Baetis tricaudatus</u>	167
27.	Linear regression of fecundity versus egg size for <u>Baetis tricaudatus</u>	170

CHAPTER 1

GENERAL INTRODUCTION

PREY PATCH SELECTION

A primary focus of ecology is to identify the factors producing spatial and temporal patterns displayed by plants and animals. Within this context, animals display a diverse array of patterns associated with energy allocation, mate selection, life histories and feeding (Krebs and Davies 1978, 1984, 1991). For example, animals display a wide variety of patterns associated with where and when to feed, and which and how many prey items to ingest (Pyke 1978, 1981, Sih 1982, Stamps 1983, Allan 1984, Lima et al. 1985, Holomuzki 1986, Dill 1987, Pierce 1988, Culp 1989, Scrimgeour and Winterbourn 1989, Lima and Dill 1990, Helfman and Winkelman 1991).

Foraging patterns are thought to vary in response to a diversity of factors including heterogeneity in food abundance and predation risk. In response to spatial heterogeneity in food abundance many foragers, including stream insects, exhibit area restricted search, that is they allocate a high proportion of time to feeding within

relatively small areas (Hassell and May 1974, Smith 1974, Krebs 1979, Hart 1985, Holmes 1984, Kohler 1984, Wiley and Kohler 1984). For example, Kohler (1984) found that mayfly larvae of Baetis tricaudatus Dodds spent 70% of their foraging time within periphyton patches although such areas accounted for only 20% of the total foraging area. This feeding pattern resulted because B. tricaudatus turned more frequently while feeding in and immediately after leaving small patches of high food abundance (Kohler 1984). In fact, the ability of mayfly larvae to respond to spatial variation in algal biomass in this fashion, may explain larger scale spatial patterns in the field where mayfly abundance has been reported to be positively related to algal biomass (Richards and Minshall 1988).

Foragers also display a variety of spatial and temporal patterns in response to predators including increased time allocated to vigilance, shifts in habitat use, and reduced feeding rates and attack distances (Stein and Magnuson 1976, Sih 1980, 1982, Dill and Fraser 1984, Cerri and Fraser 1983, Werner et al. 1983a, 1983b, Cooper 1984, Fraser and Emmons 1984, Lima 1985, Power 1987, Harvey et al. 1988, Holomuzki and Short 1988, Holomuzki and Short 1990, Turner and Mittlebach 1990). During the 1970's and early 1980's the factors producing foraging patterns associated with selection of prey patches were investigated within the construct of optimal foraging theory. These spatial

foraging models assume a forager attempts to maximize rate of net energy intake (Reviewed by Pike 1984, Stephens and Krebs 1986). Numerous tests of optimal foraging models indicate that many foragers appear to select individual prey or patches of prey in accordance with predictions of optimal foraging models (Stephens and Krebs 1986, Krebs and Davies 1991, but see Pierce and Ollason 1987, Rapport 1991, for an alternative viewpoint).

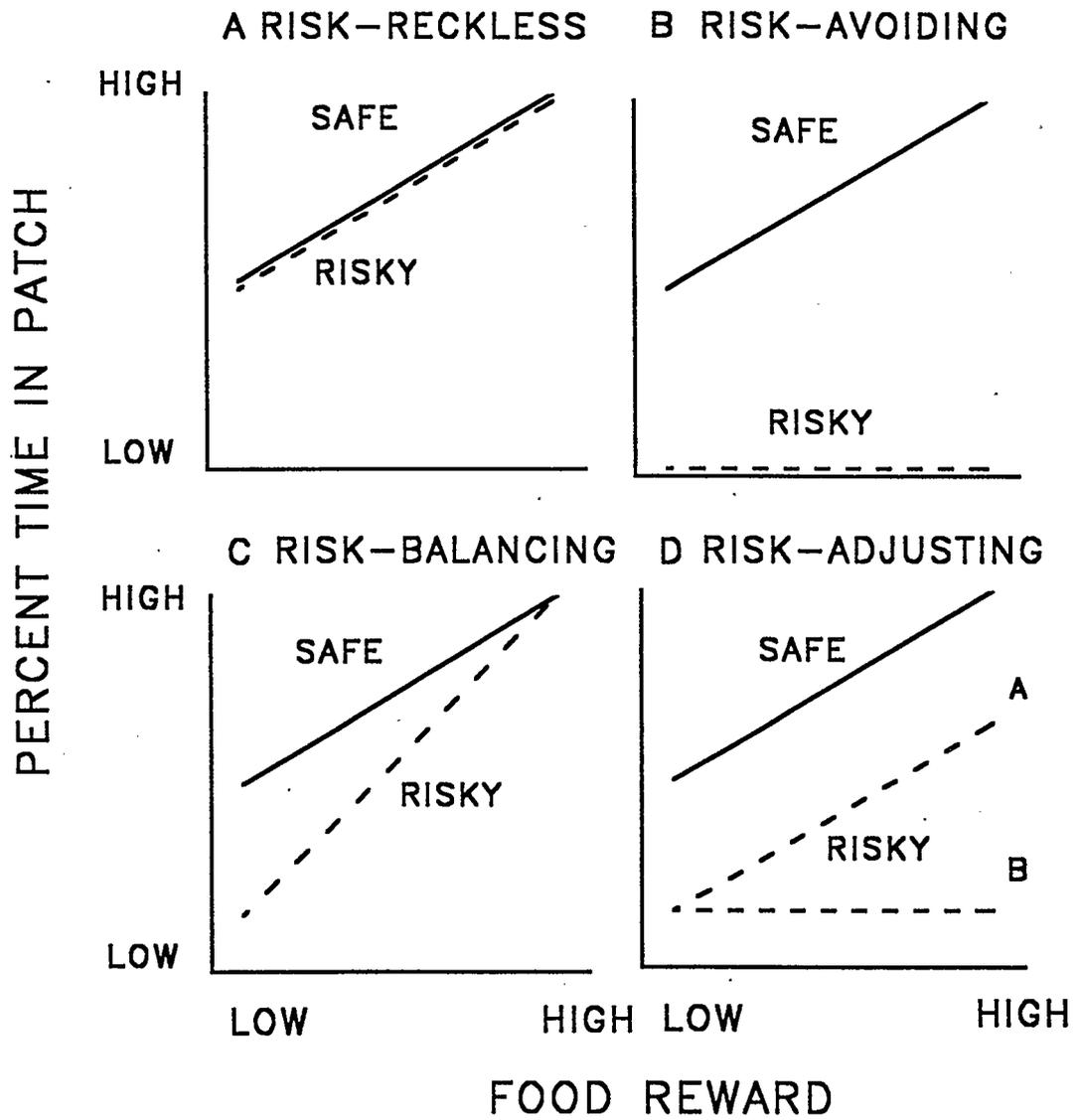
Early optimal foraging models were reasonably successful at predicting foraging patterns in simple situations, that is, where foraging decisions were based solely on food reward. However, the simplicity of these models has limited their range of application (Dill 1987). Recent foraging models have focused on more complex scenarios including the behavioural trade-off between foraging efficiency and predator avoidance (Fraser and Huntingford 1986, Pitcher et al. 1988, Kohler and McPeck 1989). Most foragers are themselves subject to predation risk while foraging. Thus, foraging decisions likely involve an evaluation of foraging benefits, in terms of food intake, versus the probability of being eaten while foraging. In fact, foraging patch selection by many foragers should be based on an evaluation of these two factors if the best foraging patches are those which make the forager vulnerable to predators (i.e., a conflicting demand scenario) (Sih 1980).

CONFLICTING DEMAND SCENARIOS

Numerous studies demonstrate that foragers trade-off predation risk against food reward when selecting feeding patches (Holbrook and Schmitt 1988, Newman et al. 1988, Pitcher et al. 1988, Bowers 1990). Few studies, however, have examined this relationship quantitatively (Abrahams and Dill 1989, Nonacs and Dill 1990). Fraser and Huntingford (1986) provide a conceptual framework to evaluate four possible trade-off strategies between predation risk and food reward on selection of prey patches where the foragers have simultaneous access to safe and risky patches of variable food quantity. They identify: 1) risk-avoiding, 2) risk-reckless, 3) risk-balancing, and 4) risk-adjusting trade-off strategies (Figure 1).

Risk-reckless foragers select patches based solely on food reward and do not distinguish between risky (i.e., predator present) and safe patches (i.e., predator absent) (Figure 1a). Risk-avoiding foragers minimize the risk of being preyed upon while foraging, by selecting only safe foraging patches irrespective of food reward levels in risky patches (Figure 1b). The major distinction between risk-reckless and risk-avoiding strategies is the forager always maximizes food reward in the risk-reckless strategy and

Figure 1. The four predation risk-food reward trade-off strategies described by Fraser and Huntingford (1986) when foragers are provided with spatial variation in predation risk and food reward. The response variable is percent time allocation. Individual figures show a subset of predictions for each of the four trade-offs. Solid line equals time allocation in safe patches (i.e., predator absent), dashed line equals time allocation in risky patches (i.e., predator present). The two lines in the risk-adjusting strategy (A and B) indicate two common expectations of this trade-off, although a range of slopes between these lines is possible.



maximizes safety in the risk-avoiding strategy.

In contrast, risk-balancing and risk-adjusting strategies do not involve a single, overriding criterion. Foragers adopting these trade-offs are always willing to accept some predation risk when choosing patches and the level of risk accepted may depend upon food reward. For instance, although risk-balancers spend significantly less time in risky patches when the patch contains low food, they spend proportionately more time in risky patches when the patch contains high food. Thus for risk-balancers, the reduction in the use of risky patches is inversely related to food reward, potentially culminating in a risk-reckless strategy in high food patches (i.e., equal use of risky, high food and safe, high food patches) (Figure 1c). In contrast, risk-adjusters will spend a certain proportion of time in risky patches, with the reduction in the use of these patches being proportional to risk but independent of food reward (Figure 1d). Risk-adjusters spend significantly less time in risky patches compared to safe patches, irrespective of food reward. Thus, the reduction in the use of risky patches is not inversely related to food reward. Further discussions of risk-reward trade-off models are provided by Cerri and Fraser (1983), Milinski (1985), Fraser and Huntingford (1986), Gilliam and Fraser (1987), Holbrook and Schmitt (1988) and Pitcher et al. (1988).

Several studies have investigated the behavioural trade-off between predation risk and food reward on foraging patch selection. These studies indicate that colonial ants Lasius pallitarsis (Fabricius) (Nonacs and Dill 1990) and schooling minnows (Phoxinus) (Cope) (Pitcher et al. 1988) are risk-balancers, whereas solitary, three-spined sticklebacks (Gasterosteus aculeatus) Linnaeus (Fraser and Huntingford 1986) are risk-adjusters. However, no studies have examined whether the form of the trade-off is influenced by forager size.

A forager size-specific trade-off may occur if the level of predation risk or food reward is dependent upon forager body size. In fact, several studies indicate that the degree to which foragers avoid risky patches is positively related to their vulnerability to predators and that the anti-predator behavioral response can be forager-size specific (Stein and Magnuson 1976, Sih, 1980, 1982, Werner et al. 1983a, Power 1984).

Differences in the level of predation risk imposed on foragers should also vary with predator species. In fact, Peckarsky (1980) provides evidence that behavioural responses by foragers to predators is specific to predator species. She found that mayfly larvae of Ephemerella infrequens McDunnough and Baetis bicaudatus Dodds evaded contact with the insectivorous perlid stonefly Megarcys signata (Hagen) significantly more often than with the

omnivorous pteronarcid stonefly Pteronarcella badia (Hagen) (Peckarsky 1980). These behavioural responses could result in different time allocation patterns among feeding patches if time allocation is inversely related with mortality risk. Thus, a forager might spend more time in risky patches when the level of risk imposed by a predator species is low compared to when risky patches contain a different species of predator which imposes higher risk. It is not known whether (1) differences in mortality risk due to different predators, or (2) associated with forager size-specific levels of mortality risk from the same predator, results in quantitative differences in time allocation patterns.

The behavioural trade-off models described by Fraser and Huntingford (1986) require foragers to allocate feeding effort (e.g., time allocation) among simultaneously available prey patches which differ in both predation risk and food reward. Thus, foragers must trade-off the benefits of increased food intake against the potential cost of mortality risk due to predation. The costs and benefits of the four trade-off strategies should be subject to selective pressure such that the particular trade-off adopted is that which maximizes fitness. Short-term experiments are predominantly used to examine behavioural trade-offs. This precludes the investigator from addressing whether the behavioural choices affect the foragers fitness and whether these consequences are consistent with the trade-off.

THE ALGAL - MAYFLY - PREDATOR FOOD WEB.

Mayfly larvae of Baetis tricaudatus, its algal prey and two of their predators the longnose dace, Rhinichthys cataractae (Valienciennes) and stonefly Claassenia sabulosa (Banks) represent a potential food web in which to investigate foraging trade-offs (Figure 2). Baetis tricaudatus is a herbivorous mayfly which inhabits fast flowing, stony bottom streams throughout Alberta and grazes on algae, bacteria and associated particulate material on upper surfaces of stones.

The life history of B. tricaudatus is similar to other mayfly species (Edmunds et al. 1976, Borror et al. 1981, Britain 1982). Eggs deposited in water hatch, larvae grow and moult numerous times before they undergo partial metamorphosis from the larval stage to emerge as sexually inactive subimagoes. Subimagoes rapidly moult to adults (imagoes), mate, oviposit and die (Lehmkuhl 1976, Borror et al. 1981, Brittain 1982). Reproduction is restricted solely to the adult stage which often lasts only a few days whereas the larval stage may last over one year. Because adults do not feed, body size characteristics of adults are determined through feeding of the larval stage. For example, fecundity is directly related to adult body size measured either as body length or body mass (Clifford 1970, Borror et al. 1981, Brittain 1982, Sweeney et al. 1986).

Figure 2. The algal - mayfly - predator food web: a paradigm to investigate behavioural trade-off strategies. Larvae of Baetis tricaudatus prey upon algal biomass but are in turn subject to predation from Rhinichthys cataractae and Claassenia sabulosa. Figures of animals and the algal mat modified from Scott and Crossman (1973), Minshall (1978), Pennak (1978) and Clifford (1991).

THE PREDATORS

VERTEBRATE

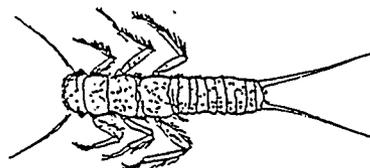
INVERTEBRATE

LONGNOSE DACE

STONEFLY LARVA

(Rhinichthys cataractae)

(Claassenia sabulosa)

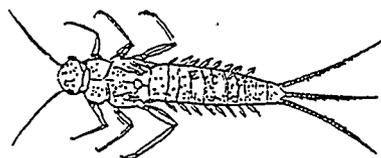


THE FORAGER



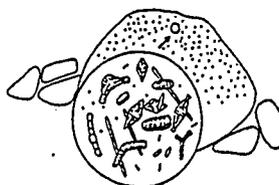
MAYFLY LARVA

(Baetis tricaudatus)



THE PREY

ALGAL MAT



In the Bow River (51° 03' N, 114° 03' W) and its tributary Jumpingpound Creek (51° 9' N, 114° 31' W), B. tricaudatus is bi-voltine with a fast growing summer generation (July-September) and a slower growing winter generation which develop from fall (October) and emerge to reproduce the following spring (April-June) (Scrimgeour unpubl. data). Both generations are present during the spring when individuals of the winter generation are larger (>3.0 mm body length) than individuals of the spring generation (<3.0 mm body length) (Scrimgeour unpubl. data).

Larval B. tricaudatus are preyed upon by a variety of vertebrate (e.g. fish) and invertebrate (e.g. stonefly) predators. In several Albertan streams R. cataractae and C. sabulosa are among the most abundant fish and stonefly predators (Culp et al. in press, Glozier 1989, Scrimgeour unpubl. data). R. cataractae are nocturnal predators consuming a diversity of benthic macroinvertebrates including B. tricaudatus larvae (Culp et al. 1988, Culp 1989). Similarly, C. sabulosa consume a diversity of macroinvertebrates, including mayfly larvae predominantly during the hours of darkness (Chapter 2) as has been reported for other perlid stoneflies (Vaught and Stewart 1974, Johnson 1981, Allan 1982).

Several lines of evidence suggest that this food web represents an ideal system to test the hypothesis that the behavioural trade-offs between predation risk and food reward is forager size-specific. First, preliminary data indicate that predation risk from R. cataractae is forager (i.e. B. tricaudatus) size-specific with small larvae experiencing higher risk than large larvae. Second, small and large B. tricaudatus differ in the length of their feeding bouts. Small larvae feed continuously throughout a diel period whereas large larvae feed exclusively at night (Chapter 2). Additionally, there appears to be marked differences in the level of mortality risk imposed on B. tricaudatus by R. cataractae and C. sabulosa (Chapter 2). R. cataractae impose almost twice the mortality risk than by C. sabulosa. When taken together, these observations indicate an opportunity to test the hypothesis that the behavioural trade-off adopted by a forager is predator-specific.

The behavioural trade-off between food reward and predation risk for B. tricaudatus probably occurs at two different spatial scales. First, at a within-stone level where foragers trade-off differences in food reward and predation risk between the top and bottom surfaces of individual stones. Foragers can obtain more food by feeding on stone tops, but in doing so increase their vulnerability to predation by fish. Second, foraging trade-offs could be

based among stones whose upper surfaces differ in food reward and/or vulnerability to predators. The present study focuses on the behavioural trade-off that B. tricaudatus displays between predation risk and food reward at the among-stone level.

GENERAL OBJECTIVES

The objectives of this study were:

(1) To confirm the preliminary field observation that the algal mat - B. tricaudatus - predator food web is appropriate to test Fraser and Huntingford's (1986) behavioural trade-off models. This was determined by documenting the diel feeding periodicity of B. tricaudatus and C. sabulosa. The diel feeding periodicity of R. cataractae was not determined because they are known to be nocturnal predators in the Bow River system (Culp 1989). Lastly, I estimated mortality risk that R. cataractae and C. sabulosa impose on small and large B. tricaudatus (Chapter 2).

(2) To determine the extent of spatial variation in food reward levels (i.e., algal biomass) on upper stone surfaces in the field and examine whether this variation among stones could produce significantly different rates of food intake by B. tricaudatus. I also determined the

functional response of B. tricaudatus grazing on monocultures of the diatom Navicula (Chapter 3). Thus, I could establish low and high food reward levels for prey patch choice experiments in the laboratory.

(3) To perform short term laboratory experiments to test the hypotheses that the trade-off strategy between predation risk and food reward adopted by the forager B. tricaudatus was independent of forager size (Chapter 4) and predator species (i.e., R. cataractae or C. sabulosa) (Chapter 5).

(4) To conduct long-term laboratory experiments to determine whether spatial variation in predation risk and food reward significantly affected the fitness correlates of growth, time to adult, adult biomass, fecundity and egg size of B. tricaudatus (Chapter 6). Lastly, I determined whether these effects were consistent with the behavioural trade-offs displayed by B. tricaudatus revealed in Chapters 4 and 5.

CHAPTER 2

DIEL FEEDING PERIODICITY OF Baetis tricaudatus,
Claassenia sabulosa AND FIELD ESTIMATES OF MORTALITY RISK

INTRODUCTION

Foragers face conflicting demands when the best feeding patches, in terms of food reward, are those which make them vulnerable to predation (Sih 1980, Kohler and McPeck 1989, Nonacs and Dill 1990). In this situation, selection of prey patches by foragers is likely to be affected by both food reward and predation risk. These effects on prey patch selection by a forager can be determined by reference to Fraser and Huntingford's (1986) four trade-off strategies (Chapter 1).

Several studies have documented that some foragers are risk-balancers (Pitcher et al. 1988, Nonacs and Dill 1990) and others are risk-adjusters (Fraser and Huntingford 1986). Whether these trade-offs are forager size-specific or are induced by a particular predator species remains unknown. The ability of an investigator to test these hypotheses requires information on the diel activity pattern of the

forager and its predators to determine if the predators impose risk during the forager's feeding period. If the diel feeding periods of the forager and the predator overlap temporally, then the forager's selection of food patches might be based on a trade-off between predation risk and food reward. The hypothesis that the trade-off between predation risk and food reward is affected by predator species can only be tested if predation risk is predator specific.

Numerous studies have shown that many predatory fish and stoneflies are size-specific predators (Werner and Hall 1974, Ringler 1979, Malmqvist and Sjostrom 1980, Bence and Murdoch 1986, Scrimgeour 1986, Allan et al. 1987). Preliminary observations in two Albertan streams suggest that predation risk to B. tricaudatus from R. cataractae and C. sabulosa is predator-specific. Predation risk from R. cataractae is twice that from C. sabulosa but this observation is based on a small sample size (Scrimgeour unpubl. data).

The objectives of this chapter were to document the diel feeding periodicity of small and large B. tricaudatus and C. sabulosa and to determine temporal overlap between the forager (i.e., B. tricaudatus) and its predators. Because R. cataractae was known to be a nocturnal predator in this drainage system (Culp 1989), its diel activity pattern was not investigated. Second, I estimated a monthly

level of mortality risk due to predation of small and large B. tricaudatus by R. cataractae and C. sabulosa.

METHODS

Diel feeding periodicity of Baetis tricaudatus and Claassenia sabulosa.

The activity of B. tricaudatus was determined by examining use of upper stone surfaces and changes in mayflies gut content mass. Use of upper stone surfaces was determined by counting the number of B. tricaudatus on upper surfaces of all stones within at least 10 quadrats (0.06 m² area). Observations were made at 1-4 h intervals over diel cycles on 12-13 July 1989, 24-25 April 1990 and 9-10 May 1991 in the Bow River. Transparent viewing boxes were used to facilitate viewing. By approaching quadrat areas from downstream and by avoiding casting shadows on the sample area during the day, mayfly behaviour was not altered detectably by the viewing process. To enable accurate observations between dusk and dawn a low intensity red light was used to illuminate the substrate.

Diel changes in gut mass of small (2-3 mm body length) and large (5-6 mm body length) B. tricaudatus was determined through gut content analysis. At least ten small and ten large individuals were collected at 2-4 h intervals over diel cycles on 12-13 May 1989 in Jumpingpound Creek and on

2-3 June 1989 in the Bow River. Individuals were preserved in 10% formalin and the entire gut removed by dissection under 25x magnification. Mayfly larvae did not regurgitate their gut contents. Guts and their contents were dried to constant mass at 60 °C, and weighed to the nearest 0.01 mg with a Cahn 25 automatic electrobalance. The dry mass (DM) of stomach contents was estimated by subtracting the mass of the stomach wall (SW) from the combined mass of the stomach and its contents using the equations: large B. tricaudatus $SW = -0.0769 + 0.0264 \text{ body length (BL)}$ ($n = 26, r^2 = 0.83, P < 0.001$); small B. tricaudatus $SW = -0.016 + 0.0105 \text{ BL}$ ($n = 20, r^2 = 0.88, P < 0.001$). These equations were derived by dissecting B. tricaudatus larvae collected during previous diel collections from the Bow River. Stomach fullness was estimated as dry mass of stomach contents (DM) / body mass (DM).

Feeding periodicity of C. sabulosa (> 15 mm body length) was determined by collecting at least 12 individuals at 2-4 h intervals over diel cycles in spring (2-3 May, 1989) and fall (31 August - 1 September) in 1989 and performing gut content analyses. I only collected large individuals (i.e., > 15 mm body length) because smaller larvae ingest low numbers of B. tricaudatus (Scrimgeour unpubl. data). Stonefly larvae were preserved in 10% formalin and the foregut removed by dissection under 12x magnification. Preserving stoneflies in formalin did not

cause regurgitation of their gut contents. Individual prey items were placed into one of four digestive categories based on the amount of internal tissue present: (1) fresh, prey item intact with < 25% loss of internal tissue (i.e. < 25%, (2) partially digested (i.e. 25% - 75% loss of internal tissue), (3) digested, (< 75% of internal tissue present), and (4) well-digested, no internal tissue, arthropods consisting solely of exoskeleton (modified from Scrimgeour and Winterbourn 1987).

Field estimates of predation risk of Baetis tricaudatus to Rhinichthys cataractae and Claassenia sabulosa.

Per-capita mortality risk of small and large B. tricaudatus from R. cataractae and C. sabulosa was estimated from the equation:

$$q_p = (n_p \times P) / N$$

where (q_p) is the per-capita mortality risk of B. tricaudatus, n_p is the daily mean number B. tricaudatus eaten per predator, P is the density of the predators and N is the density of B. tricaudatus. The study was conducted in Jumpingpound Creek on 8 April, 1987. Density of small and large B. tricaudatus and large C. sabulosa were determined by collecting stone faunal samples from 11 replicate large cobbles (maximum diameter 125-156 mm) with a fine mesh net (0.25 mm). Density of small and large B.

tricaudatus and C. sabulosa per large cobble was converted to an areal basis by correcting for the stone profile in the stream (Wrona et al. 1986). Benthic samples were preserved in formalin for sorting and identification in the laboratory. Longnose dace density was obtained from Jumpingpound Creek on 20 June 1987 following Culp et al. (1991).

The daily intake of B. tricaudatus by each predator type (R. cataractae or C. sabulosa) (n_p) was determined through examination of gut contents. A total of 15 R. cataractae were collected immediately after dawn and their gut contents removed by gut flushing following Culp et al. (1988). Gut contents of 15 C. sabulosa were determined by collecting larvae at 0200 h (MDST) approximately half way through their feeding bout. This protocol probably underestimated the total number of B. tricaudatus ingested during a complete night's feeding. I corrected for this underestimation by multiplying the mean number of prey ingested by C. sabulosa by two. This assumes that sampling frequency (i.e., number of samples collected during a diel cycle) is adequately describes feeding activity.

RESULTS

Feeding behaviour of Baetis tricaudatus and Claassenia sabulosa.

Temporal use of upper stone surfaces by B. tricaudatus in the Bow River was dependent upon forager size. The number of small B. tricaudatus on upper stone surfaces was not significantly affected by time of day in May (Repeated Measures ANOVA: $F = 0.07$, d.f. = 5, 45, $P > 0.05$) or in July (Repeated Measures ANOVA: $F = 1.55$, d.f. = 5, 54, $P > 0.05$) indicating that small larvae use upper stone surfaces throughout a 24 h period (Figure 3). In contrast, large larvae grazed on upper stone surfaces only during hours of darkness (i.e. 8 hours) and the number of large larvae on upper stone surfaces differed significantly throughout a 24 h period in April (Repeated Measures ANOVA: $F = 156.95$, d.f., 5, 55, $P < 0.001$) and May (Repeated Measures ANOVA: $F = 62.18$, d.f. = 5, 54, $P < 0.001$) (Figure 3).

Temporal patterns in gut mass also differed between small and large larvae (Figure 4). Gut mass of large B. tricaudatus feeding in the Bow River and Jumpingpound Creek varied significantly over a 24 h period in May ($F = 6.85$, d.f. = 10, 94, $P < 0.001$) and June ($F = 8.16$, d.f., = 5, 54, $P < 0.001$) and was consistently highest during the night (Figure 4). In contrast, there was no significant difference change in gut mass of small B. tricaudatus (May $F = 2.06$, d.f. = 9, 94, $P > 0.05$; June $F = 1.86$, d.f. = 5,

54, $P > 0.05$) indicating that small larvae feed throughout a 24 h period. When these data are combined with temporal changes in the use of upper stone surfaces, they indicate that the use of upper stone surfaces is associated with food ingestion.

Figure 3. Diel changes in mean ($\bar{x} \pm se$) density (No./0.1 m²) of (A) small and (B) large Baetis tricaudatus on upper stone surfaces in the Bow River. Solid horizontal line indicates hours of darkness. Δ = 9-10 May 1991, \square = 12-13 July 1989, \blacktriangle = 24-25 April 1990, \bullet = 9-10 May 1991.

NO. ON UPPER STONE SURFACES

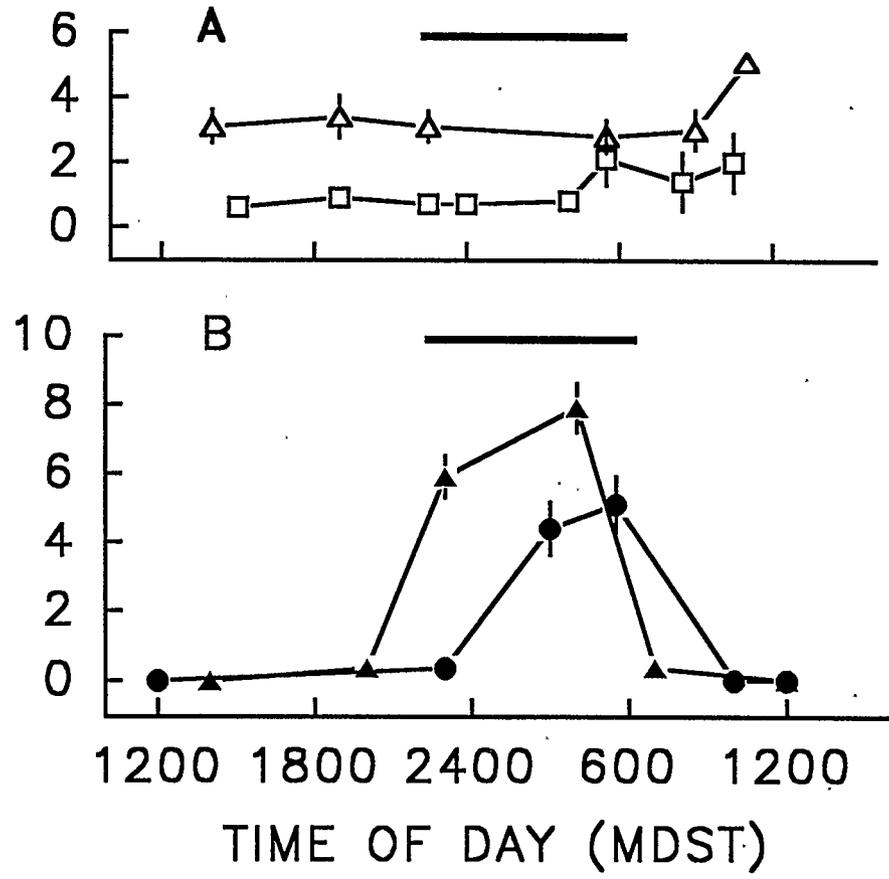
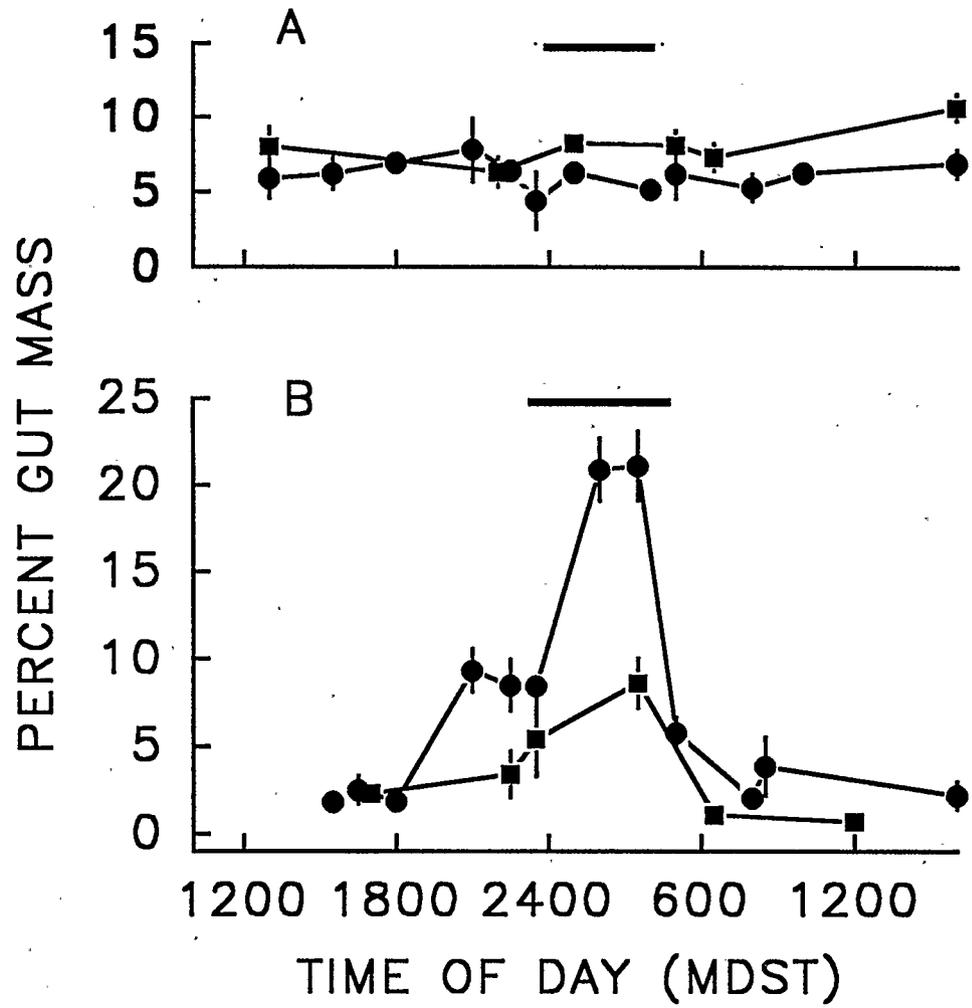
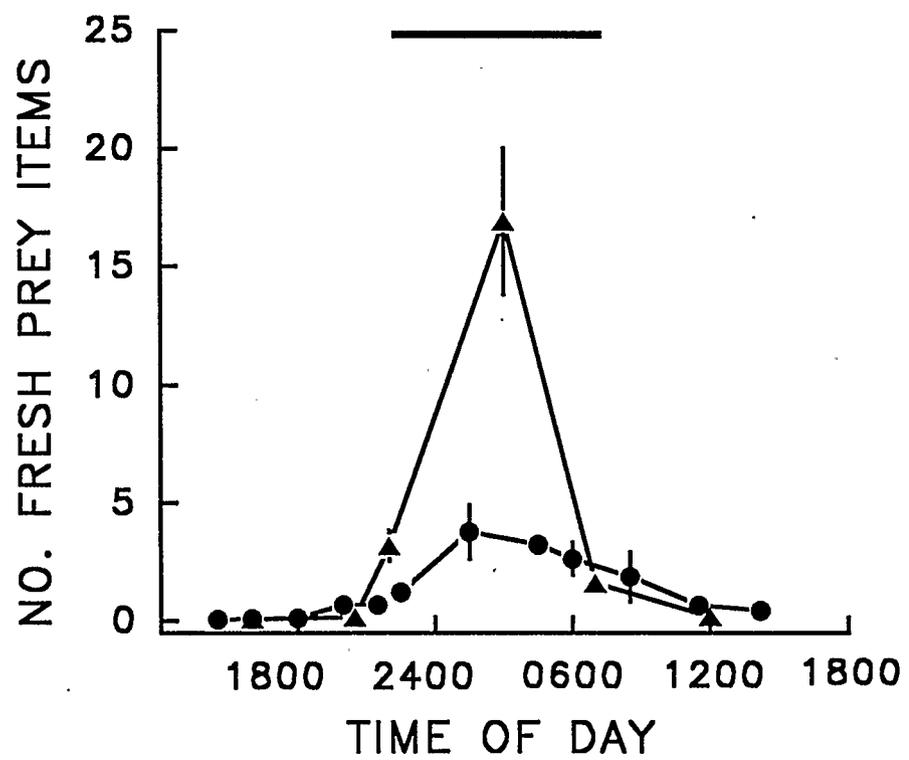


Figure 4. Diel changes in mean percent ($\bar{x} \pm se$) gut mass of (A) small and (B) large Baetis tricaudatus collected from the Bow River and Jumpingpound Creek, 1989. Solid line indicates hours of darkness. • = 12-13 May (Jumpingpound Creek), ■ = 2-3 June (Bow River).



Stonefly larvae of C. sabulosa ingested a diversity of benthic invertebrates with mayfly (Ephemerella spp., Paraleptophlebia spp., and B. tricaudatus), chironomid larvae and oligochaetes numerically dominant comprising > 90% of all prey items ingested. Number of fresh prey items in the gut of C. sabulosa varied significantly throughout diel periods in spring ($F = 10.76$, d.f. = 12, 174, $P < 0.001$) and fall ($F = 76.67$, d.f. 5, 64, $P < 0.001$). On each occasion, the number of fresh prey items in the gut during the day were significantly lower than during the night indicating that C. sabulosa are nocturnal predators (Figure 5).

Figure 5. Diel changes in mean number of fresh prey items ($\bar{x} \pm se$) in the foregut of Claassenia sabulosa from Jumpingpound Creek. Solid line equals hours of darkness. • = 2-3 May (1989), ▲ = 31 August - 1 September (1991).



Field estimates of predation risk of Baetis tricaudatus to Rhinichthys cataractae and Claassenia sabulosa.

Stomach content analysis indicated that R. cataractae and C. sabulosa ingested a diversity of benthic prey including mayfly, caddisfly, dipteran and stonefly larvae. Larvae of B. tricaudatus were numerically dominant comprising 40% and 65% of all prey items ingested by R. cataractae and C. sabulosa, respectively on April, 1987.

Field estimates indicated marked differences in density between R. cataractae, C. sabulosa larvae and between small and large B. tricaudatus (Table 1). Larvae of C. sabulosa were at least five times more abundant than R. cataractae and small larvae were almost seven times more abundant than large B. tricaudatus. When these data are combined with mean number of small and large B. tricaudatus ingested by R. cataractae and C. sabulosa, they indicate marked differences in: (1) mortality due to predation between R. cataractae and C. sabulosa, and (2) mortality risk imposed by R. cataractae and C. sabulosa on small and large B. tricaudatus. When daily estimates of mortality rate are converted to a thirty day mortality risk, assuming an exponential decay in larval survival, mortality risk of small B. tricaudatus was approximately twice that of large larvae to R. cataractae and C. sabulosa predators. Mortality risk of small and large B. tricaudatus from R. cataractae was almost twice that from C. sabulosa (Table 1).

Table 1. Field estimates of predation risk of small and large Baetis tricaudatus by Rhinichthys cataractae and Claassenia sabulosa. Predation risk estimates based on the equation $q_p = (n_p \times P)/N$ where n_p is the daily mean number Baetis tricaudatus eaten per predator, P is the density of the predator (No./m²), and N is the density of Baetis tricaudatus (No./m²).

Predator type	Forager size	n_p	P	N	30 day q_p
<u>Claassenia sabulosa</u>					
	small	1.46±0.64	11.3±0.2	5441±141	0.09
	large	0.12±0.22	11.3±0.2	813±174	0.05
<u>Rhinichthys cataractae</u>					
	small	12.23±2.58	2.3±0.1	5441±141	0.16
	large	0.84±0.36	2.3±0.1	813±174	0.06

DISCUSSION

Studies investigating the potential trade-off between predation risk and food reward must document close temporal overlap in habitat use by the forager and its predators. Additionally, the ability to establish whether a forager trade-off of risk and reward is forager size-specific and predator-specific needs to be based on the knowledge of risk to confirm that mortality risk is a function of these factors.

Baetid mayfly larvae display a diversity of diel activity patterns and are reportedly diurnal (Graesser and Lake 1984, Statzner and Mogel 1985, Allan et al. 1986, Wilzbach 1990), nocturnal (Elliott 1968, Kovalak 1979, Ploskey and Brown 1980) or aperiodic (Kovalak 1979, Kohler 1983, 1985). I recorded diel activity patterns of small and large B. tricaudatus by measuring use of upper stone surfaces, and diel changes in gut mass. My results indicate that the use of upper stone surfaces by small and large B. tricaudatus is associated with feeding since spatial use of these surfaces coincided with the presence of algal material in guts. While both small and large larvae foraged on upper stone surfaces, they differed in the length of their feeding period. Large larvae were clearly nocturnal feeders, consuming algal material almost exclusively at night, whereas small larvae were aperiodic.

Differences in diel activity patterns of small and large B. tricaudatus could reflect diel changes in abiotic factors such as dissolved oxygen concentrations (Kovalak 1979, Wiley and Kohler 1980), water temperature (Allan et al. 1986) or biotic factors which include diel changes in predation risk (Ploskey and Brown 1980, Malmqvist 1988, Rader and Ward 1990, Cowan and Peckarsky in press, Flecker in press). It is unlikely that diel changes in water temperature or dissolved oxygen concentrations explain size-related differences in feeding of B. tricaudatus because small and large larvae were often found feeding on the same stones. One hypothesis which may explain the size-specific foraging patterns is that levels of mortality risk from day active salmonid predators which are present in the Bow system (Culp et al. in press) is positively related with B. tricaudatus size. Large B. tricaudatus may be constrained to feeding at night when predation risk from day active, visual feeders is low. Size-specific predation on mayfly larvae from day active, drift feeding fish is thought to explain ontogenetic changes from aperiodic to nocturnal drift periodicity (Allan 1978, 1984, Flecker in press, Cowan and Peckarsky, in press). The shift from aperiodic to nocturnal has only been observed in streams containing visually active fish, further supporting the fish predation hypothesis (Malmqvist 1988, Flecker in press).

Analysis of gut contents of C. sabulosa indicated significant changes in the number of fresh prey items over diel cycles in both spring and fall. The number of fresh prey items in foreguts was significantly higher during the hours of darkness strongly suggesting a nocturnal feeding pattern. This nocturnal pattern is consistent with the studies of Vaught and Stewart (1974), Johnson (1981, 1983) and Allan (1982) who reported nocturnal activity patterns for several species of perlid stoneflies. At present, ultimate factors controlling the nocturnal periodicity of C. sabulosa are unknown but potentially include a behavioural response to diel changes in the activity of their macroinvertebrate prey or a response to reduce their vulnerability to day active fish predators.

Comparison of field estimates of mortality risk due to predation by R. cataractae and C. sabulosa on B. tricaudatus indicated marked differences between predator types (R. cataractae or C. sabulosa) and between B. tricaudatus sizes (small or large). Predation risk of B. tricaudatus from R. cataractae was twice that from C. sabulosa. The factors producing predator-specific and forager size-specific differences in mortality are unknown. However, these results indicate that the algal - B. tricaudatus - R. cataractae and C. claassenia food web represents a model system in which to test the hypotheses that a forager trade-off between predation risk and food reward is dependent on

forager size and predator species.

CHAPTER 3.

ESTABLISHING THE CONFLICTING DEMAND SCENARIO: FIELD AND
LABORATORY ESTIMATES OF FOOD REWARD LEVELS.

INTRODUCTION

Foraging theory attempts to predict how, where and when a forager should feed and to identify the underlying mechanisms producing these patterns. Optimal foraging theory has been relatively successful at predicting selection of prey patches when a forager has simultaneous access to patches which differ in food reward (reviewed by Pyke 1984, Stephens and Krebs 1986). These studies demonstrate that some foragers select prey or patches of prey in accordance with predictions of optimal foraging theory, that is, maximizing their net rate of energy intake. The generality of these models is questioned when foragers evaluate patch quality on factors other than energy intake. For example, foraging patches often differ in mortality risk of prey to predators and the presence or absence of predators is known to affect the selection process (Fraser and Huntingford 1986, Holbrook and Schmitt 1988, Pitcher et al. 1988).

Fraser and Huntingford (1986) identify four behavioural

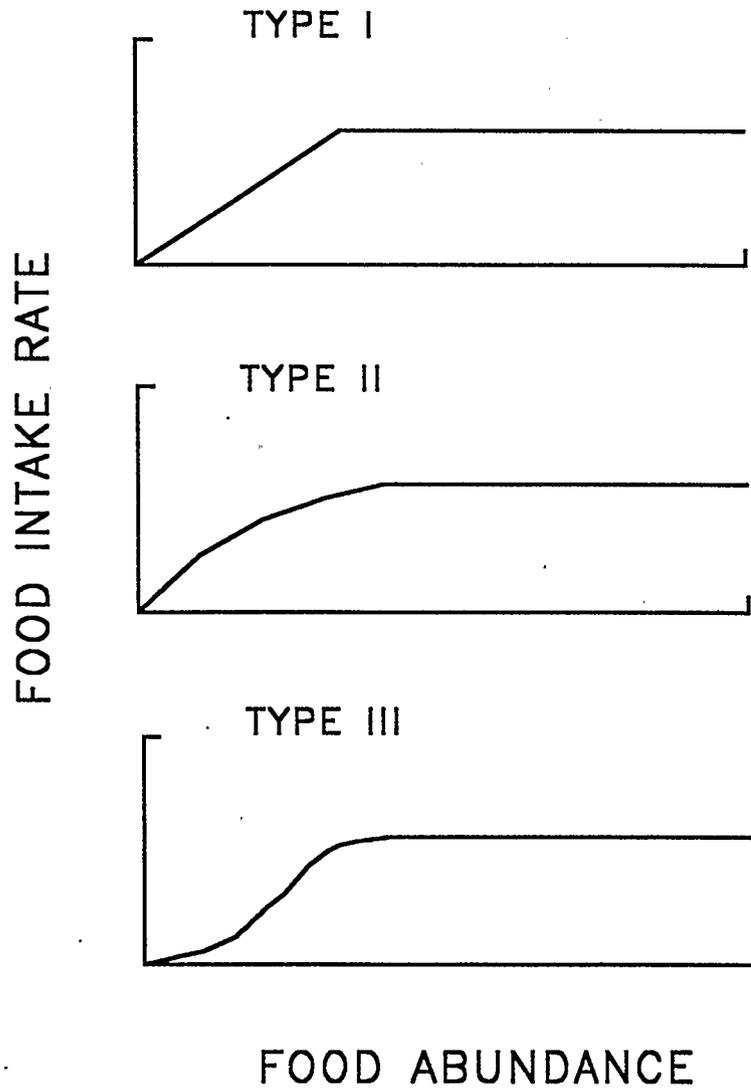
trade-off models that evaluate the combined effects of predation risk and food reward on selection of prey patches (Chapter 1). The trade-off adopted by a particular forager can only be identified if the experimental design includes two levels of food reward representing biologically different feeding rates (i.e. low and high food reward levels). While several studies have quantified food reward based on estimates of per-capita intake (Holbrook and Schmitt 1988), or growth (Nonacs and Dill 1990) at different levels of food abundance, this approach is not generally used (Pitcher et al. 1988).

Different levels of food abundance representing different levels of food reward can be determined by identifying a forager's functional response. The functional response describes the relationship between food abundance and per-capita food intake rate. Additionally, the ability to discriminate between Fraser and Huntingford's risk-adjusting and risk-balancing trade-offs requires the identification of a low and a high food reward level, and use of the asymptotic feeding rate as the high food reward level. Foragers most typically display one of three functional responses which can describe the relationship between prey availability and numbers of prey ingested. These functional responses are defined as Type I, Type II, and Type III (Holling 1959) (Figure 6). Each curve is characterized by an increasing function to an asymptotic

feeding rate, but the three models differ in the slope of the curve to the asymptote. Irrespective of the functional response type, they all allow the identification of low and high food reward levels.

The objectives of this chapter were two-fold. First, I determined whether variation in food reward levels in the field represent significantly different rates of food reward for small and large B. tricaudatus. This was accomplished by measuring algal biomass on the upper stone surfaces. This was followed by a set of feeding trials where I measured food intake at three algal biomass representing intake at 25%, median and 75% quartiles of algal biomass observed in the Bow River in May. Second, I identified the functional response of small and large B. tricaudatus grazing in the laboratory on a standardized food source, the diatom Navicula. Results of functional response experiments enabled me to identify two diatom biomasses representing low and high food reward levels to be used in patch choice experiments (Chapters 4-5).

Figure 6. Type I, II, III functional response curves of food intake rate versus food abundance.



METHODS

Field estimates of algal biomass and rate of food intake by Baetis tricaudatus.

Spatial variation in algal biomass on upper stone surfaces of stones in the Bow River was determined in Spring (May) and Fall (April) by scraping algal material from stones with a stiff from an area delimited with a 1.0 cm² neoprene disk. Stone surface scrapings were dried to constant mass at 60°C, ashed at 550°C for 1 h and ash free dry mass (AFDM) was estimated. I determined whether variation in algal biomasses observed in the field in May produced significantly different rates of food intake by comparing food ingestion at three algal biomasses representing 25% quartile, median, and 75% quartile values.

Small (mean body length = 3.0±0.3 mm) and large (5.2±0.5 mm) larvae of B. tricaudatus were collected from the Bow River. Individuals were maintained for 1 week prior to experiments in laboratory holding tanks with turbulent water at 11°C and a 16:8 h day:night cycle. During this period, larvae were fed an ad libitum supply of algal mats from the Bow River (biomass > 20 mg/cm² AFDM).

Feeding trials consisted of allowing individual larvae to feed on the upper surfaces of five small stones (width and length = 2.5 × 1 cm) collected from the field two days prior to the start of experiments. Individual stones were

attached to the bottom of experimental streams with silicone sealant. Thus, larvae could only graze algal mats on upper stone surfaces. Experiments were conducted in small (0.25 L, 50 cm² planar area), plexiglas streams (Walde and Davies 1984) to which filtered and oxygen saturated water was circulated (water velocity $\bar{x} \pm se = 6.7 \pm 0.3$ cm/s; water temperature 11°C). Since small and large B. tricaudatus feed during the night, experiments were conducted in the dark between 0800-1600 h MDST. Larvae experienced a reversed day/night light cycle for 48 h (2 complete day/night cycles) prior to experiments. Diatom biomasses were determined by scraping a 9 mm² area from the upper surfaces of each stone. These algal samples were dried at 60°C for 2 days and then weighed to the nearest 0.01 mg.

Larvae were acclimated to experimental conditions for 24 h prior to experiments then starved for an additional 24 h to clear foreguts. A pilot study showed that there was no significant difference in ingestion rates of starved (starvation period = 24 h) and fed animals (starvation period = 0 h) (small B. tricaudatus $t = -0.45$, d.f. = 10, $P > 0.05$; large B. tricaudatus $t = -0.17$, d.f. = 10, $P > 0.05$). Each feeding trial consisted of allowing an individual to forage for a 1 h period. After this time, larvae were removed from streams and preserved in 10% formalin. Recently ingested material forms a distinct bolus in the foregut, and was removed under 12x magnification.

Experiments were replicated four times at each of the three algal biomasses for both small and large B. tricaudatus. Ingested algal material was dried to constant mass at 60°C and weighed to the nearest 0.001 mg.

Functional response experiments for Baetis tricaudatus feeding on Navicula.

Small (2.8 ± 0.4 mm) and large (5.4 ± 0.4 mm) larvae of B. tricaudatus were collected from the Bow River and maintained for 2-4 weeks in holding tanks prior to experiments. During this period, larvae were fed an ad-libitum supply of Navicula sp., a pennate diatom which is an important food source for B. tricaudatus (Scrimgeour unpubl. data).

Feeding trials of mayflies on diatom patches were conducted in the same small plexiglas streams as described previously. Food in each stream was present on the top surface of five plexiglas substrates (length, width and height = $2 \times 1 \times 1$ cm). Algal mats were produced for the trials by inoculating plexiglas substrates with Navicula, and algal biomass was manipulated by varying the length of time that substrates were maintained in culture. Diatoms were cultured in still water as pilot studies showed this method produced diatom layers of uniform biomass (mean coefficient of variation [CV] = 12% calculated for all five diatom biomass levels).

By culturing diatoms in still water, I assumed that meal size was not significantly affected by diatom culture method (i.e. still versus flowing water). To test this hypothesis, I conducted an experiment where individual larvae were allowed to feed for a 1 h period on diatom mats cultured in either flowing (small plexiglas streams) or still water (Pyrex dishes). Experiments were conducted in small streams (0.25 L) containing five plexiglas substrates (2 x 1 x 1 cm) with upper surfaces covered with a diatom mat (diatom biomass = 0.42 mg/cm²) and replicated five times. The hypothesis that ingestion rates were not significantly affected by diatom culture method was tested with a two sample t-test.

Larvae were acclimated to experimental conditions for 48 h prior to experiments, including a 24 h starvation period to clear foreguts. Each feeding trial consisted of allowing an individual to forage for a 1 h period. Larvae were removed from streams, preserved in 10% formalin and the food bolus in the foregut removed under 12x magnification. Food was absent from other areas of the gut. The remaining algae on grazed substrates was removed with a scalpel. Total patch depletion equalled the difference between initial and final diatom biomass, and ingestion equalled the mass of gut contents. Experiments were replicated five or six times at each of the five diatom biomass levels. Algae scraped from all substrates in a given stream and ingested

material were dried at 60°C and weighed to the nearest 0.001 mg.

Non-linear curve fitting (Williams and Juliano 1985; Trexler et al. 1988) using the Quasi-Newton method on SYSTAT (Wilkinson 1988) was used to discriminate among functional response models I, II, and III and to calculate model parameters: a (attack coefficients, T_h (handling times) and their respective 95% confidence limits. The hypothesis that ingestion rates were not significantly affected by diatom biomass levels was tested with a single factor ANOVA on \log_{10} transformed data to remedy inequality of variances. For all analyses an alpha of < 0.05 was used.

RESULTS

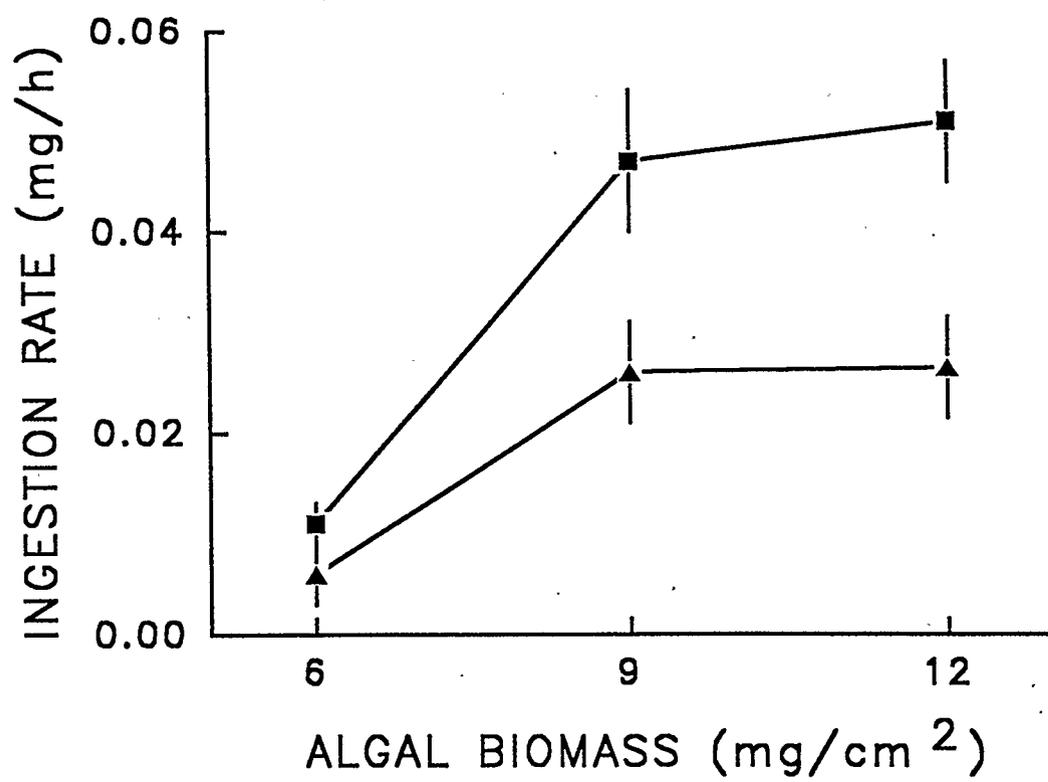
Field estimates of algal biomass and rate of food intake by Baetis tricaudatus.

Algal biomass (AFDM) (9.02 ± 0.6 mg AFDM/cm², N = 43) on upper stone surfaces in the Bow River in May was highly variable among stones (CV = 36%). Analysis of the frequency distribution indicated that 25% quartile, median, and 75% quartiles in the field represented algal biomasses of 6 mg AFDM/cm², 9 mg AFDM/cm² and 12 mg AFDM/cm² biomasses, respectively. Mean algal biomass on upper stone surfaces in August (40.1 ± 3.5 mg AFDM/cm², N = 19, CV = 38%) was significantly higher than in May ($t = 12.08$, d.f. 60, $P < 0.05$). Qualitative analysis of stone scrapings in May and August indicated that algal mats consisted predominantly of Navicula, Diatoma, Achnanthes, Cocconeis, and Gomphonema.

Small and large B. tricaudatus ingested significantly different amounts of algal material when grazing on 25%, median and 75% quartiles of algal abundance observed in the field in May (single factor ANOVA: small larvae, $F = 21.429$, d.f. = 2,9, $P < 0.001$; large larvae $F = 12.442$, d.f. = 2,9, $P < 0.005$) (Figure 7). Comparison of treatment means with Tukey's test indicated that small and large B. tricaudatus ingested significantly more algal material when grazing on algal mats of 9 mg AFDM/cm² and 12 mg AFDM/cm² than 6 mg AFDM/cm². This suggests that an algal biomass of 9 mg

AFDM/cm² represents asymptotic feeding rates for small and large B. tricaudatus (Figure 7). Differences in ingestion rates among these algal biomasses cannot be due to depletion since total algal biomass during trials was reduced by < 20%. Feeding trials were not performed at algal biomasses observed in the fall because on average they were five times higher than asymptotic feeding rates. Thus, it is unlikely that feeding trials performed at the higher biomasses in the fall would have resulted in higher ingestion rates.

Figure 7. Mean ingestion rates ($\bar{x} \pm se$) of small (\blacktriangle) and large (\blacksquare) Baetis tricaudatus when grazing on natural algal mats representing 25%, median, and 75% quartiles of algal biomasses observed in the Bow River in May.



Functional response of Baetis tricaudatus grazing on Navicula.

Ingestion rates for small and large B. tricaudatus were significantly affected by diatom biomass (Single factor ANOVA: small B. tricaudatus $F = 6.71$, d.f.=4,25, $P < 0.001$; Large B. tricaudatus: $F = 15.58$, d.f. 4,25, $P < 0.001$). Based on comparison of coefficients of determination, residual analysis and curve fitting, small and large B. tricaudatus displayed a Type II functional response, that is, a decelerating rise to a positive asymptote (Figure 8). This model is described as:

$$p(x) = ax/(1+aT_h x)$$

where p is the predator's functional response, x is prey density, a is the attack coefficient, and T_h is handling time (Holling 1959). This model accounted for more of the variation in foraging rate (small B. tricaudatus $r^2 = 0.94$, large B. tricaudatus $r^2 = 0.96$) than a Type I (small B. tricaudatus $r^2 = 0.63$, large B. tricaudatus $r^2 = 0.57$) or Type III model (small B. tricaudatus $r^2 = 0.90$, large B. tricaudatus $r^2 = 0.55$).

Upper asymptotic feeding rates for small and large B. tricaudatus were reached when diatom biomass was 0.43 mg/cm^2 (Figure 8). Attack coefficients for small and large B. tricaudatus were not significantly different, but there were

significant differences in handling times as indicated by non-overlap of their respective 95% confidence intervals (Table 2). Analysis of the functional responses of small and large B. tricaudatus grazing on the diatom Navicula indicate that two diatom biomasses can be selected to represent low and high food intake rates of small and large B. tricaudatus (Table 3).

Mean diatom depletion was <27% of the initial diatom biomass and B. tricaudatus satiation probably did not occur since recently ingested material filled <10% of the foregut region. Additionally, loss of diatoms from control streams due to dislodgement by the current was low (< 2% diatom biomass across all diatom biomass levels). Diatom culture method (flowing versus still water culturing) did not significantly affect ingestion rates for small (mean food ingestion ($\bar{x} \pm se$) flowing water = 0.028 ± 0.002 , still water = 0.022 ± 0.004 , $t = -0.13$, d.f. = 8, $P > 0.05$) or large B. tricaudatus (flowing water = 0.043 ± 0.006 , still water 0.042 ± 0.006 , $t = -0.90$, d.f. = 10, $P > 0.05$).

Figure 8. Functional response curves (mean ingestion rate \pm se) of small (\blacktriangle) and large (\blacksquare) Baetis tricaudatus when grazing on patches of the diatom prey, Navicula.

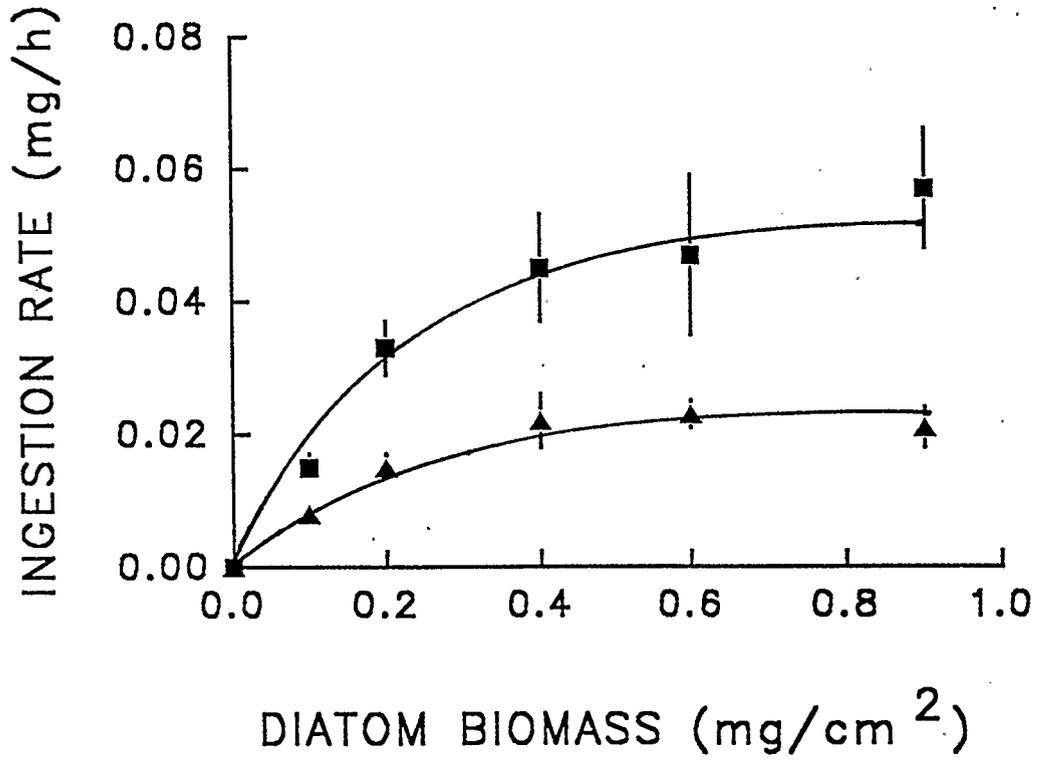


Table 2. Attack coefficients (mg/h) (a) and handling times (mg/h) (T_h) (\pm 95% confidence intervals) of small and large Baetis tricaudatus grazing diatoms in laboratory streams. Equation parameters based on a Type II functional response.

<u>Baetis tricaudatus</u> size	a	T_h
Small	0.18 \pm 0.04	18.9 \pm 2.6
Large	0.18 \pm 0.07	11.7 \pm 4.0

Table 3. Low and high food reward levels predicted from examination of functional response curves of small and large Baetis tricaudatus feeding on the diatom, Navicula.

Food reward	Diatom biomass (mg/cm ²)	Predicted mean ingestion rate (mg/h)	
		Small	Large
Low	0.12	0.007	0.013
High	0.80	0.027	0.052

DISCUSSION

Foragers likely evaluate the conflicting demands of feeding efficiently versus minimizing predation risk when prey patches display spatial variation in both food reward and predation risk. Three lines of evidence indicate that the algal - B. tricaudatus - predator food web is an appropriate system in which to investigate risk-reward trade-offs. First, analysis of algal biomass on upper stone surfaces in the Bow River and food intake rates of B. tricaudatus feeding on such surfaces indicate significant differences in foraging benefits in terms of food intake among stones. Second, activity patterns of B. tricaudatus and C. sabulosa (Chapter 2) and results of Culp (1989) indicate temporal overlap of B. tricaudatus with their R. cataractae and C. sabulosa predators. Third, per-capita estimates of mortality risk of B. tricaudatus from R. cataractae and C. sabulosa (Chapter 2) suggest that these predators impose risk on B. tricaudatus. Thus, foraging patch selection by B. tricaudatus is likely to involve a behavioural trade-off between maximizing food intake and minimizing predation risk.

Determining the behavioural trade-off that B. tricaudatus and other foragers exhibit when prey patches display variation in predation risk and food reward requires the experimenter to select two food reward levels which

represent significantly different feeding rates. One protocol to satisfy this requirement is to identify the functional response displayed by a forager. My results indicate that small and large B. tricaudatus displayed a Type II functional response when foraging on the diatom Navicula. This response type is often observed in herbivore-plant interactions (Hatto and Harper 1969, Downing 1981). This decelerating function is produced because the proportion of time spent handling food (i.e. pursuing, subduing, consuming and cleaning mouthparts) increases with food density and ultimately limits ingestion rate (Holling 1959). For grazing mayflies such as B. tricaudatus, the increase in handling time may result from increased time spent brushing diatoms from the substrate and processing these cells.

Asymptotic feeding rates of small and large B. tricaudatus foraging on Navicula were similar to those obtained when larvae foraged on natural stone surfaces, despite a 22 fold difference in diatom biomass (asymptotic feeding rate on natural stones = 9 mg AFDM/cm², Navicula on plexiglas substrates 0.43 mg DM/cm² = 0.40 mg AFDM/cm²; Scrimgeour unpubl. data). Differences in diatom biomass producing asymptotic feeding rates could reflect differences in vulnerability of diatom species to grazing (i.e., Navicula versus multi-species diatom assemblages) or differences in substrate texture (i.e., plexiglas versus

natural stone surfaces). Vulnerability of diatoms to invertebrate grazers is diatom species-specific reflecting differences in size, attachment, and placement of diatoms within the algal matrix (Nicotri 1977, Hart 1985, Lehman and Sandgren 1985). In general, relatively large, loosely attached species diatom species (e.g., Nitzschia, Navicula) are thought to be removed from stone surfaces more easily than species such as Gomphonema, Achnanthes, Cocconeis, and Diatoma (Sumner and McIntire 1982, Colletti et al. 1987, Hill and Knight 1987, Lamberti et al. 1987, Steinman et al. 1987). Diatom assemblages on upper stone surfaces from the Bow River consisted of several adnatly attached species including Gomphonema, Achnanthes, Cocconeis and Diatoma. Thus, high biomasses of these species could result in low ingestion rates by B. tricaudatus because of their resistance to grazing. In contrast, lower biomasses of Navicula could produce similar ingestion rates because they form a loosely attached algal mat which may be easily grazed.

Differences in diatom biomasses producing similar asymptotic feeding rates also could reflect differences in substrate texture between natural stone and plexiglas surfaces. Electronmicrographs of natural stones (Rounick and Winterbourn 1983, Winterbourn et al. 1985, Dudley and D'Antonio 1991) and plexiglas surfaces (Scrimgeour unpubl. data) indicate that natural stone surfaces display greater

surface complexity in terms of surface roughness. These structural differences could create spatial refugia for some algal species (Dudley and D'Antonio 1991), thus producing a quantitatively different relationship between diatom biomasses and diatom availability to grazers. Presently, I am unable to determine the importance of these two mechanisms to explain why different diatom biomasses produced similar asymptotic feeding rates. However when taken together, they indicate the need to consider effects of algal species and substrate type when establishing food reward levels for grazers such as B. tricaudatus. In the present study, the potentially confounding effects of substrate type and algal species on rates of food intake by B. tricaudatus were minimized because I established food reward rates separately for both small and large B. tricaudatus feeding on natural substrates and monocultures of Navicula.

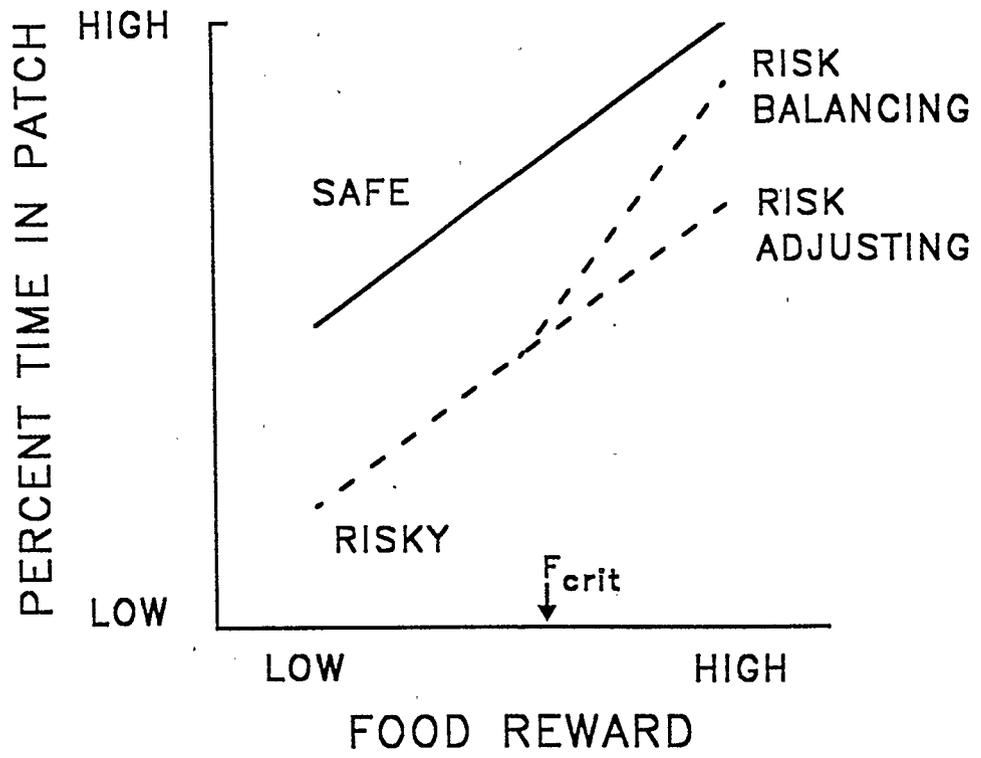
Algal biomasses in the Bow River and other streams display high spatial and temporal variability (Fisher et al. 1982, Winterbourn et al. 1985, Morikawa 1988, Richards and Minshall 1988; Scrimgeour et al. 1988; Scrimgeour and Winterbourn 1989). Analysis of cumulative frequency distributions of algal biomass in the Bow River in spring and fall suggest that such variation changes the proportion of stones which would provide high food reward patches (i.e., algal biomass on upper stone surfaces > 9 mg

AFDM/cm²). In spring 50% of upper stone surfaces of stones would be expected to provide high levels of food reward for B. tricaudatus compared to 90% in the fall. This suggests that the behavioural trade-off between predation risk and food reward for B. tricaudatus likely varies with season. In the fall the trade-off may simplify to choosing between high food, safe patches and high food, risky patches because algal biomasses are high. Moreover, this scenario may represent an ideal test of Gilliam and Fraser's prey patch choice model where foraging patches are thought to be selected based on minimizing the ratio of mortality risk to foraging returns (Gilliam and Fraser 1987).

The ability to discriminate among risk-balancing and risk-adjusting requires the selection of asymptotic feeding rates as the high food reward level. A forager adopting a risk-balancing trade-off will accept proportionately greater risk for higher food reward. However, the ability to discriminate between risk-balancing and risk-adjusting is complicated if a forager accepts proportionately greater risk above some threshold reward level (F_{crit}) (Figure 9). For example, consider the situation where a forager allocates a certain proportion of time to feeding in risky patches below a threshold food reward level but accepts proportionately more risk above a threshold food reward level. In this situation unless the asymptotic feeding rate is chosen as the high food reward level the forager might be

incorrectly identified as risk-adjuster because the high food reward is below the level initiating a risk-balancing trade-off. This potential error can be overcome if the asymptotic feeding rate is selected as the high food reward level. In this situation, the critical food reward level initiating acceptance of proportionately greater risk for higher food reward would be exceeded. Thus, I suggest that the identification of a foragers functional response is essential to discriminate among Fraser and Huntingford's behavioural trade-off models.

Figure 9. Risk-balancing and risk-adjusting trade-offs when foragers experience spatial variation in both food reward and predation risk. The response variable is percent time allocation. Solid line represents safe patches, dashed lines represents risky patches. F_{crit} represents the potential point where a forager could accept proportionately greater risk (i.e. proportional increase in time allocation in risky, high food patches) for higher food reward resulting in a risk-balancing trade-off.



CHAPTER 4

EFFECTS OF PREDATION RISK AND FOOD REWARD ON FORAGING PATCH
SELECTION BY THE LOTIC MAYFLY Baetis tricaudatus: EVIDENCE
FOR A RISK-ADJUSTING TRADE-OFF.

INTRODUCTION

Considerable attention over the last decade has focused on the factors affecting the selection of prey foraging patches (reviewed by Pyke 1984, Stephens and Krebs 1986). Although classical optimal foraging models predict individuals should select prey patches based solely on the net rate of energy intake, an increasing body of evidence indicates that other qualities, including the risk of predation while feeding, affect the selection process (Fraser and Emmons 1984, Fraser and Huntingford 1986, Gilliam and Fraser 1987, Holbrook and Schmitt 1988, Pitcher et al. 1988, Kohler and McPeck 1989, Nonacs and Dill 1990). For some foragers, patch selection is based on an evaluation of predation risk and food reward (i.e., rate of energy intake) because feeding in the highest quality patches makes them vulnerable to predators, leading to a conflicting

demand scenario.

While numerous studies have shown foragers to trade-off predation risk against food reward when selecting a feeding patch (Newman et al. 1988, Pitcher et al. 1988, Bowers 1990), few have examined this relationship quantitatively (Abrahams and Dill 1989, Nonacs and Dill 1990). Fraser and Huntingford (1986) provide a conceptual framework to evaluate four possible trade-offs between predation risk and food reward on selection of foraging patches where the foragers have simultaneous access to safe and risky patches of variable food quantity (Chapter 1).

Although a few studies have investigated these trade-offs (Fraser and Huntingford 1986, Pitcher et al. 1988, Nonacs and Dill 1990), none have examined whether the form of the trade-off is influenced by forager size or ontogenetic development. For instance, a forager size-specific trade-off may occur if the level of predation risk or food reward is dependent upon forager body size. Several studies indicate that the degree to which foragers avoid risky patches is positively related to their vulnerability and that anti-predator responses can be forager-size specific (Stein and Magnuson 1976, Sih, 1980, 1982, Werner et al. 1983a, Power 1984). However, at present it is not known whether these size-specific attributes reflect qualitatively different behavioral trade-offs.

The algal prey - B. tricaudatus - R. cataractae lotic

food web provides an ideal system for evaluating foraging trade-off models. Baetid mayflies inhabit fast flowing, stony bottom streams and graze on algae, bacteria and associated particulate material on upper stone surfaces. Thus, they potentially face a conflict because feeding on upper surfaces of stones where algal biomass is highest, increases their vulnerability to predators, such as benthic foraging sculpins or minnows (Kohler and McPeck 1989). In such situations, algal patch selection by baetid mayflies probably involves an assessment of both predation risk and food reward (Kohler and McPeck 1989). My field observations on diel changes in gut mass and temporal use of upper stone surfaces by small and large B. tricaudatus further indicates mayfly size-specific differences in the timing and duration of the feeding period and the level of predation risk from R. cataractae. Predation risk from R. cataractae is inversely related with B. tricaudatus size, such that large B. tricaudatus experience lower predation risk than small B. tricaudatus (Chapter 2). Additionally, the length of the feeding period is size specific with large B. tricaudatus have a short 8-10 h feeding period, whereas small larvae feed on upper stone surfaces throughout day and night (i.e., a 24 h period) (Chapter 3).

Based on these observations, I hypothesize that ontogenetic differences in predation risk and food reward will produce different time allocation patterns among

simultaneously available patches. If differences in foraging time allocation patterns of small and large B. tricaudatus are sufficiently large, they should produce qualitatively different trade-offs (sensu Fraser and Huntingford 1986). If time allocation in risky patches is inversely related to mortality risk then time allocation in risky patches by large B. tricaudatus will exceed that by small B. tricaudatus which experience higher risk (Chapter 2). These differences could potentially culminate in large B. tricaudatus adopting a risk-balancing trade-off whereas small larvae could display a risk-adjusting trade-off.

These predictions were tested in a laboratory stream system where food reward and predation risk was manipulated experimentally in artificial streams. Food intake rates and time allocation patterns among simultaneously available patches were measured for both small and large B. tricaudatus. Because B. tricaudatus can vary patch residence times by drifting out of risky patches, I measured drift rates in safe (predator absent) versus risky (predator present) streams. Moreover, because foragers can alter patch residence times by varying the distance at which they flee from a predator, I measured flight initiation distances of B. tricaudatus to R. cataractae. Based on the findings, I determined which of the four possible foraging trade-off models proposed by Fraser and Huntingford (1986) apply and identified some of the proximal mechanisms involved.

METHODS

Experimental animals

Small (2.5 ± 0.3 mm) and large instar larvae (5.4 ± 0.3 mm) of B. tricaudatus were collected from the Bow River during 20 April-3 May, 1990. Individuals were maintained at 11 °C for 2-4 weeks prior to experiments in aerated, flowing water holding tanks in the laboratory with a 14:10 h day:night cycle. During this period larvae were fed an ad libitum supply of the diatom, Navicula sp., which was cultured following Scrimgeour et al. (1991).

A stock population of R. cataractae was collected from the Bow River on 29 April 1990 and maintained at 11°C on a diet of B. tricaudatus in the laboratory until utilized in the patch choice trial experiments. Individual dace were used only once per treatment.

Patch choice trials

Patch choice trials for small and large B. tricaudatus were conducted in circular streams (diameter = 25 cm, water volume = 6 L, planar area = 470 cm²) partitioned into four equal-sized compartments (i.e., foraging patches) with mesh screen (Figure 10). These compartments (patches) represented spatial variation in both food reward (low,

high) and predation risk (safe (S), risky (R)). Risky patches were established by placing a single R. cataractae in each of the two patches designated as risky. Predators were absent from safe patches. Low (0.10 mg/cm^2 of Navicula sp. (LF)) and high food reward (0.90 mg/cm^2 (HF)) levels were based on results of functional response experiments as described in Chapter 3 (Table 4). Thus, larvae had access to four simultaneously available patches: LF+R, LF+S, HF+R, HF+S where each patch contained a single $4 \times 4 \times 1 \text{ cm}$ plexiglas artificial substrate with the top surface (16 cm^2) covered with the appropriate biomass of Navicula (Figure 10).

Water temperature (day:night = $14^\circ\text{C}:9^\circ\text{C}$) and diel light cycle (light:dark = 14:10 h) within the streams were based on spring field conditions. In addition, although water circulation jets were present in only two of the four patches, mean water velocities ($\bar{x} \pm \text{se}$) measured directly above artificial substrates with a Novonics micro-current meter did not vary significantly among patches containing water jets ($8.73 \pm 0.6 \text{ cm/s}$) or jet absent patches ($9.58 \pm 0.8 \text{ cm/s}$) (single factor ANOVA, $F = 0.97$, $P > 0.05$).

Each patch choice experiment involved placing 30 larvae, either small or large, in each artificial stream for a 38 h acclimation period prior to the addition of the predator. The acclimation period therefore consisted of two

Figure 10. Design of circular stream (4 L, planar area = 470 cm²) used to determine the effects of predation risk and food reward on time allocation among four simultaneously available patches (quadrants). Each patch contains a single 16 cm² feeding patch with the upper surface covered with the diatom, Navicula. Mesh screens prevent fish predators from moving among patches while allowing free movement of mayfly larvae.

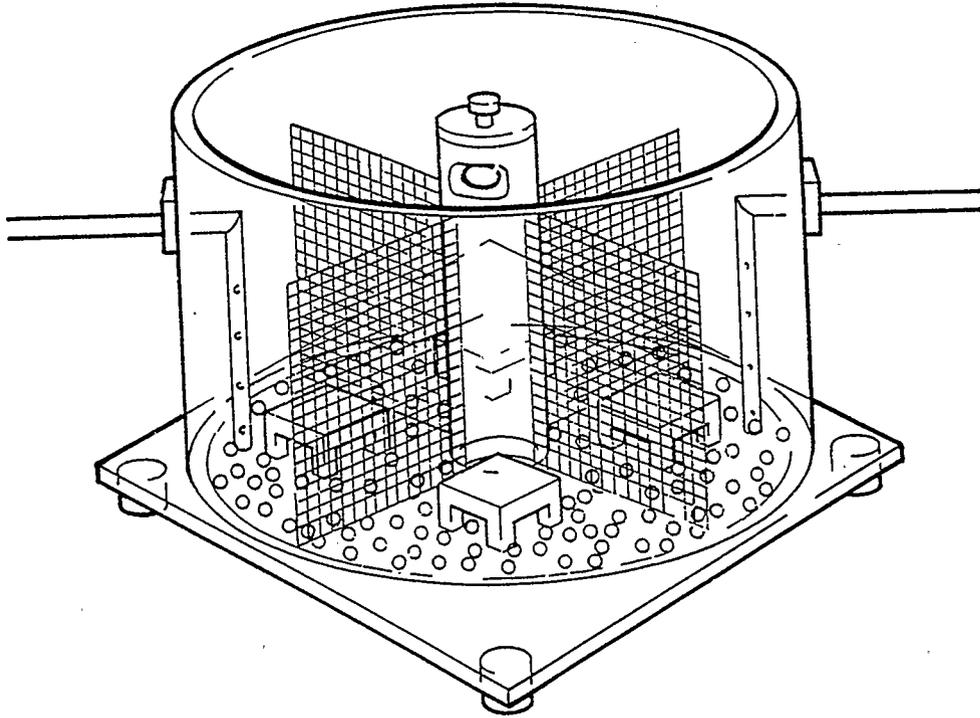


Table 4. Summary of food reward levels based on examination of the functional response of small and large Baetis tricaudatus grazing on the diatom prey, Navicula.

Food reward	Diatom biomass (mg/cm ²)	Predicted mean ingestion rate (mg/h)	
		Small	Large
Low	0.12	0.007	0.013
High	0.80	0.027	0.052

diurnal and one nocturnal interval. Five minutes after the start of the dark period each stream was videotaped for one minute to determine the mayfly patch distribution in the absence of predators and to determine whether mayflies could distinguish amongst the diatom biomass levels (i.e., low versus high food patches). Approximately five minutes after this initial filming period and thus 10 minutes into the dark period, a single adult R. cataractae (63 ± 1.4 mm) was placed into each of the two patches designated randomly as risky. The entire stream was again videotaped under infrared light for 1 h. Patch choice trials were replicated four times.

During the predator treatment period, R. cataractae could attack mayflies only in the risky patch as 5 mm mesh screens prevented them but not the mayflies from moving among patches. These individuals selected randomly from the stock population were acclimated to stream conditions for 38 h prior to the experiment. The presence of R. cataractae in one patch did not appear to alter behaviours of mayflies, such as drift rate or position of larvae on top, bottom, and sides of substrates in other patches. This result is consistent with the previous observation that B. tricaudatus do not respond to R. cataractae odours in terms of drift rates and positioning on artificial substrates (Scrimgeour unpubl. data). Nevertheless, the placement of safe and risky patches were rotated 90° after each replicate trial to

control for possible patch position effects. To avoid accumulation of predator odours streams were scrubbed with hot water and detergent between trials.

Experimental substrates were removed from streams and replaced with clean (i.e., diatom absent) substrates during the final 4 h light acclimation period prior to the experimental dark photoperiod and the onset of the experiment. This protocol ensured that diatoms ingested during the previous night of the acclimation period would be digested and cleared from the foregut. Substrates covered with a fresh diatom mat of appropriate biomass were placed into each of the four stream compartments. I quantified the amount of food ingested during the experimental period by measuring the gut mass of individual mayflies and the total loss of Navicula from each substrate (initial biomass minus final biomass).

For each 1 h trial I calculated time allocated to each patch by the 30 mayflies by dividing time allocation by mayflies in each of the four patches by the total time that all mayfly larvae spent foraging in all patches (30 larvae \times 1 h = 30 h total foraging time). Cumulative estimates of patch use were determined by stopping the videotape every 30 seconds of the 1 h trial and counting numbers of mayflies in each patch of the four patches (n=120).

The number of mayflies in the drift (measured over a 1 minute period) was determined every 3 minutes to identify

possible drift responses by larvae to predators. On each occasion, I counted the number of larvae drifting past a vertical line in the high food, safe patch extending from the mid-point of the outer wall to the drainage column located in the centre of the stream. Because foragers can alter patch residence times by varying the distance at which they flee from a predator, I measured the distance between B. tricaudatus and R. cataractae that initiated the drift response.

At the end of each trial at least five mayflies were selected randomly (when possible) from all patches and preserved in 10% formalin so that food intake could be determined through gut content analysis. Depletion of diatom patches during the experiment (initial biomass - final biomass) was determined by scraping diatoms from plexiglass substrates. Loss of diatoms due to current velocity is minimal under this experimental set-up (Chapter 3). Diatoms removed from foreguts and from plexiglas scrapings were dried to a constant mass at 40°C and weighed to the nearest 0.01 mg on a Cahn electrobalance.

Statistical analyses

I discriminated amongst the four risk-reward trade-offs for small and large B. tricaudatus using the following analyses. Time allocation budgets (i.e., the number of larvae multiplied by patch residence) in each of the four concurrently available patches and patch-specific food ingestion rates were calculated. Using these data, the hypotheses that patch use in terms of time allocation and food ingestion rates were not significantly affected by predation risk (safe, risky), food reward (low, high) was tested with a repeated measures, model 1, two-factor ANOVA after an arcsine square-root transformation.

The hypothesis that mean drift rate was not significantly affected by predation risk (safe, risky), mayfly size (small, large), time since the start of the trial (covariate) was tested using a model 1, two-factor ANCOVA on \log_{10} transformed data followed by comparison of slopes (Zar 1984, Neter et al. 1990). Finally, the hypothesis that the mean distance initiating flight into the drift was not significantly affected by food reward (low, high), mayfly size (small, large) was tested using a model 1, two-factor ANOVA.

RESULTS

In the absence of a predator, B. tricaudatus discriminated among food reward patches distributing themselves in proportion to relative food reward levels. The total number of small (22.5 ± 0.7) and large (23 ± 0.7) mayflies in high food patches was approximately four times higher than in low food patches (small 5.3 ± 0.3 , large 4.8 ± 0.5). Additionally, in the absence of risk mean ingestion rates of larvae fed on the high biomass were four times higher those on the low diatom biomass; these differences were significant for both small and large B. tricaudatus (small $t = 25$, d.f. = 8, $P < 0.001$; large $t = 11.0$, d.f. = 8, $P < 0.01$). Differences in the total numbers of larvae among simultaneously available patches which differ in food reward were not significantly different from a 4:1 ratio (high food reward:low food reward) (Yates Continuity χ^2 : small $\chi^2 = 0.10$, d.f. = 1, $P > 0.05$; large $\chi^2 = 0.18$, d.f. = 1, $P > 0.05$). This ratio is predicted if mayflies adopted an ideal free distribution, that is, a 1:1 relationship between the proportion of available resources and the proportion of foragers utilizing those resources (Fretwell and Lucas 1970, Parker and Sutherland 1986). Lastly, because I was able to account for >90% of all larvae within each stream at any one time, so the strong food response accounts for a high proportion of larvae in

experimental streams.

Total time allocation in safe, high food reward patches after introduction of predators remained four times higher than in safe, low food patches. For both mayfly size classes, these proportions were not significantly different from a predicted 4:1 ratio (Yates Continuity Chi square: small $\chi^2 = 0.25$, d.f. = 1, $P > 0.05$; large $\chi^2 = 1.40$, d.f. = 1, $P > 0.05$) based on the ideal free distribution.

The majority of foraging time by small B. tricaudatus after the introduction of predators was spent in safe, high food patches and time allocation in safe patches exceeded that in risky patches (Figure 11). This result likely explains the significant interaction between predation risk and food reward on time allocation among patches (Table 5). Time allocation in risky patches remained low irrespective of food reward levels, indicating that while small B. tricaudatus used risky patches, the presence of risk lowered patch use approximately by a constant proportion. Consequently, the reduction in the use of risky patches was not lowest in patches containing high food reward levels (as predicted under the risk-balancing trade-off and this difference was significant ($t = 25$, d.f. = 6, $P < 0.001$) (Figure 12).

Similarly, the percentage of total time allocation among foraging patches by large B. tricaudatus was significantly affected by the interaction between food

reward and predation risk (Table 5). Time allocation in safe patches exceeded that in risky patches and the majority of foraging time was spent in safe, high food patches (Figure 11). Time allocation in risky patches was almost three times higher when they contained high food reward (15.6 ± 1.4 %) compared with low food reward (5.8 ± 2.3 %). Moreover, the reduction in the use of risky patches was significantly higher when patches contained low food reward ($t = 9.14$, d.f. = 6, $P < 0.001$) (Figure 12).

Figure 11. Effect of predation risk (safe, risky) and food reward (low, high) on mean percent time allocation ($\bar{x} \pm se$) in patches by (A) small and (B) large Baetis tricaudatus. Data have been plotted separately for risky patches (o) and safe patches (•) when larvae had simultaneous access to patches with different spatial combinations of predation risk and food reward. Standard error not shown if included in the symbol.

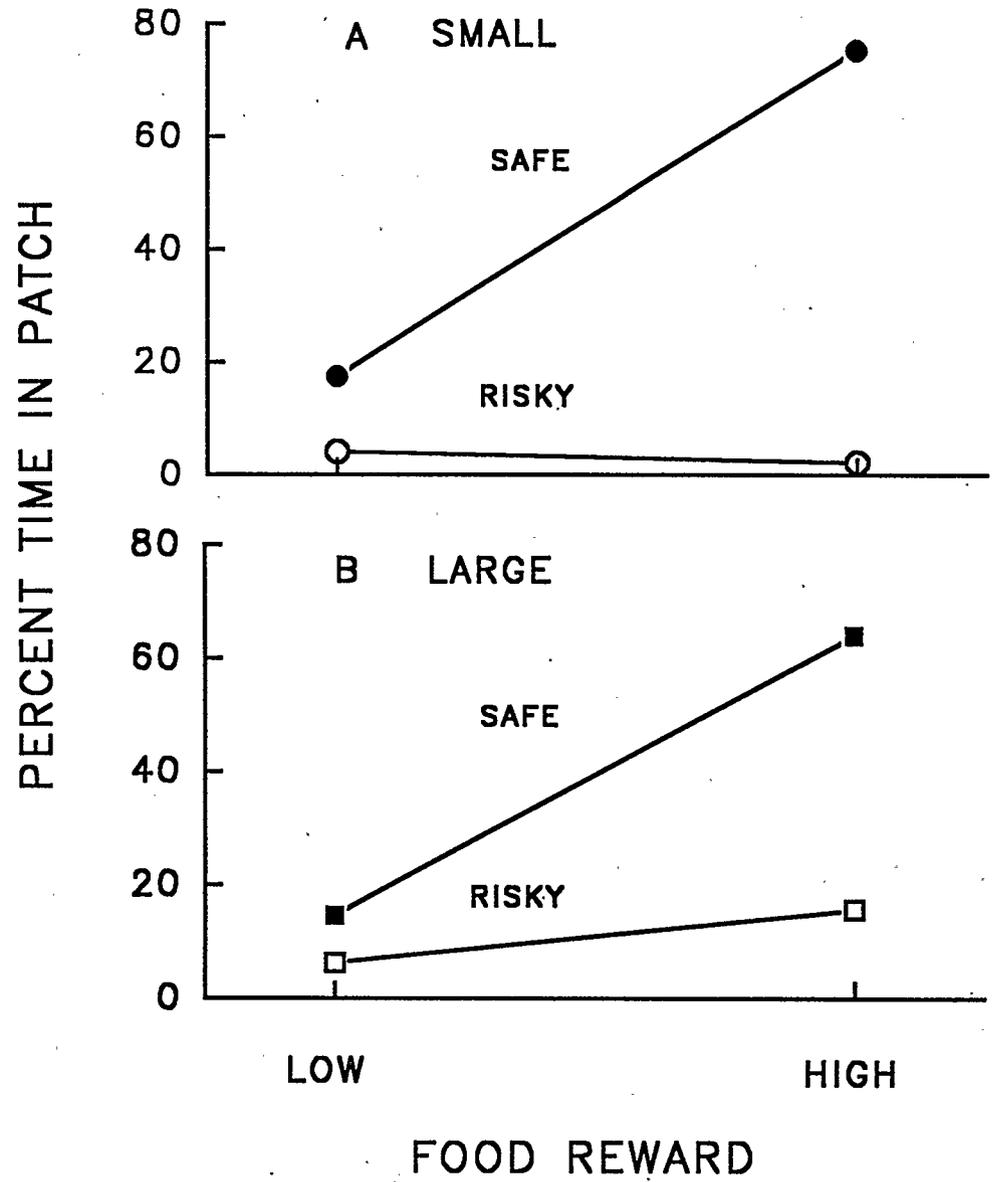
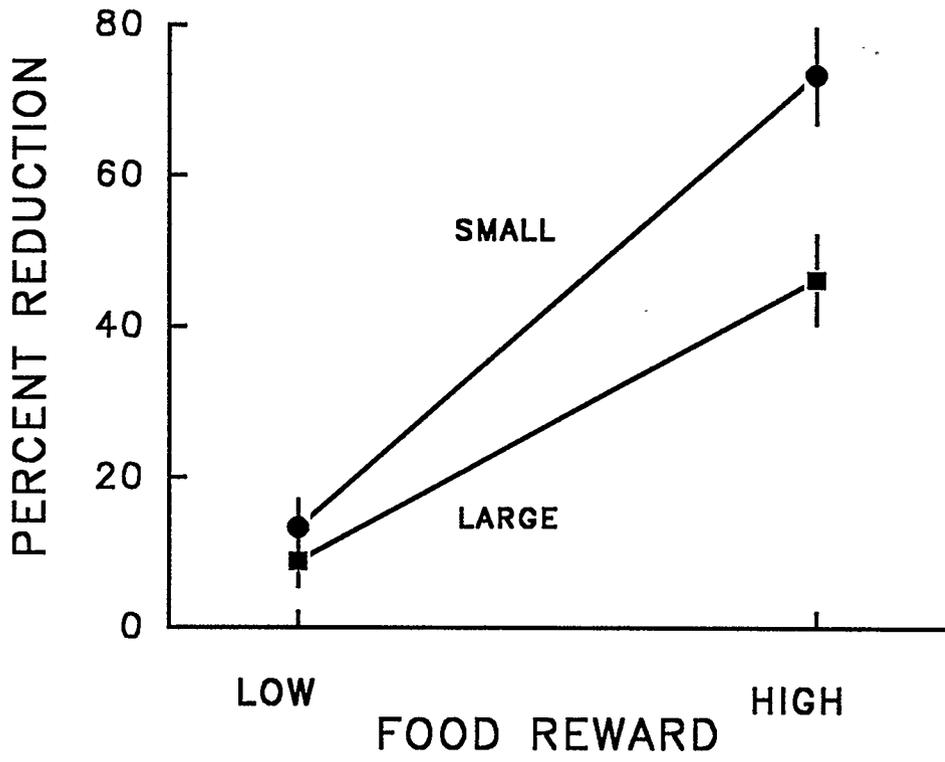


Table 5. Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on time allocation in simultaneously available foraging patches by small and large Baetis tricaudatus.

Source	df	MS	F	Significance
Small larvae				
Risk	1	1.254	647.33	P < .0001
Food	1	0.38	195.47	P < .0001
Risk × Food	1	0.40	208.63	P < .0001
Error	12	0.02		
Large larvae				
Risk	1	0.46	156.04	P < .001
Food	1	0.50	169.30	P < .001
Risk × Food	1	0.13	44.68	P < .001
Error	12	0.04		

Figure 12. Mean percent reduction ($\bar{x} \pm se$) in time allocation in risky patches compared to equal food in safe patches for small (●) and large Baetis tricaudatus (■). Standard error not shown if included in the symbol.



As very low numbers of small B. tricaudatus were present in risky patches at the end of trials, comparisons of algal ingestion rates could only be performed on larvae from safe patches. Small B. tricaudatus ingested significantly more food in safe, high food patches (0.023 ± 0.001 mg/h) than in safe, low food patches (0.006 ± 0.002 mg/h) ($t = 6.9$, d.f. = 8, $P < 0.001$). In contrast, mean ingestion rates for large B. tricaudatus were significantly affected by the interaction of food reward and predation risk (Table 6); mean ingestion rates were highest in safe, high food patches (Figure 13). Mean ingestion rates in risky patches were low irrespective of food reward levels, indicating that the presence of risk lowered algal consumption by an approximately constant proportion. Consequently, the reduction in food ingestion in risky low food patches (0.013 ± 0.002 mg/h) was significantly higher (two sample t-test on log transformed data: $t = 7.7$, d.f. = 6, $P < 0.005$) than in risky high food patches (0.056 ± 0.005 mg/h). Differences in food ingestion and time allocation in foraging patches between small and large B. tricaudatus can not be due to size-related differences in mayfly satiation or depletion of algal biomass. Small and large B. tricaudatus foraged throughout the 1 h trials, and depletion of the diatom mat (<10% initial biomass) and reduction in numbers of B. tricaudatus (<2 individuals per stream) during trials were low. Additionally, because R. cataractae did

not satiate, it is presumed that levels of predation risk did not vary appreciably throughout the experimental period.

Introduction of R. cataractae into streams caused a significant increase in drift rates compared to controls (predator absent) (Figure 14). However, the presence of a stationary R. cataractae did not cause drift behaviour to increase. Drift rates were highest three minutes after the introduction of R. cataractae into streams and coincided with the beginning of rooting (probing the substrate with snout) and swimming foraging behaviours (Beers and Culp 1990). ANCOVA indicated a significant two-way interaction between time (i.e., covariate) and predation risk, suggesting that drift rates changed in a quantitatively different manner through time in predator present versus predator absent treatments (Table 7). Although drift rates of B. tricaudatus were not significantly affected by B. tricaudatus size, the flight drift response produced a significant two-way interaction between B. tricaudatus size and food reward (Table 8). Mean flight distance of small B. tricaudatus to R. cataractae was similar in low (4.1 ± 0.2 cm) and high food reward patches (3.8 ± 0.3 cm) (Figure 15). Flight initiation distance for large B. tricaudatus, declined by four-fold in low food reward (4.3 ± 0.3 cm) compared to high food reward patches (1.1 ± 0.1 cm).

Table 6. Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on food consumption rates of large Baetis tricaudatus in simultaneously available foraging patches.

Source	df	MS	F	Significance
Risk	1	4.94	84.98	P < .001
Food	1	7.85	134.88	P < .001
Risk × food	1	3.05	52.36	P > .05
Error	57	0.06		

Figure 13. Effect of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) food ingestion rates of large Baetis tricaudatus. Data are plotted separately for risky (●) and safe patches (■) when larvae had simultaneous access to patches with different spatial combinations of predation risk and food reward. Standard error not shown if included in the symbol.

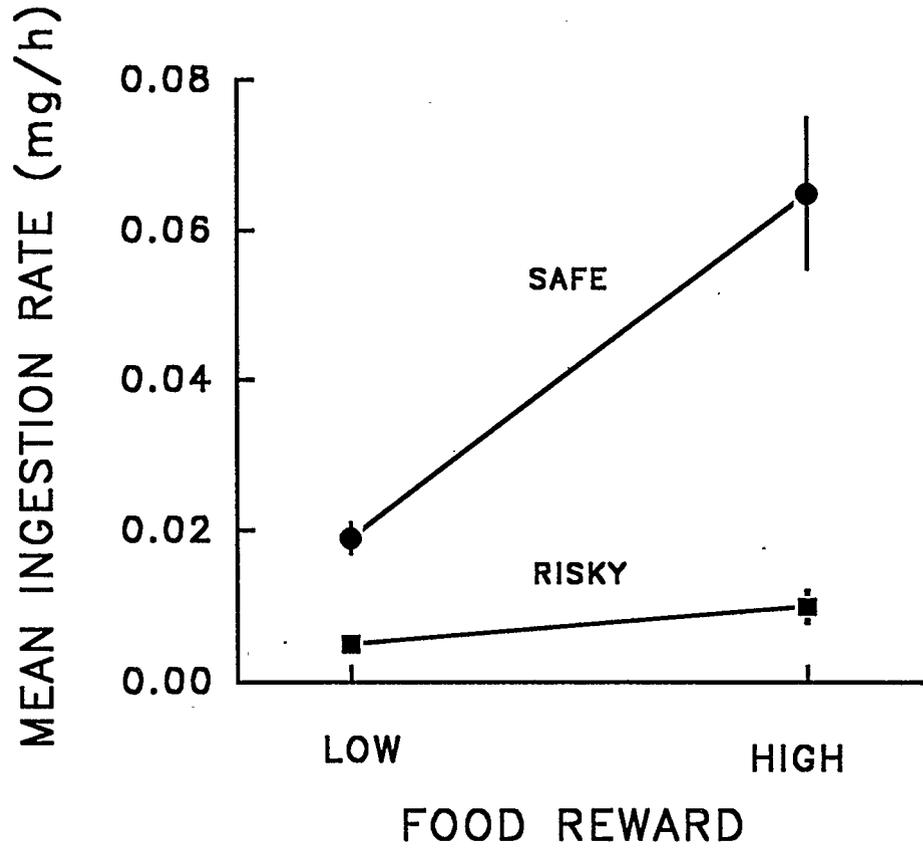


Figure 14. Log_{10} mean drift rates ($\bar{x} \pm \text{se}$) of (A) small and (B) large Baetis tricaudatus in streams containing predators (●) compared to streams without predators (■). Standard error not shown if included in the symbol.

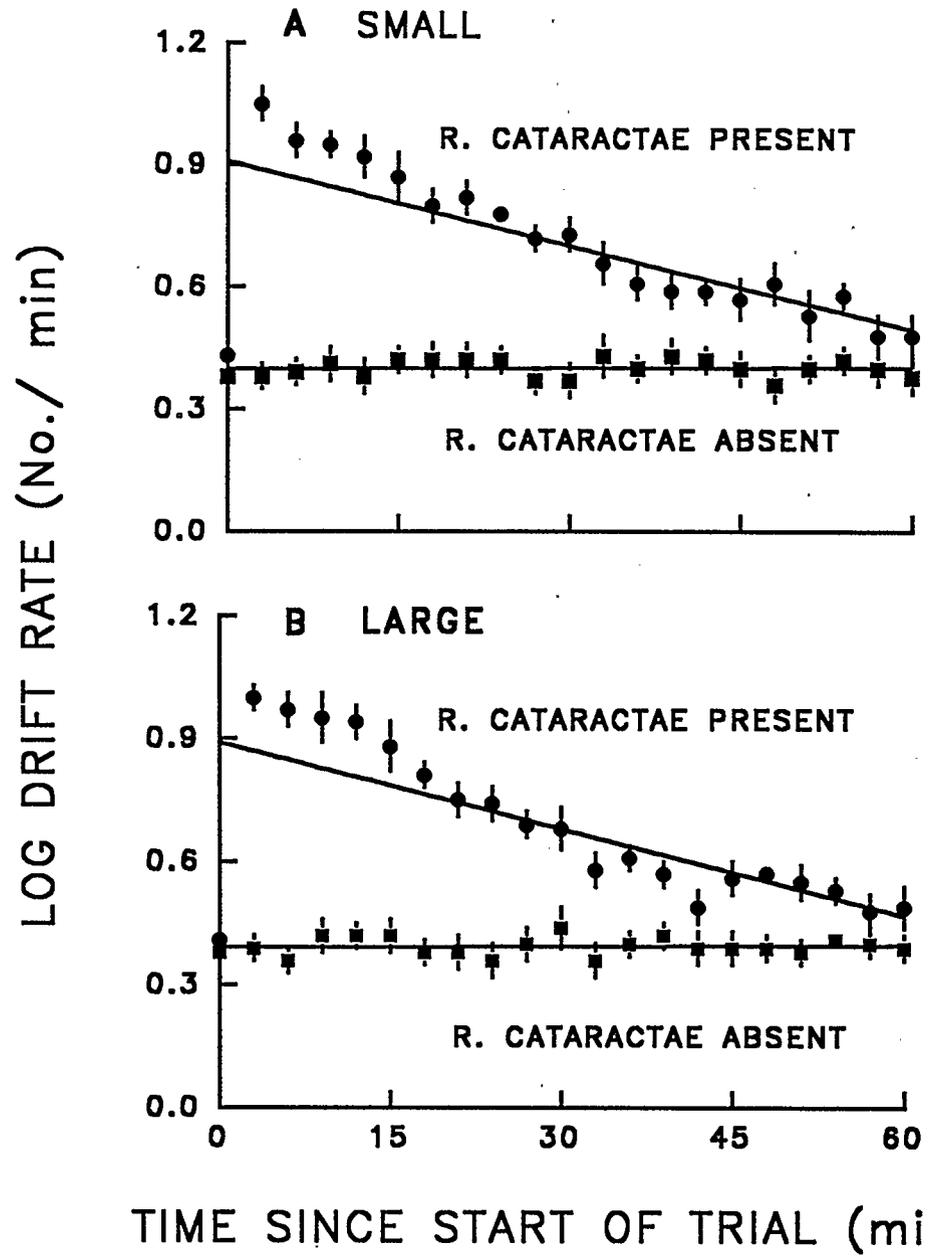


Table 7. Results of ANCOVA determining the effects of Baetis tricaudatus size (small, large), predation risk (safe, risky) and the interaction of these effects on \log_{10} drift rate (covariate).

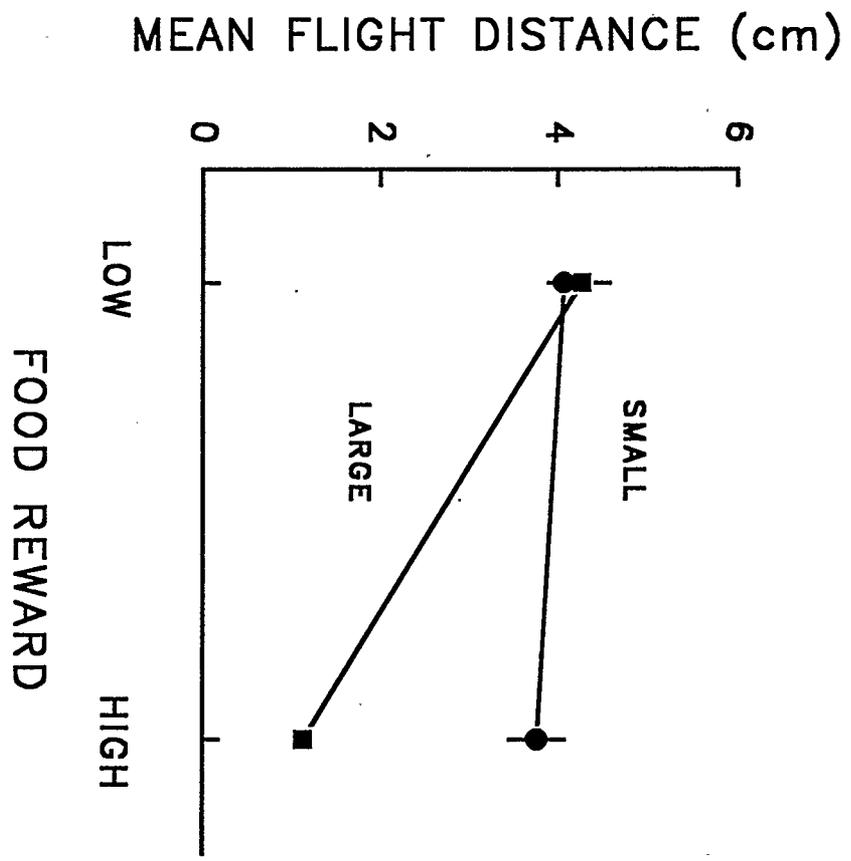
Comparison	d.f.	MS	F	Significance
Size	1	0.003	0.32	P > .05
Risk	1	6.588	685.91	P < .001
Time	1	2.202	229.31	P < .0001
Size × Risk	1	0.002	0.03	P > .05
Time × Risk	1	2.114	220.09	P < .0001
Time × Size	1	0.0002	0.02	P > .05
Size × Time	1	0.005	0.48	P > .05
× Risk				

Comparison	Intercept	P	Slope	Significance
Risky	0.992	< .0001	-0.0092	< .0001
Safe	0.402	< .0001	-0.0001	> .05

Table 8. Results of two-factor ANOVA determining the effects of Baetis tricaudatus size (small, large), food reward (low, high), and the interaction of these effects on mean distance initiating a flight response to Rhinichthys cataractae.

Source	df	MS	F	Significance
Size	1	3.50	40.28	P < .0001
Food	1	2.54	29.22	P < .0001
Size × Food	1	4.28	49.36	P < .0001
Error	211	0.09		

Figure 15. Effect of food reward (low, high) on mean flight distance ($\bar{x} \pm se$) by small (\bullet) and large (\blacksquare) Baetis tricaudatus to Rhinichthys cataractae. Standard error not shown if included in the symbol.



DISCUSSION

Predation risk has profound effects on spatial and temporal foraging patterns, the extent of which are often prey size-dependent (Stein and Magnuson 1976, Stein 1979, Sih 1980, 1987, Werner et al. 1983a, Power 1984, Dixon and Baker 1988). I hypothesized that size-related differences in per capita risk and feeding period of small and large B. tricaudatus would produce different time allocation patterns. If these differences were sufficiently large then large B. tricaudatus should have adopted a risk-balancing trade-off whereas small B. tricaudatus should have adopted a risk-adjusting trade-off. I predicted that large B. tricaudatus would accept proportionately greater risk when risky patches contained high food (i.e., risk-balance), because in contrast with small B. tricaudatus, they feed only during the night and experience low risk from R. cataractae.

Analysis of patch use by small and large B. tricaudatus in the absence of predators showed that both the numbers of mayflies and time allocation within patches conformed to predictions of the Ideal Free Distribution, establishing that B. tricaudatus is capable of discriminating between low and high quantity food patches. Thus, foraging patch selection can potentially involve an evaluation of food reward, a necessary requirement for the risk-balancing,

risk-adjusting, and risk-reckless strategies. Risk and food reward experiments revealed that foraging patch selection, with respect to time allocation and consumption rates, involved an evaluation of both food reward and predation risk. Fraser and Huntingford (1986) provide a two factor, factorial ANOVA design to operationally define their four trade-offs. However, this factorial design alone can not be used to discriminate among the four trade-offs as the significance of main effects (predation risk and food reward) and the interaction term are identical for several trade-offs. I discriminated among the four trade-offs based on an ANOVA design on time allocation and per-capita ingestion rates, and combined these results with the relationship between the reduction in use of risky patches and food reward levels. While large B. tricaudatus consumed more food and spent more time in risky patches when they contained high food reward, they did not accept proportionately greater risk for high food reward (i.e., they did not risk-balance). Similarly, small B. tricaudatus apportioned less time to risky habitats irrespective of food reward levels. When these results are compared with predictions of the four trade-off models (Figure 1), they indicate that both small and large B. tricaudatus are risk-adjusters. Hence, taken alone, these data indicate that the risk-reward trade-off by B. tricaudatus is fixed with respect to forager size.

Nevertheless, large body size does appear to confer an increased ability to accept increased exposure to risk under high food conditions. This result produced different time allocation patterns in risky patches between small and large larvae. For example, exposure to R. cataractae reduced patch use by small B. tricaudatus by a constant proportion, whereas large B. tricaudatus increased time allocation to risky areas when patches contained high food reward. Differences in length of feeding period and predation risk may explain quantitative differences in time allocation in risky, high food patches. Because small B. tricaudatus feed continuously throughout a diel cycle, the cost of reduced food intake due to the appearance of a nocturnal predator may be negated by food intake during the day. This compensatory foraging response of small individuals is unavailable to large B. tricaudatus because they feed exclusively during the night, presumably to avoid high mortality from day active trout predators. In fact, the shift from diurnal to a nocturnal activity pattern by B. tricaudatus is consistent with the findings of several other studies (Allan 1978, Flecker in press, Cowan and Peckarsky in press) and is hypothesized to be a general response to size-selective predators, such as trout, which feed during the day (Allan 1978, Flecker in press). Thus, the abundance of trout in the Bow River system (Culp et al. in press) may be indirectly determining the nature of the behavioral

trade-off that large B. tricaudatus adopt at night.

Foragers can determine patch residence times by varying the distance at which they initiate a flight response to an approaching predator (Ydenberg and Dill 1986, Dill and Ydenberg 1987, Dill and Houtman 1989). A general prediction is that time in a patch is inversely related to the distance at which prey initiate a flight response to a predator. My findings indicate that time allocation in risky patches by large B. tricaudatus is associated with a food dependent, predator-induced flight response to R. cataractae. Although the distance at which small B. tricaudatus flee from R. cataractae was constant with respect to food reward levels, flight initiation for large B. tricaudatus was reduced by four-fold when patches contained high food reward. Numerous studies have clearly demonstrated the importance of flight into the drift as an anti-predator response to invertebrate (Peckarsky 1980, Peckarsky 1987, Soluk and Collins 1988, Malmqvist and Sjostrom 1988) and fish predators (Kohler and McPeck 1989, Culp et al. 1991). In addition to predator avoidance, drift is a mechanism by which foragers can vary patch residence times in response to patch quality. The ability to vary flight initiation distances should be adaptive because it allows grazers, such as B. tricaudatus, to exploit a food resource which shows high spatial and temporal variability (Richards and Minshall 1988, Scrimgeour and Winterbourn 1989). This may be an important mechanism

affecting patch residence time, especially when the predator, like R. cataractae, has a short reactive distance (< 2 cm) (Beers and Culp 1990).

Size-specific differences in flight initiation distance could represent size-related differences in the ability of B. tricaudatus to discriminate among food reward levels. My findings do not support this contention because both larval sizes distinguished between food reward levels by adopting an ideal free distribution. Rather, the size-specific differences in flight initiation distance may result from age-related changes in sensory abilities of B. tricaudatus to perceive R. cataractae. Perception of stonefly and fish predators by mayfly larvae is thought to involve olfactory and hydrodynamic cues (Kohler and McPeck 1989, Peckarsky and Wilcox 1989, Culp et al. 1991). The intensity of water borne cues and hydrodynamic waves is likely related inversely with distance to the predator. Hence, one possible hypothesis to explain a size-specific flight initiation response is that the ability to discriminate among the intensity of these cues is related to sensory development or experience through previous encounters. More data are required for a complete understanding of the mechanisms producing the observed size-specific difference in allocation of foraging time among simultaneously available patches.

Presently I am unable to explain unequivocally why small and large B. tricaudatus adopted a risk-adjusting strategy compared to the other three alternatives. The adaptive value of risk-adjusting may be related to the value of increased food intake associated with foraging in risky, high food patches. In contrast to risk-reckless and risk balancers, risk-adjusters always obtain less food in the presence of a predator compared to equivalent food in a safe patch (Fraser and Huntingford 1986, Pitcher et al. 1988). In fact, a cost-benefit model may be valuable to predict foraging trade-offs in conflicting demand scenarios. For example, risk-adjusting may be the predominant response when the cost of feeding in a risky patch in terms of probability of being eaten and reduced food intake exceeds the benefits derived from the patch (i.e., an increase in food intake). B. tricaudatus forage by moving across the substrate accompanied by lateral movements of the abdomen. These behaviours may not be compatible with minimizing predation risk because perception of mayfly prey by R. cataractae likely involves detection of hydrodynamic cues created by mayfly movement and flow distortion around a stationary mayfly (Beers and Culp 1990, Culp et al. 1991). Thus, the risk-adjusting strategy adopted by B. tricaudatus may be optimal because the cost of staying in a risky patch (reduced food intake, increased probability of being attacked) exceeds the benefits derived from increased food

intake. How these processes affect other fitness correlates such as rates of growth, time to adult and fecundity will require longer term studies.

CHAPTER 5

EFFECTS OF PREDATOR TYPE ON THE BEHAVIOURAL TRADE-OFF BY
THE LOTIC MAYFLY Baetis tricaudatus.

INTRODUCTION

Spatial and temporal foraging patterns are strongly affected by the presence of predators (Stein and Magnuson 1976, Sih, 1982, Dill and Fraser 1984, Cerri and Fraser 1983, Werner et al. 1983a, Cooper 1984, Lima 1985, Power 1987, Harvey et al. 1988, Holomuzki and Short 1990). For example, the presence of a predator often reduces the length of time that foragers spend in patches (Sih 1980, Cerri and Fraser 1983, Holbrook and Schmitt 1988, Macchiusi and Baker in press). While the above studies demonstrate that time allocation patterns by foragers are reduced by predators, none have determined whether the reduction in use of risky patches is dependent on predator species.

Time allocation patterns by a forager might be specific to a particular predator species if the level of mortality risk imposed on a forager differs with predator species. In

fact, numerous studies indicate that the degree to which foragers avoid predators is positively related to their vulnerability (Stein and Magnuson 1976, Peckarsky 1980, Sih, 1980, 1982, Werner et al. 1983a, Power 1984). For example, Peckarsky (1980) found that mayfly larvae of Ephemera infrequens McDunnough and Baetis bicaudatus Dodds evaded contact with the insectivorous perlid stonefly Megarcys signata (Hagen) significantly more often than with the omnivorous pteronarcid stonefly Pteronarcella badia (Hagen). It therefore seems likely that differences in the level of mortality imposed on a forager could alter time allocation patterns among feeding patches containing different predator species. A general prediction is that time allocated to feeding by foragers in risky patches is inversely related to mortality risk.

The level of mortality risk imposed on a forager by a predator species can be affected by the presence or absence of other predator species. For example, the presence of two predator species feeding in the same area can produce additive or synergistic effects on the level of mortality risk imposed on a forager (Soluk and Collins 1989, Rahel and Stein 1988). For example, Rahel and Stein (1988) found that crayfish (Orconectes rusticus) (Girard) and small mouth bass (Micropterus dolomieu Lacepede) ingested significantly more johnny darters (Etheostoma nigrum Rafinesque), a small fish, when they foraged together than when they foraged

separately. The question remains, however, whether differences in mortality risk among different predator species, either feeding alone or with another species, results in different time allocation patterns by their prey (i.e., a forager). If differences in time allocation patterns by foragers when risky patches contain different predator species are sufficiently large they will result in foragers displaying qualitatively different trade-offs between predation risk and food reward (sensu Fraser and Huntingford's trade-off models (Chapter 1)).

The algal prey - mayfly grazer (B. tricaudatus Dodds) - stonefly (C. sabulosa) - minnow predator (R. cataractae) food web provides an ideal system to determine whether behavioural trade-offs differ according to predator species. Baetid mayflies are preyed upon by both R. cataractae and C. sabulosa but the levels of mortality risk on B. tricaudatus are predator specific. Mortality risk on B. tricaudatus from R. cataractae is twice that from C. sabulosa (Chapter 2). If time allocation in risky patches is inversely related to predation risk, B. tricaudatus should allocate more time to feeding in risky patches containing C. sabulosa than in risky patches containing R. cataractae. If the presence of both predator species (i.e., C. sabulosa and R. cataractae) in the same patch increases mortality risk to B. tricaudatus then time allocation in risky patches should be further reduced. If differences in time allocation patterns

are sufficiently large they will result in B. tricaudatus displaying a qualitatively different trade-off depending upon the predator involved (e.g., risk-adjusting versus risk-balancing).

These hypotheses were tested in a laboratory stream system where B. tricaudatus had simultaneous access to foraging patches which differed in predation risk and food reward. While small and large B. tricaudatus are risk-adjusters (Chapter 4), I only investigated the effects of predator species on time allocation patterns by large B. tricaudatus because only large B. tricaudatus displayed a food-dependent flight (i.e., drift) initiation response (Chapter 4). This response represents a potential mechanism to vary time allocation patterns. For each trial I measured time allocated to feeding in each of the four simultaneously available patches to determine whether differences in predator species resulted in quantitative or qualitative differences in time allocation patterns for the grazer. Drift rates in safe (predator absent) versus risky (predator present) streams and the distance at which larvae initiated a flight response (i.e., drift) to predators were also measured. Based on these findings, I determined which of the four foraging trade-offs proposed by Fraser and Huntingford (1986) applied when B. tricaudatus experienced predation risk from the three predator combinations (C. sabulosa; R. cataractae; C. sabulosa with R. cataractae) and

identified some of the proximal mechanisms involved.

METHODS

Experimental animals

Large instar larvae (5.4 ± 0.3 mm) of B. tricaudatus were collected from the Bow River, Calgary, Alberta, during 20 April-3 May, 1990. Individuals were maintained at 11 °C for 2-4 weeks prior to experiments in aerated, flowing water holding tanks in the laboratory with a 14:10 h day/night cycle. During this period larvae were fed an ad libitum supply of the diatom, Navicula sp., which was cultured as described earlier (Chapter 3).

Stock populations of R. cataractae and C. sabulosa were collected from the Bow River on 29 April 1990 and maintained at 11°C in laboratory streams. These predators were fed an ad libitum diet of B. tricaudatus larvae until utilized in the patch choice trial experiments. Individual predators were used only once per treatment.

Patch choice trials

Patch choice trials to determine the effect of predator species on the behavioural trade-off adopted by B. tricaudatus were conducted in large, circular streams that were partitioned into four equal-sized compartments (i.e., foraging patches) representing spatial variation in both

predation risk (safe (S), risky (R)) and food reward (low food reward - 0.10 mg/cm² of Navicula sp. (LF), high food reward - 0.90 mg/cm² (HF)) as described in Chapter 4.

Briefly, mayflies had access to four concurrently available patches (LF+R, LF+S, HF+R, HF+S) where each patch contained a single 4 × 4 × 1 cm feeding patch covered with the appropriate biomass of Navicula. Risky patches contained one of the following treatments: either (1) one R. cataractae (63±1.4 mm), (2) one C. sabulosa (28±4.1 mm) or (3) one C. sabulosa and one R. cataractae at the same time. Water temperature, and diel light cycle within the streams were based on spring field conditions and food reward levels were based on results of functional response experiments (Chapter 3).

Each patch choice experiment involved placing 30 mayflies in each artificial stream for a 38 h acclimation period prior to the addition of the predator. Prior to adding predators, each stream was videotaped for 1 min in the dark to determine the mayfly patch distribution in the absence of predators and to determine whether mayflies could distinguish amongst the diatom biomass levels (i.e., low versus high food patches). Approximately five minutes after this initial filming period and commencement of the dark photoperiod, an individual R. cataractae or of C. sabulosa or one individual of each species was placed randomly into a patch designated randomly as risky. The entire stream was

again videotaped under infrared light for 1 h to measure allocation of foraging time by B. tricaudatus among the four foraging patches.

Predators could only attack mayfly larvae in the risky patch as 5 mm mesh screens prevented them but not the mayflies from moving among patches. Predators were acclimated to stream conditions for 38 h prior to the experiment and the presence of a predator in one patch did not appear to alter behaviours of mayflies, such as drift rate or position of larvae on top, bottom, and sides of substrates, in other patches.

For each 1 h trial I calculated the amount of time that larvae spent in each of the four patches by the total amount of foraging time available during the 1 h trials (i.e. 30 larvae multiplied by 1 h = 30 h foraging time). These data provide information on the relative occupation of the four patches. This was accomplished by pausing the video tape player every thirty seconds and counting the number of larvae in each of the patches. Video play back also enabled me to calculate per capita attack rates (No. of attacks/No. of larvae in a patch/h) for each of the predator treatments. The number of mayflies in the drift (measured over a 1 minute period) was determined every 3 minutes to identify possible drift responses to predators as described in Chapter 4. Foragers can alter patch residence times by varying the distance at which they flee from a predator.

Thus, I measured the distance between B. tricaudatus and the predator that initiated the drift response. When the predator treatment included both a single R. cataractae and a C. sabulosa in the same compartment, I assumed that any drift event was a response to the nearest predator.

Statistical Analyses

I determined whether quantitative differences in time allocation patterns resulted in qualitatively different trade-offs by B. tricaudatus by measuring time allocation budgets in each of the four patches (Chapter 4). Patch-specific food ingestion rates were not calculated, since I had shown previously shown that time allocation in patches and rates of food intake are closely related (Chapter 4). The hypotheses that patch use in terms of time allocation was not significantly affected by predation risk (safe, risky), food reward (low, high) and the interaction of these terms was tested with a repeated measures, model 1, two-factor ANOVA on arcsine square-root transformed data which was applied separately for each of the three combinations of predators. The hypothesis that per capita attack rates on B. tricaudatus by C. sabulosa and/or R. cataractae was not significantly affected by predator species, food reward and the interaction of these factors was tested with a repeated measures, two factor ANOVA.

The hypothesis that mean drift rate was not significantly affected by predation risk (control, R. cataractae, C. sabulosa, C. sabulosa and R. cataractae) was tested with a model 1, single factor ANOVA with repeated measures in time. Finally, the hypothesis that the mean distance between the predator and B. tricaudatus initiating the flight response was not significantly affected by food reward (low, high), and predator combination (R. cataractae only, C. sabulosa, C. sabulosa and R. cataractae) was tested with a repeated measures, model 1, two factor ANOVA.

RESULTS

In the absence of predators, B. tricaudatus larvae discriminated among food patches distributing themselves in proportion to food reward levels. The total number of mayflies in high food patches prior to the introduction of R. cataractae ($23 \pm 0.7\%$) (Chapter 4), C. sabulosa ($21.4 \pm 0.7\%$), R. cataractae and C. sabulosa ($21.6 \pm 0.7\%$) was approximately four times higher than in low food patches prior to the introduction of R. cataractae ($4.8 \pm 0.5\%$) (Chapter 4, C. sabulosa ($5.0 \pm 0.3\%$), R. cataractae and C. sabulosa ($5.2 \pm 0.4\%$). These proportions are not significantly different from a 4:1 ratio when risky patches contained R. cataractae (Yates Continuity $\chi^2 = 0.18$, d.f. = 1, $P > 0.05$); C. sabulosa ($\chi^2 = 0.04$, d.f. = 1, $P > 0.05$) or both predators ($\chi^2 = 0.01$, d.f. = 1, $P > 0.05$). This ratio is predicted if mayflies adopted an ideal free distribution, that is, a 1:1 relationship between the proportion of available resources and the proportion of foragers utilizing those resources (Fretwell and Lucas 1970, Parker and Sutherland, 1986).

The total amount of time allocated to safe, high food reward patches remained four times higher than in safe, low food reward patches for all three predator combinations. These proportions were again not significantly different from a predicted 4:1 ratio for all three predator

combinations (R. cataractae $\chi^2 = 1.40$, d.f. = 1, $P > 0.05$; C. sabulosa $\chi^2 = 2.82$, d.f. = 1, $P > 0.05$; both predators combined, $\chi^2 = 0.31$, d.f. = 1, $P > 0.05$).

After the introduction of predators, time allocation in safe patches exceeded risky patches and the majority of foraging time was spent in safe, high food patches (Figure 16). The percentage of total time allocation among foraging patches by large B. tricaudatus larvae was significantly affected by the interaction between food reward and predation risk for all three predator combinations (Table 9). Time allocation in risky patches was almost three times higher when they contained high food reward (R. cataractae $\bar{x} = 15.6 \pm 1.4\%$, C. sabulosa $\bar{x} = 19.89 \pm 1.2\%$, both predators present $\bar{x} = 16.38 \pm 1.9\%$), compared with low food reward (R. cataractae $\bar{x} = 5.8 \pm 2.3\%$, C. sabulosa $\bar{x} = 3.89 \pm 1.9\%$, both predators present $\bar{x} = 3.63 \pm 1.3\%$). Moreover, the reduction in the use of risky patches was significantly higher when patches contained low food reward (R. cataractae: $t = 9.14$, d.f. = 6, $P < 0.001$; C. sabulosa $t = 12.33$, d.f. = 8, $P < 0.0001$; both predators present: $t = 10.28$, d.f. = 8, $P < 0.001$).

Mean time allocated to feeding varied little in risky patches containing R. cataractae (low food (LF) = $6.3 \pm 2.3\%$, high food (HF) = $16.4 \pm 1.4\%$), C. sabulosa (LF = $3.9 \pm 0.6\%$, HF = $19.9 \pm 1.1\%$), and both predators at the same time (LF = $3.6 \pm 0.7\%$, HF = $16.4 \pm 1.4\%$). Based on Fraser and

Figure 16. Effects of predation risk and food reward on mean time allocation ($\bar{x} \pm se$) in patches by Baetis tricaudatus when risky patches contained (A) one Claassenia sabulosa and/or one Rhinichthys cataractae. Data are plotted separately for safe and risky patches when Baetis tricaudatus had simultaneous access to patches with different spatial combinations of predation risk and food reward. Standard error not shown if included in the symbol.

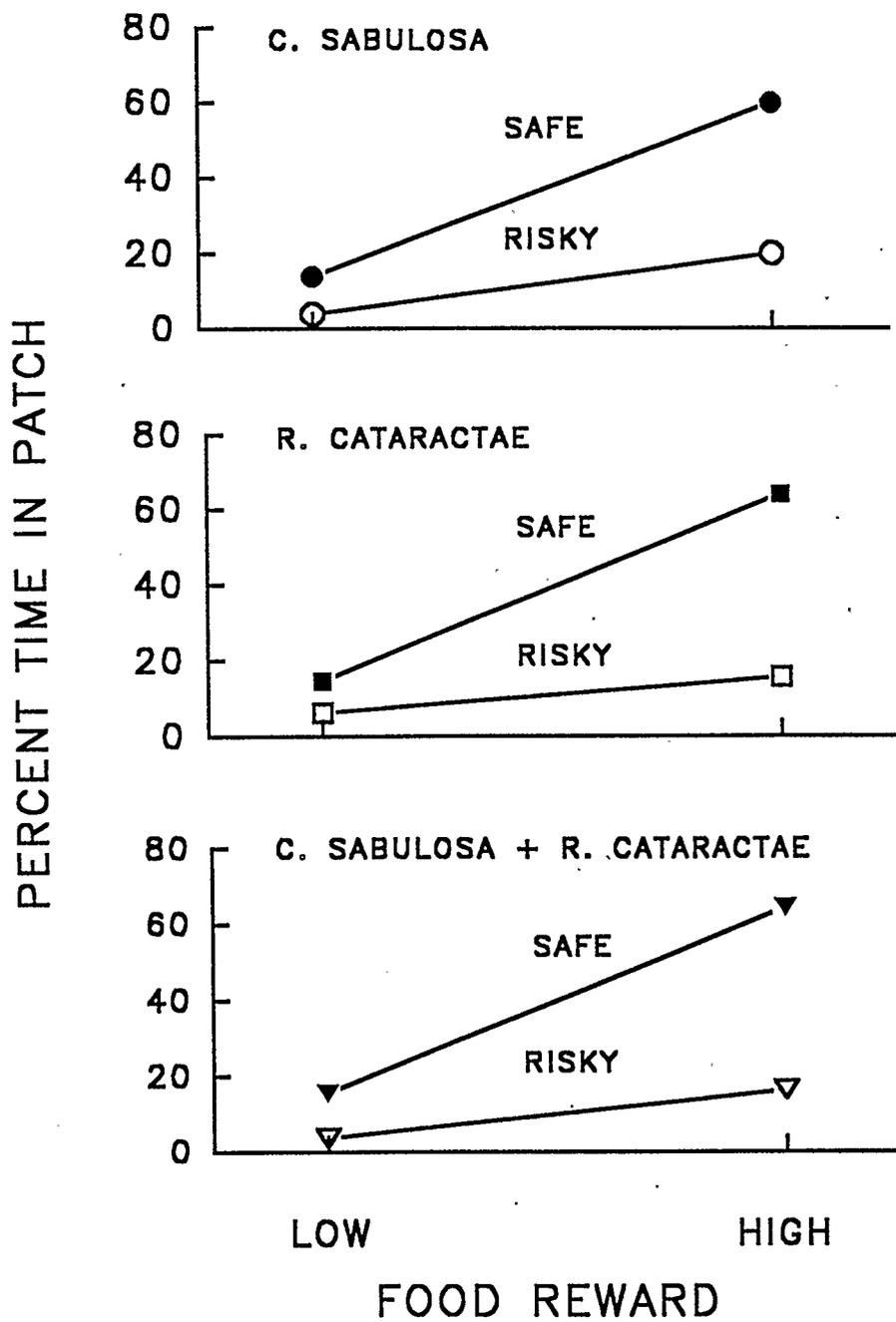


Table 9. Two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on time allocation in simultaneously available foraging patches by large Baetis tricaudatus larvae when risky patches contained a single Rhinichthys cataractae, and/or a single Claassenia sabulosa.

Source	d.f.	MS	F	Significance
<u>Rhinichthys cataractae</u> as predator				
Risk	1	1.25	647.33	P < .001
Food	1	0.38	195.47	P < .001
Risk × Food	1	0.04	208.63	P < .001
Error	12	0.02		
<u>Claassenia sabulosa</u> as predator				
Risk	1	0.51	506.94	P < .001
Food	1	0.74	742.96	P < .001
Risk × Food	1	0.07	71.81	P < .001
Error	16	0.01		
<u>Rhinichthys cataractae</u> and <u>Claassenia sabulosa</u> as predators				
Risk	1	0.67	362.60	P < .001
Food	1	0.71	382.63	P < .001
Risk × Food	1	0.11	60.04	P < .001
Error	16	0.03		

Huntingford's trade-off models B. tricaudatus adopted a risk-adjusting trade-off (Fig. 1) irrespective of predator species.

Per capita attack rates on B. tricaudatus by predators were significantly affected by predator species and food reward (Table 10). Per capita attack rates were highest when risky patches contained a single R. cataractae and both predators at the same time (i.e., R. cataractae and C. sabulosa) and lowest when patches contained a single C. sabulosa (Figure 17). Per capita attack rates in low food reward patches were significantly higher than in high food patches probably because while the total number of attacks on B. tricaudatus were similar in low and high food patches, low food patches contained fewer larvae. Additionally, these results indicate that mortality risk from R. cataractae is higher than from C. sabulosa (Figure 17).

While B. tricaudatus larvae were attacked more frequently when risky patches contained R. cataractae and both R. cataractae and C. sabulosa at the same time, the number of attacks by R. cataractae on B. tricaudatus did not differ when they were foraging alone or with C. sabulosa (two sample t-test: $t = 0.24$, d.f. = 16, $P > 0.05$). In contrast, C. sabulosa attacked significantly fewer B. tricaudatus when R. cataractae were present in a patch ($t = 3.35$, d.f. = 18, $P < 0.005$) (Table 11).

Drift rates of B. tricaudatus were significantly affected by the interaction of time since start of trial and predation risk (Table 12). Drift in control streams (i.e., predator absent) was low and constant through time whereas drift in streams was initially high then decreased (Figure 18). This drift pattern likely explains the significant interaction between predation risk and time. Comparison of sample means using Tukey's Test, indicated that drift rates were not significantly different when streams contained either R. cataractae, C. sabulosa or both predators at the same time (Figure 18).

Mean drift initiation distances were significantly affected by food reward (Table 13). Drift flight distances of B. tricaudatus to all three predator combinations were higher when foraging patches contained low food reward but declined by four-fold when patches contained high food (Figure 19). Flight initiation distances were not significantly related to number of B. tricaudatus in risky, low food patches (linear regressions $y = 4.15 - 4.83x$, $N = 52$, $r^2 = 0.01$, $P > 0.05$) or risky, high food reward patches $y = 1.09 - 0.012x$, $N = 56$, $r^2 = 0.01$, $P > 0.05$) when patches contained R. cataractae) (Figure 20).

Figure 17. Effect of predator species and food reward on mean ($\bar{x} \pm se$) per capita attack (No. attacks/individual/h) on Baetis tricaudatus larvae when risky patches contained a single Rhinichthys cataractae, a single Claassenia sabulosa, or both predators at the same time.

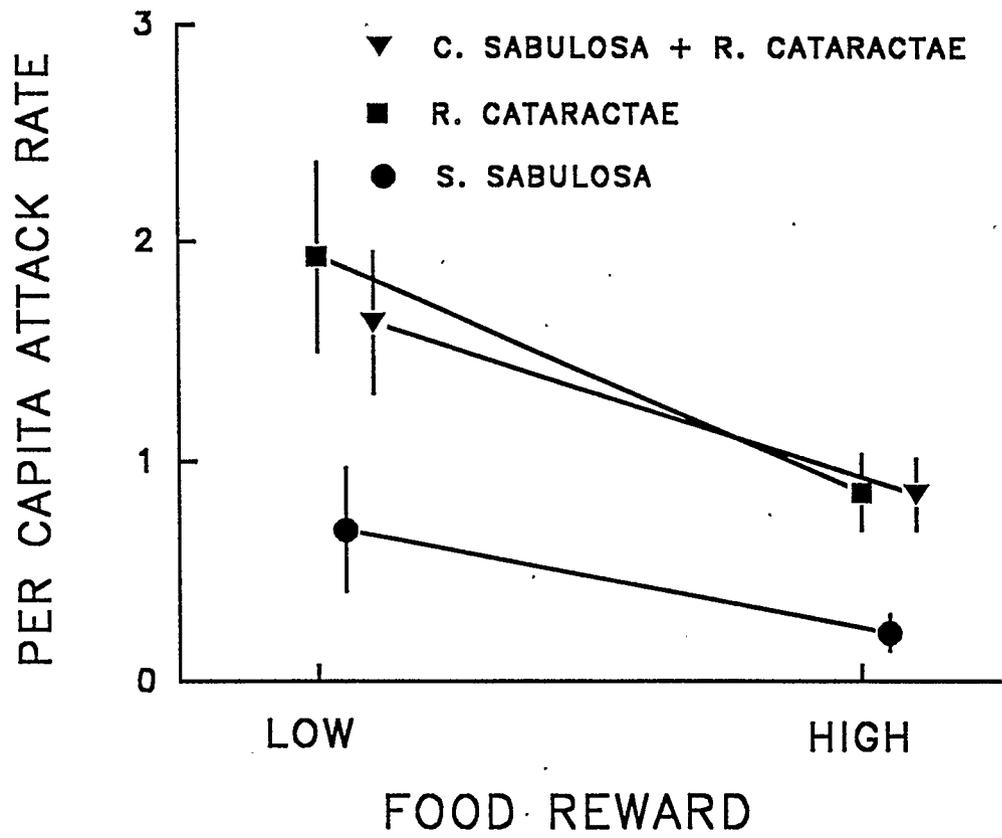


Table 10. Two factor ANOVA showing the effects of predator species (Rhinichthys cataractae, Claassenia sabulosa, Rhinichthys cataractae and Claassenia sabulosa) and food reward (low, high) on mean per capita attack rate ($\bar{x} \pm se$) on large Baetis tricaudatus larvae during patch choice trials.

Source	d.f.	MS	F	Significance
Risk	2	0.137	10.67	P < .001
Food	1	0.150	12.25	P < .001
Risk × Food	2	0.003	0.21	P > .05
Error	22	0.012		

Table 11. Mean number ($\bar{x} \pm se$) of times Baetis tricaudatus larvae were attacked when risky patches contained Rhinichthys cataractae and/or Claassenia sabulosa. Data represent number of attacks in low and high food patches combined.

Predator	Number of attacks \bar{x}	se
<u>Rhinichthys cataractae</u> only	3.13	0.35
<u>Rhinichthys cataractae</u> with <u>Claassenia sabulosa</u>	3.00	0.37
<u>Claassenia sabulosa</u> only	1.10	0.23
<u>Claassenia sabulosa</u> with <u>Rhinichthys cataractae</u>	0.20	0.13

Figure 18. Comparison of mean drift rate ($\bar{x} \pm se$) of large Baetis tricaudatus larvae in streams without predators (\blacktriangle) to those containing Rhinichthys cataractae (\blacksquare), Claassenia sabulosa (\bullet) and both predators at the same time (\blacktriangledown).

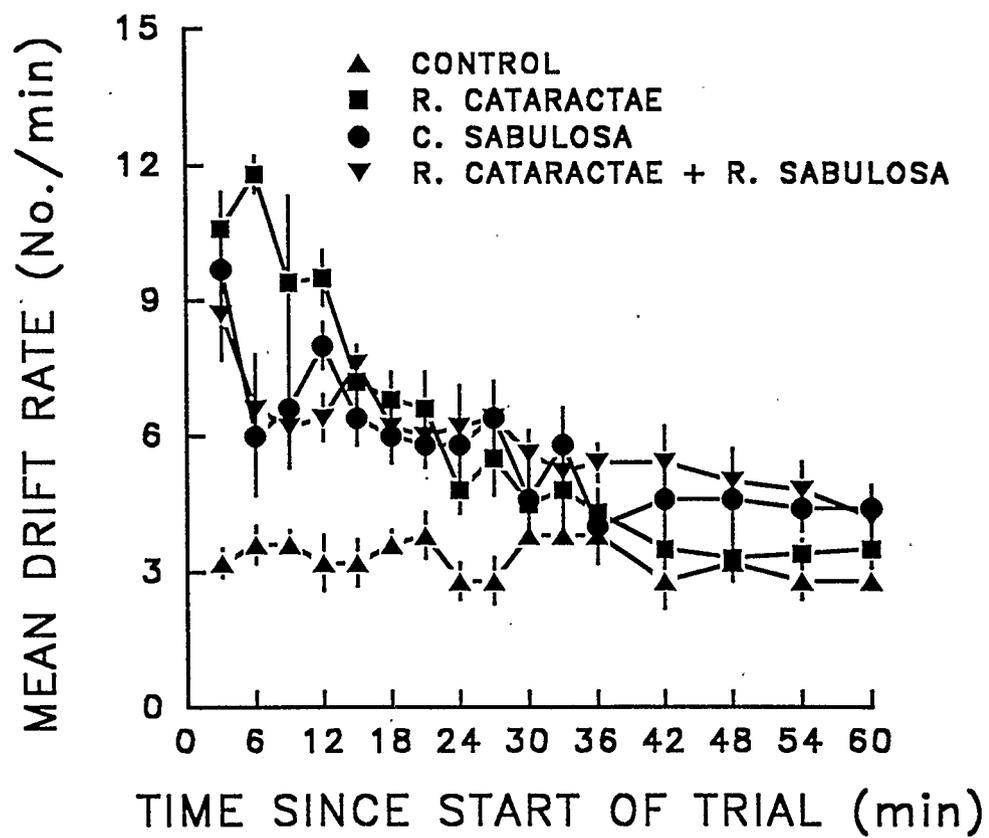


Table 12. Results of (A) repeated measures single factor ANOVA determining the effects of predation risk (control, Claassenia sabulosa, and/or Rhinichthys cataractae on mean drift rate of Baetis tricaudatus and (B) comparison of treatment means using Tukey's Studentized Range test. Values with the same letter are not significantly different from one another.

(A)				
Source	d.f.	F	Significance	
Time	2,14	96.63	P < .05	
Risk	3,15	11.43	P < .0001	
Time × Risk	12,42	3.29	P < .05	

(b) Predation Risk	Mean drift rate	SE	N
	(No./ minute)		
Control (Predators absent)	3.22 ^a	0.10	5
<u>Rhinichthys cataractae</u>	5.87 ^b	0.18	4
<u>Claassenia sabulosa</u>	5.91 ^b	0.18	5
<u>Rhinichthys cataractae</u> with <u>Claassenia sabulosa</u>	5.81 ^b	0.50	5

Figure 19. Effect of food reward (low, high) and predator species (■ Rhinichthys cataractae, • Claassenia sabulosa, ▼ both predators present at the same time) on mean flight initiation distance ($\bar{x} \pm se$) by Baetis tricaudatus.

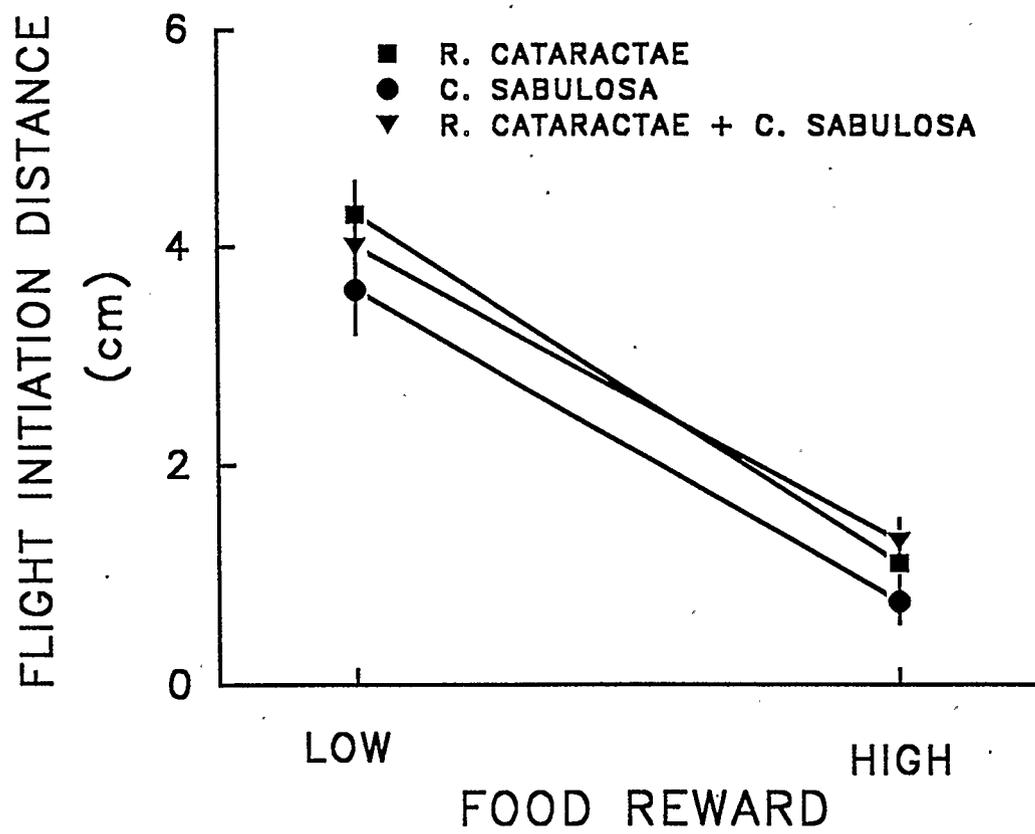
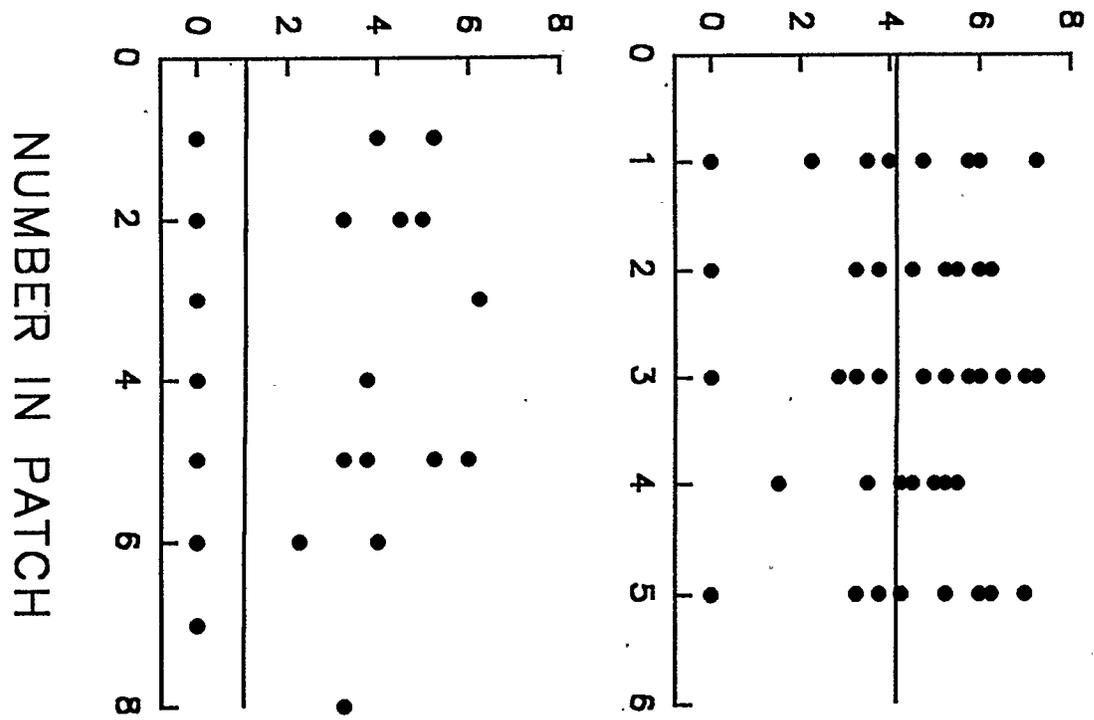


Table 13. Results of two factor ANOVA determining the effects of food reward (low, high) and predation risk (Rhinichthys cataractae, and/or Claassenia sabulosa) and the interaction of these factors on mean distance initiating a flight response by large Baetis tricaudatus.

Source	d.f.	MS	F	Significance
Food	1	12.94	153.86	P < 0.001
Predator	1	0.31	1.87	P > 0.05
Food× Predator	2	0.13	1.49	P > 0.05
Error	322	0.08		

Figure 20. Linear regressions of flight initiation distances versus number of Baetis tricaudatus in (A) low food patches and (B) high food patches containing Rhinichthys cataractae.

FLIGHT INITIATION DISTANCE (cm)



DISCUSSION

Predators exert strong spatial and temporal effects on foraging patterns of their prey, and the extent of these effects are often predator-dependent (Charnov et al. 1976, Peckarsky 1980, Rankin 1986, Soluk and Collins 1988, Rahel and Stein 1988, Diamant and Shpigel 1985). I hypothesized that predator-specific rates of mortality risk on B. tricaudatus by R. cataractae and/or C. sabulosa would produce quantitatively different time allocation patterns among risky patches. If these differences were sufficiently large B. tricaudatus would produce qualitatively different trade-offs (sensu Fraser and Huntingford's (1986) trade-off models) among predator species.

Patch use by large B. tricaudatus larvae in the absence of predators indicates that both the numbers of mayflies and time allocation within patches conformed to predictions of the Ideal Free Distribution. Thus, B. tricaudatus is capable of discriminating between low and high quality food patches (Chapter 4). Hence, foraging patch selection by B. tricaudatus can potentially involve an evaluation of food reward, a necessary requirement for the risk-balancing, risk-adjusting, and risk-reckless strategies.

Vulnerability of foragers to predators is strongly dependent upon predator species and can be complicated further if while avoiding one predator, a forager increases its vulnerability to another predator species (Charnov et al. 1976, Peckarsky 1980, Diamant and Shpigel 1985, Soluk and Collins 1988a, Rahel and Stein 1988). The level of mortality risk imposed on their prey by two or more predators foraging in the same area depends on whether a predator enhances (+), has no effect (o), or reduces foraging success (-) of the other predator. For example, Soluk and Collins (1988) found that mottled sculpins (Cottus bairdi Girard), a small stream fish, captured twice as many mayfly larvae of Ephemerella subvaria McDunnough when perlid stonefly larvae, Agnatina capitata (Pictet) were present. The presence of both predators, however, did not result in mutual benefits since perlid stonefly larvae ingested significantly fewer mayfly larvae when sculpins were present, that is, a +,- interaction (Soluk and Collins 1988a). Rahel and Stein (1988) provide evidence for mutual enhancement, such that crayfish and small mouth bass ingested significantly more johnny darters when they foraged together than separately. The question remains, however, whether such interactions among predators affect the time allocation patterns by prey among their foraging patches.

My results clearly indicate that differences in predation risk, in terms of per capita attack rates, among predator species foraging alone or together had little effect on time allocation patterns by B. tricaudatus. In fact, quantitative differences in time allocation patterns by B. tricaudatus in risky, low food and risky, high food patches among the three predator combinations were minor (<5%). Consequently, while B. tricaudatus spent more time in risky patches when they contained high food reward, they did not accept proportionately greater risk for high food reward (i.e., they did not risk-balance). When these results are compared with Fraser and Huntingford's (1986) four trade-off models the results indicate that B. tricaudatus displayed a risk-adjusting trade-off. B. tricaudatus adopted the same qualitative trade-off when risk was imposed by a single R. cataractae, a single C. sabulosa or when both predators were present in patches at the same time. These results indicate that the risk-reward trade-off exhibited by B. tricaudatus is fixed with respect to predator species.

The lack of any measurable effects of predator specific attack rates on time allocation patterns by B. tricaudatus may be due to the strong drift response exhibited by B. tricaudatus. While drift initiation distances were affected by food reward level, B. tricaudatus predominantly vacated risky patches before predators had the opportunity to

attack. Thus, the relationship between time allocation in risky patches and per capita attack rates may be poor because mayfly larvae reduce the predators opportunity to attack. In fact, attack rates by R. cataractae and C. sabulosa on B. tricaudatus during trials were low (< 4 attacks/h).

Foragers can determine patch residence times and, therefore, foraging benefits in terms of food intake, by varying the distance at which they flee from an approaching predator (Ydenberg and Dill 1986, Dill and Ydenberg 1987, Dill and Houtman 1989). My findings indicate that time allocation in risky patches by B. tricaudatus was associated with a food dependent, predator flight response. Drift initiation distances were significantly lower when B. tricaudatus were feeding in high food reward patches.

Ydenberg and Dill (1987) present two hypotheses to explain the distance at which foragers flee from an approaching predator based on perception of the predator and initiation of the flight response. The perceptual limit hypothesis states that a forager would flee an approaching predator as soon as the predator is perceived. In contrast, the economic hypothesis states that a forager would flee some time after perceiving an approaching predator. In the second scenario, flight initiation distance could be based on the costs (e.g., lost foraging opportunities) and benefits (e.g., reduced probability of being eaten) of the

response.

The ability to discriminate between these hypotheses requires specific information on a forager's perceptual abilities. This allows the experimenter to discriminate between when a forager perceives a predator and when it initiates a flight response. Because the perceptual abilities of B. tricaudatus are poorly known, I am unable to determine which hypothesis explains the food-dependent drift response. The perceptual limit hypothesis would explain the food-dependent flight response if the ability of B. tricaudatus to perceive an approaching predator is reduced when feeding in high biomass diatom mats. Alternatively, the economic hypothesis would explain the food-dependent flight response if the perceptual abilities of B. tricaudatus are unaffected by diatom biomass. If B. tricaudatus alter flight distances on the basis of costs and benefits of leaving patches, then the cost of leaving high food patches, where food intake is high, should exceed that in low food patches. My analysis of flight distances is consistent with this prediction. Additionally, because flight initiation distances were unrelated with the number of conspecifics in a patch, the flight response is unlikely to be related to grouping dilution or encounter effects. Thus, if B. tricaudatus vary flight distances on the basis of economic decisions then the response is likely related to food reward levels. Experiments which attempt to

discriminate between these two hypotheses would be useful in identifying the mechanisms underlying the behavioural trade-offs between predation risk and food reward by B. tricaudatus.

Presently, I am unable to explain unequivocally why B. tricaudatus adopted a risk-adjusting strategy compared to the other three trade-off strategies. However, in contrast to risk-reckless and risk balancers, risk-adjusters always obtain less food in the presence of a predator compared to equivalent food in a safe patch (Fraser and Huntingford 1986, Pitcher et al. 1988). The adaptive value of risk-adjusting may be related to the lack of benefits associated with foraging in risky patches. A general prediction is that risk-adjusting would be optimal if the benefits to individual fitness (e.g., growth rates, time to adult, fecundity) associated with foraging in risky patches are less than those from feeding in safe patches. Results of short-term time allocation budgets by B. tricaudatus among simultaneously available patches indicated that time in patch followed the order of safe, high food > safe, low food = risky, high food > risky, low food. If fitness consequences are consistent with time allocation budgets then growth rates, fecundity and time to adult should differ when B. tricaudatus are reared under these conditions. Experimental tests of these predictions require long-term study under different regimes of predation risk and food

reward.

CHAPTER 6

FITNESS CONSEQUENCES OF PREDATION RISK AND FOOD REWARD FOR
Baetis tricaudatus LARVAE.

INTRODUCTION

Foraging theory is based on the assumption that natural selection favours individuals making foraging decisions which maximize fitness (Stephens and Krebs 1986). However, foraging behaviour may conflict with avoiding predators. Thus, when balancing predation risk against food reward, selection should favour individuals which adopt the trade-off maximizing fitness. Numerous studies have investigated the behavioural trade-off between predation risk and food reward (e.g., Holbrook and Schmitt 1988, Pitcher et al. 1988, reviewed by Lima and Dill 1990) and have shown that patch selection are affected by these factors. Few behavioural studies, however, have made the connection between the short-term trade-offs made by a forager and long-term fitness consequences; and whether such trade-offs are optimal or adaptive (Nonacs and Dill 1990).

The fitness of an adult can be defined as the number of its offspring that reach reproductive maturity (Lloyd 1987).

This can be very difficult to determine because of high dispersal, longevity, crypsis and if adults produce many offspring. Thus, many studies measure life history traits (i.e., fitness correlates) such as growth rates, age and size at maturity, fecundity and egg size which are related to fitness (Stearns 1980, Sibley and Calow 1986).

Fraser and Huntingford (1986) describe four trade-off strategies when foragers have simultaneous access to foraging patches which differ in predation risk and food reward: risk-avoiding, risk-adjusting, risk-balancing and risk-reckless trade-offs (Chapter 1). Larval B. tricaudatus are risk-adjusters such that they allocate a small proportion of time to feed in risky patches but the reduction in the use of these patches is not inversely related to food reward. This qualitative trade-off strategy was independent of the size of B. tricaudatus (Chapter 4) and predation risk imposed by R. cataractae and/or C. sabulosa (Chapter 5). When time allocation by small and large B. tricaudatus are combined, time in safe, high food patches exceeds that in safe, low food patches, which exceeds that in risky, high patches, which exceeds that spent in risky, low food patches. Whether time allocation affects fitness correlates and whether these effects are consistent with the risk-adjusting trade-off are unknown.

A risk-adjusting trade-off can be considered the optimal trade-off between predation risk and food reward if fitness consequences are related to how a forager allocates foraging time among patches. For example, when time allocation patterns for risk-adjusters are ranked from high to low, time spent in safe, high food patches exceeded that spent in safe, low food patches which exceeded that in risky, high food patches which exceeded that in risky, low food patches. Thus, a risk-adjusting trade-off will be optimal if these fitness correlates of animals reared under fixed levels of risk and reward display similar rankings.

This prediction was tested in a laboratory stream system where B. tricaudatus larvae were reared under different levels of food reward and predation threat (i.e., predation risk). I measured larval growth rates, time to adult, adult biomass, fecundity and egg size to determine: (1) whether these fitness correlates were affected by predation risk and food reward and, (2) whether such effects were consistent with foraging time allocation patterns displayed by B. tricaudatus.

Predation risk was imposed on B. tricaudatus with a model R. cataractae. The use of model predators is a technique commonly used in behavioural studies (Milinski and Heller 1978, Pitcher et al. 1988, Peckarsky and Wilcox 1989, Peckarsky and Penton 1989a, Angradi 1992). While the use of a model does not impose mortality risk due to predation it

does elicit a drift response and the use of refugia. Both of these behaviours are likely associated with reduction in food intake. Thus, I have assumed that predation threat imposed with a model R. cataractae is perceived by B. tricaudatus as mortality risk. As a consequence I have assumed that predation threat is synonymous with predation risk. This assumption is consistent with the contention that many aquatic foragers perceive predators by the hydrodynamic waves that the predators produce (Lang 1980, Tautz 1987, Peckarsky and Penton 1989a, 1989b, Peckarsky and Wilcox 1989, Culp et al. 1991).

METHODS

Experimental design

Mayfly larvae (body length $\bar{x} \pm se = 2.8 \pm 0.01$ mm, $N = 320$) collected from the Bow River (1-7 April, 1990) were reared in small, circular plexiglas streams in which filtered, aerated water was circulated (Chapter 3). Water was pumped into each stream from one of two large (>500 L) reservoirs. Water temperature (day = 14°C, night 10°C) and diel light cycle (12 light (day): 12 dark (night)) was cycled on a diel basis. The bottom of each stream was covered with a single layer of small glass beads (diameter = 4 mm) with five rectangular plexiglas blocks (length, width, thickness = 3 × 2 × 1 cm) elevated 1 cm above the stream bottom to provide feeding patches. Previous experiments showed that Baetis feed predominantly on feeding patches with little time spent grazing glass beads (Scrimgeour unpubl. data).

The experiment represented a two-factorial design with food reward (low, high) and predation risk (safe, risky) as factors. Groups of ten larvae were reared in separate streams under one of four combinations of predation risk and food reward: (1) safe, low food, (2) safe, high food, (3) risky, low food, or (4) risky, high food. Each combination of reward and risk was replicated eight times.

Two levels of food reward (i.e., algal biomass) were established by adding phosphorus (KH_2PO_4) into one reservoir but not the other. After addition of nutrients each stream was inoculated with a 50 ml volume of algal stock removed from the upper surfaces of stones from the Bow River. Algal growth in streams receiving water from the high nutrient reservoir grew rapidly whereas algal growth in low nutrient streams was lower. Differences in algal biomasses among streams receiving low and high nutrient water produced two significantly different algal biomasses on upper surfaces of feeding substrates after two weeks. An initial set of feeding trials (described in Chapter 3) showed that these biomasses (low biomass = 0.10 mg DW/cm^2 , high biomass = 1.10 mg DW/cm^2) represented significantly different rates of food reward by small and presumably large B. tricaudatus larvae. Mean food intake rate by small B. tricaudatus on high algal biomass ($0.04 \pm 0.005 \text{ mg DW/h}$) was four times higher than on low algal biomass ($0.01 \pm 0.002 \text{ mg DW/h}$) (t-test on log transformed data, $t = 4.41$, d.f. = 14, $P < 0.01$).

Algal biomass on plexiglas substrates in each stream was monitored during trials by removing two 16 mm^2 areas at random from two substrates in each stream at weekly intervals. The algae was dried at $40 \text{ }^\circ\text{C}$ for 2 days and weighed to the nearest 0.001 mg to determine biomass. Previous algal growth experiments in small streams have shown that algal biomasses increase through time

irrespective of nutrient additions (Scrimgeour unpubl. data). The build-up of this material enters the water column, eventually clogs the central outflow column and results in mayflies drifting out of the streams. Thus, algal mats on upper surfaces of feeding patches were reduced by gently scraping these surfaces with a stout brush. This procedure also ensures that initial levels of food reward remain constant through time.

Predation risk on B. tricaudatus was imposed using a model R. cataractae which had been dried and covered with a thin plastic film. Thus, my experiments were designed to test for sub-lethal effects of a predator disturbance on fitness correlates. While this does not allow for effects of predators on larval survival, predators can potentially alter fitness correlates by initiating a drift flight response associated with movement to refugia where a forager's feeding rate may be reduced (Culp et al. 1991).

Predation risk was imposed on B. tricaudatus by moving the model at regular intervals around the bottom of risky streams six times during darkness (i.e., once every 1.5 h). On each occasion, the model was moved in an upstream direction at a velocity of 0.70 cm/s to resemble swimming and probing foraging behaviours described by Beers and Culp (1990).

Measurement of fitness correlates

Larval size was determined by removing all ten individuals from each stream at weekly intervals with a large pipette and placing them into a petri dish. Total larval body length (posterior of abdomen to anterior of head) was measured under 12 x magnification before larvae were returned to their respective stream. This procedure took less than 20 s per individual.

Individuals were reared in streams until they emerged as adults. Fine mesh netting (aperture diameter = 2 mm) was secured over the top of streams to ensure that adults could not leave the stream. Emerging adults were collected daily from each stream and preserved in 10% formalin. Adult males were dried at 40 °C for 2 days to determine biomass. Females were removed from the 10% formalin solution after 2 days and dissected under 25x magnification so that all eggs from the internal cavity could be removed and counted. The eggs and remaining female viscera were dried in separate dishes and their dry masses combined to estimate total female mass. Mean egg size (dry weight) was calculated by dividing the total dry weight of the entire egg mass by the number of eggs.

Statistical analyses

The hypothesis that initial food reward levels remained constant through time in risky and safe patches containing low and high food reward was tested with a two factor ANCOVA with algal biomass (low, high), predation risk (safe, risky) as the factors and time as the covariate. Similarly, an ANCOVA design with time as the covariate was used to test the hypothesis that larval growth was affected by predation risk, food reward and the interaction of these factors. The hypotheses that time to adult, adult body mass, fecundity and egg mass were affected by predation risk, food reward and the interaction of these factors were tested with a model 1, two factor ANOVA. Where appropriate, data were transformed to remedy inequality of variances and to satisfy the assumption of normality. Comparisons of slopes in ANCOVA designs, information on two-factor interactions and multiple range tests were conducted by performing contrast statements within SAS (SAS 1988).

RESULTS

Algal biomass on upper surfaces of feeding blocks were significantly higher in high food reward streams (ANCOVA, $F = 527.85$, d.f. = 1,214, $P < 0.001$) but were not significantly affected by predation threat, time or the interactions of any combinations of these factors. When taken together, these results indicate that food reward levels in high food reward streams were significantly greater than in low food reward streams and did not change over time. This result was independent of whether streams were designated as risky or safe.

Growth trajectories of larvae reared under different levels of predation risk and food reward (Figure 21) were significantly affected by the interaction between time, food reward and predation risk (Table 14). Comparison of growth trajectories indicated that slopes of all lines were significantly different from each other (Table 14). Thus, larval growth rates were highest when larvae were reared under safe, high food conditions which exceeded those reared under safe, low food which exceeded those reared under risky, high food which exceeded those reared under risky, low food conditions. Thus, growth in safe streams exceeded that in risky streams and in high food exceeded that in low food streams.

Figure 21. Effects of predation risk (safe, risky) and food reward (low, high) on mean larval growth rates ($\bar{x} \pm se$) of Baetis tricaudatus. Specific symbols represent different larvae reared under different combinations of predation risk and food reward: • safe, high food, ■ safe, low food, ▼ risky, high food, ▲ risky, low food. Standard error not shown if included within symbol.

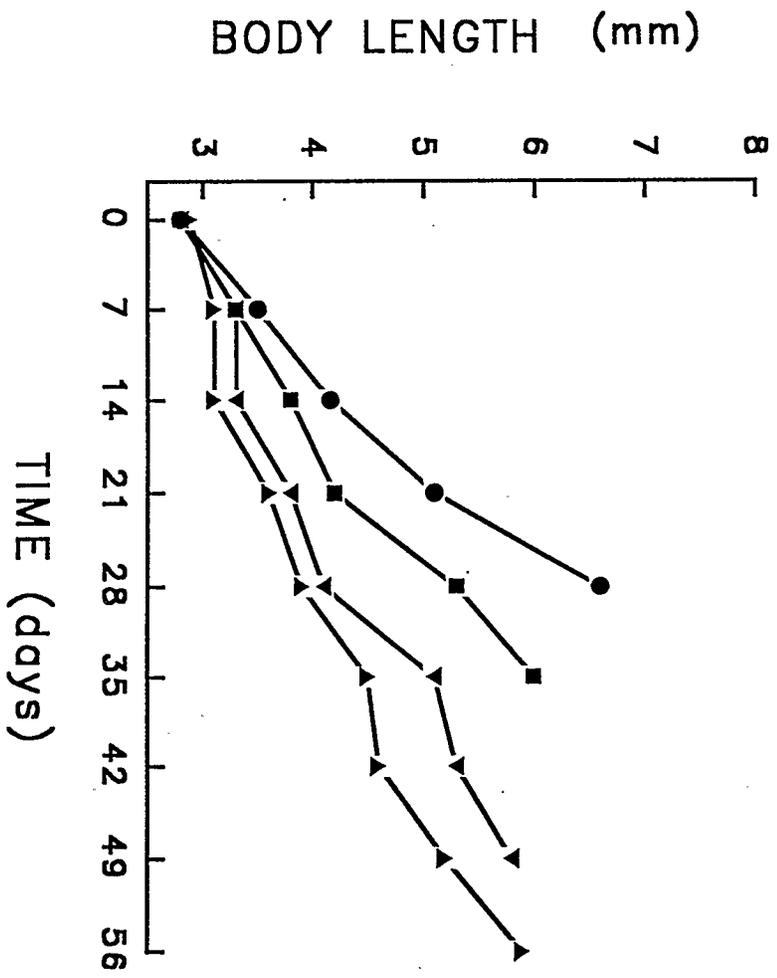


Table 14. Results of (A) ANCOVA determining the effects of predation risk (safe, risky) and food reward (low, high) and the interaction of these factors on \log_{10} mean body length of Baetis tricaudatus reared in laboratory streams and (B) comparison of growth curve slopes.

(A) ANCOVA				
Source	df	MS	F	Significance
Food	1	0.0000015	0.00	> 0.05
Risk	1	0.0070201	23.95	< 0.05
Food × Risk	1	0.0041488	14.16	< 0.05
Time	1	2.2280454	7600.46	< 0.05
Time × Food	1	0.0348749	118.97	< 0.05
Time × Risk	1	0.19937481	680.12	< 0.05
Time × Food × Risk	1	0.01695209	57.83	< 0.05
Stream (Food × Risk)	4	0.00140698	1.20	> 0.05

(B) Comparison of \log_{10} growth slopes			
Parameter	Slope	SE	Significance
Safe, high food	0.08864879	0.002	< 0.0001
Safe, low food	0.06374142	0.001	< 0.0001
Risky, high food	0.04332773	0.001	< 0.0001
Risky, low food	0.03888391	0.001	< 0.0001

Mean development time of larvae to adults (Figure 22) was significantly affected by predation risk and food reward (Table 15). Multiple range tests on main effects indicated that body mass of adults was significantly higher when reared under safe versus risky conditions and under high versus low food conditions.

Mean body mass of adult females (Figure 23) was significantly affected by predation risk and food reward (Table 16). Multiple range tests on main effects indicated that body mass of females was significantly higher when reared under safe compared with risky conditions and under high versus low food. Additionally, mean male adult mass (Figure 23) was significantly affected by the interaction between predation risk and food reward (Table 16). Analysis of contrast statements revealed a significant difference in adult mass of males reared in high food under safe versus risky conditions (Figure 23).

Mean female fecundity (Figure 24) was significantly affected by the interaction between predation risk and food reward (Table 17). Contrast statements indicated a significant difference in fecundity when larvae were reared under safe, high food conditions compared with risky, high food conditions. This result, however, is not surprising because of the positive, non-linear relationship between body mass and fecundity (Figure 25). This relationship is

Figure 22. Effects of predation risk (safe, risky) and food reward (low, high) on mean time to adult ($\bar{x} \pm se$) of (A) male and (B) female Baetis tricaudatus. Standard error not shown if included within symbol.

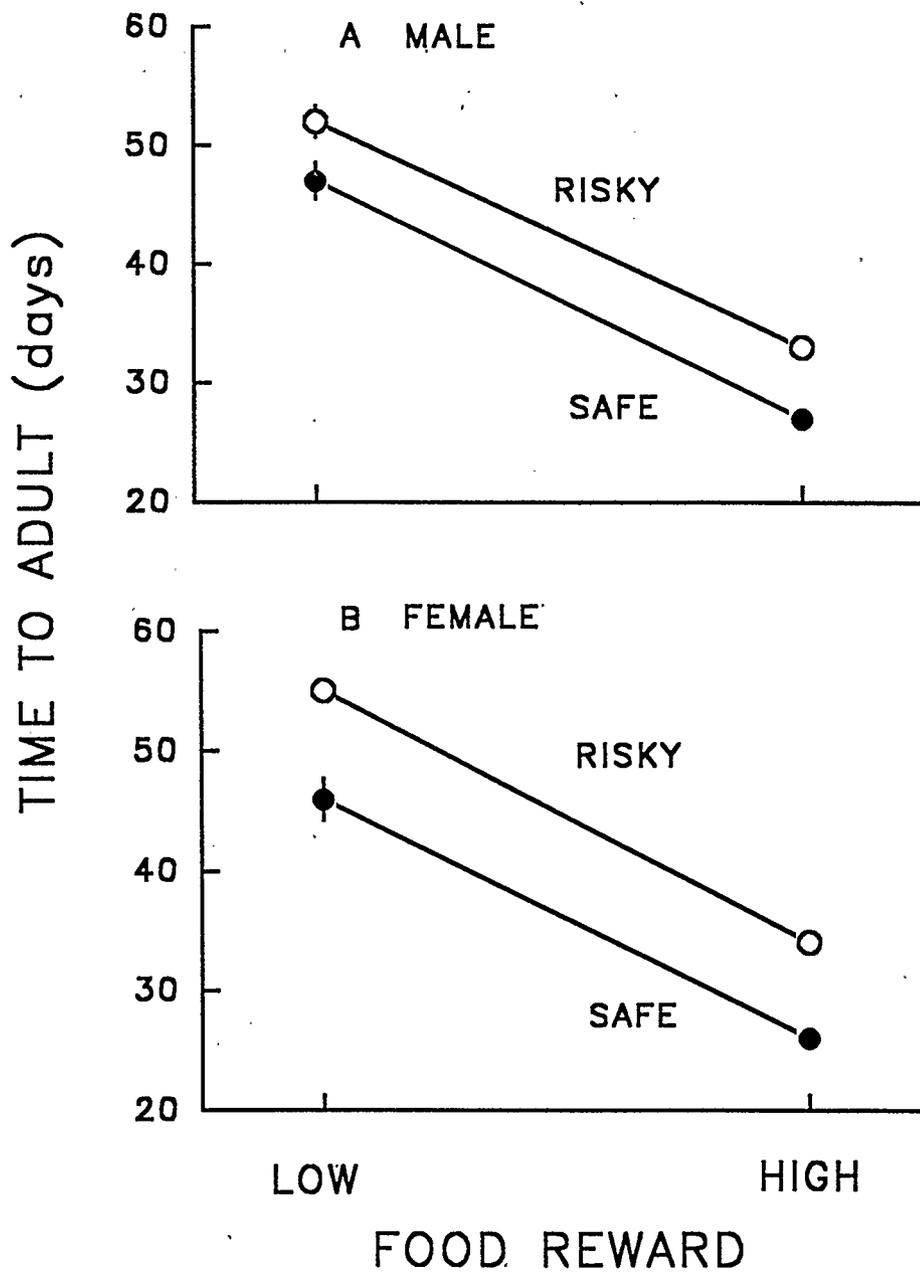


Table 15. Results of two factor ANOVA determining the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these terms on mean time to adult ($\bar{x} \pm se$) of (A) male and (B) female Baetis tricaudatus.

Source	df	MS	F	Significance
(A) Males				
Risk	1	5406.33	154.1	< 0.001
Reward	1	810.49	23.1	< 0.001
Risk × Reward	1	0.01	0.1	> 0.05
Error	99	35.09		
(B) Females				
Source	df	MS	F	Significance
Risk	1	1405.75	40.88	< 0.0001
Reward	1	9414.08	273.78	< 0.0001
Risk × Reward	1	0.31	0.01	> 0.05
Error	93	34.39		

defined as $\text{Log}_{10} \text{ fecundity} = 2.24 + 0.38 \text{ body mass (mg)}$ ($N = 104$, $r^2 = 0.89$, $P < 0.0001$). Thus, small differences in body mass observed when larvae were reared under safe, low food versus risky, high food conditions can produce large differences in fecundity.

Mean egg size (Figure 26) was significantly affected by the interaction of predation risk and food reward (Table 18). Contrast statements revealed significant differences in mean egg size of adults reared under safe, high food conditions compared with all other combinations of risk and reward. Additionally, mean egg size of adults from safe, low food streams was significantly higher than in risky, high food streams. There was no significant difference in mean egg size from adults reared under risky, low food and risky, high food patches. This latter result likely explains the significant interaction between predation risk and food reward (Table 18). Egg size was significantly related to fecundity (Linear regression: $\text{egg size (mg)} = 0.00049 + 0.0000025 \text{ fecundity}$, $N = 101$, $r^2 = 0.45$, $P < 0.01$).

Figure 23. Effects of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) body mass (dry weight) of (A) male and (B) female adult Baetis tricaudatus. Standard error not shown if included within symbol.

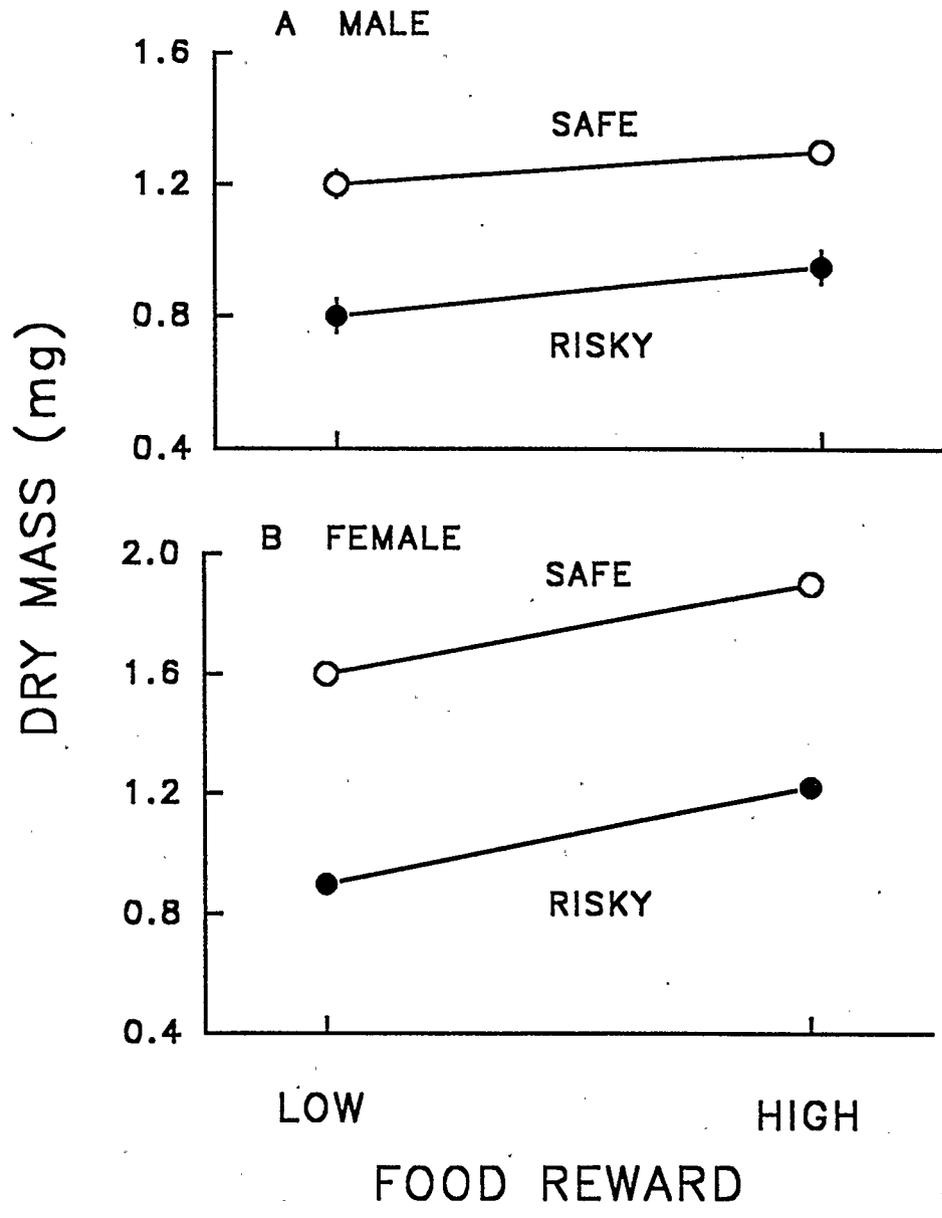


Table 16. Results of two factor ANOVA determining the effects of predation risk (safe, risky) food reward (low, high) and the interaction of these terms on mean mass of (A) male and (B) female Baetis tricaudatus.

Source	df	MS	F	Significance
(A) Male				
Risk	1	3.35	1000.00	< 0.001
Reward	1	0.56	215.92	< 0.0001
Risk × Reward	1	0.02	8.57	< 0.005
Error	100	0.002		
(B) Female				
Source	df	MS	F	Significance
Risk	1	12.23	741.50	< 0.0001
Reward	1	2.38	144.18	< 0.0001
Risk × Reward	1	0.01	0.40	> 0.05
Error	100	0.02		

Figure 24. Effects of predation risk (safe, risky) and food reward (low, high) on mean fecundity ($\bar{x} \pm se$) of Baetis tricaudatus. Standard error not shown if included within symbol.

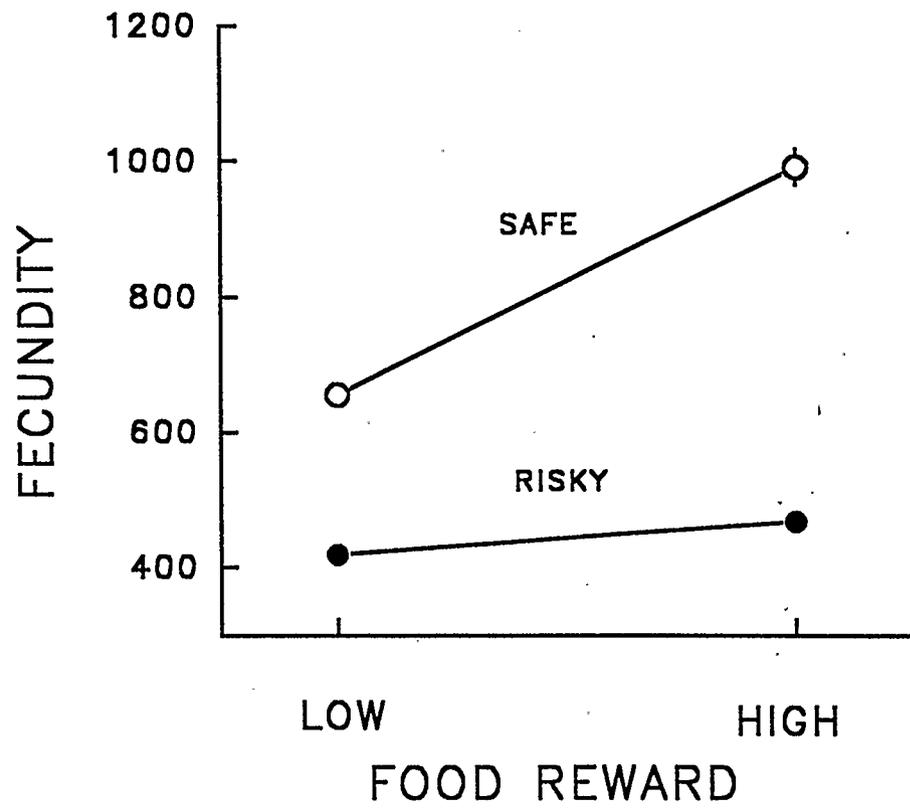


Table 17. Results of two factor ANOVA showing the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these factors on mean fecundity of Baetis tricaudatus.

Source	df	MS	F	Significance
Risk	1	3979180.3	426.9	< 0.0001
Reward	1	1002718.2	107.6	< 0.0001
Risk × Reward	1	53940.7	57.4	< 0.0001
Error	101	9321.2		

Figure 25. Relationship between body mass and fecundity for Baetis tricaudatus reared in laboratory streams under different regimes of predation risk (safe, risky) and food reward (low, high). Specific symbols represent larvae reared under different combinations of predation risk and food reward. • risky, low food, ■ risky, high food, ▲ safe, low food, ▼ safe, high food.

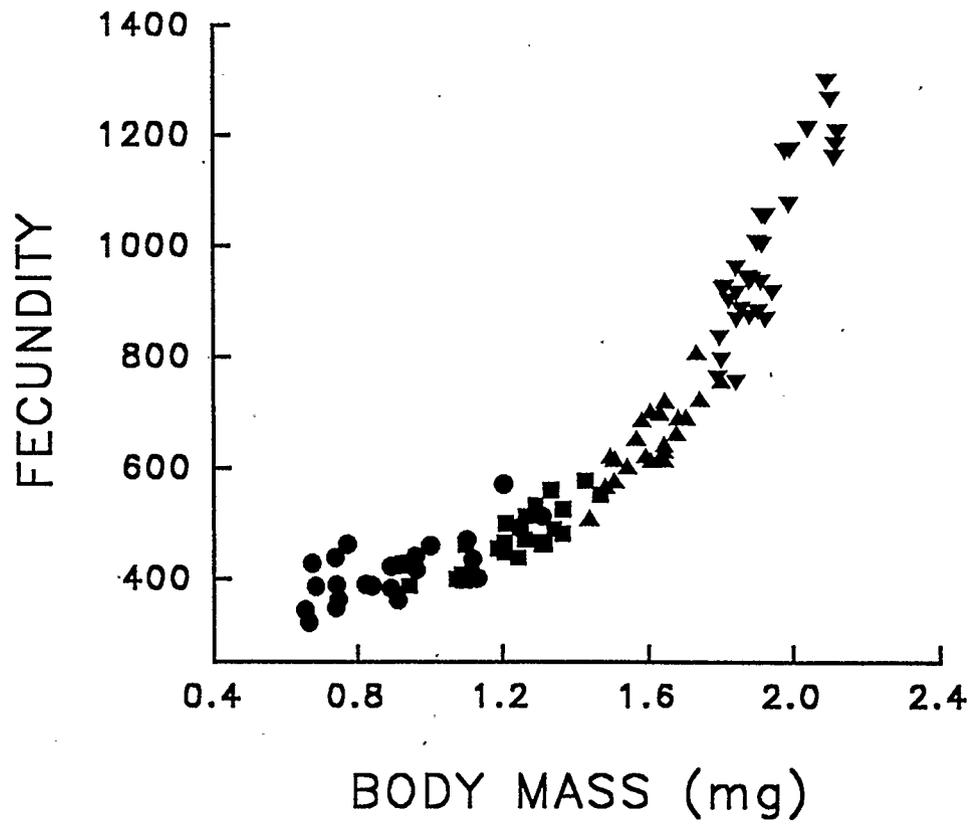


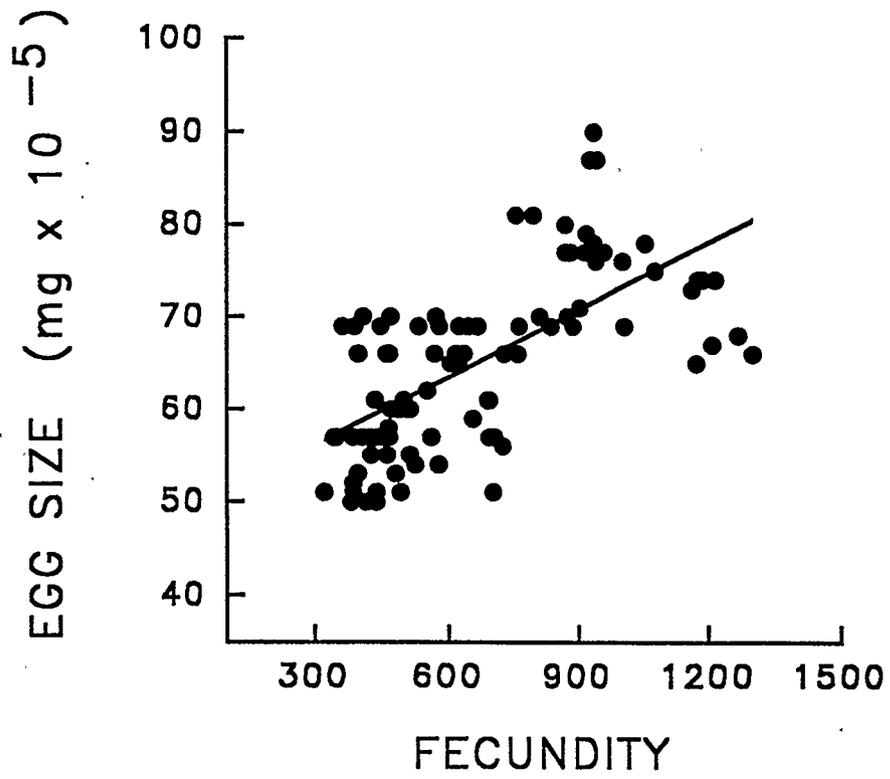
Figure 26. Effects of predation risk (safe, risky) and food reward (low, high) on mean ($\bar{x} \pm se$) egg size of adult Baetis tricaudatus. Standard error not shown if included within symbol.



Table 18. Results of two factor ANOVA showing the effects of predation risk (safe, risky), food reward (low, high) and the interaction of these terms on mean egg size of Baetis tricaudatus.

Source	df	MS	F	Significance
Risk	1	3.308×10^{-7}	90.46	< 0.0001
Reward	1	1.000×10^{-7}	27.35	< 0.0001
Risk \times Reward	1	7.997×10^{-8}	8.00	< 0.0001
Error	99	3.511×10^{-7}		

Figure 27. Linear regression of egg size versus fecundity for Baetis tricaudatus.



DISCUSSION

Foraging theory is based on the assumption that foraging decisions affect an individual's fitness. When foraging choices involve a trade-off between predation risk and food reward, foragers should adopt the trade-off which maximizes fitness. Despite the importance of this central tenet to foraging theory, few studies have determined whether behavioural trade-offs adopted by foragers are adaptive or optimal (Nonacs and Dill 1990). For example, several studies have clearly demonstrated that patch use by foragers is affected by predation risk and food reward (Holbrook and Schmitt 1988, Pitcher et al. 1988, Kohler and McPeck 1990). While these studies provide valuable information on factors affecting patch use and the proximate mechanisms involved, they do not determine whether patches differing in predation risk or food reward affect an individual's fitness.

Numerous studies demonstrate that predators alter life history characteristics of their prey (e.g., Crowl and Covich 1990, Ludwig and Rowe 1990, Skelly and Werner 1990, Blanckenhorn 1991, Feltmate and Williams 1991, Rowe and Ludwig 1991, Skelly 1991, Travers and Sih 1991). Water borne odours released by freshwater crayfish (Orconectes virilis Hagen) increased growth rates and delayed reproduction by the snail (Physella virgata) (Say) (Crowl

and Covich 1990). Skelly and Werner (1990) provided evidence that Bufo americanus Holbrook tadpoles metamorphosed at smaller sizes in the presence of the predatory anisopteran Anax junius.

Results of my study clearly demonstrate that disturbance by a model R. cataractae significantly affected larval growth, development time and adult size, fecundity, and egg mass of B. tricaudatus. Reduced growth rates of aquatic insect larvae are important for at least two reasons. First, because feeding is often restricted to larval stages (Borror 1981, Brittain 1982), adult characteristics, such as body size, are directly influenced by foraging decisions made by the larvae. Second, because fecundity is positively and non-linearly related to body size (Butler 1984, Sweeney 1984, Sweeney et al. 1986) small differences in body mass attained during larval development can produce large differences in adult fecundity.

Studies on life history patterns of larval aquatic insects have demonstrated the importance of temperature and food quantity and quality on larval growth and body size characteristics of adults (Sweeney and Vannote 1978, Anderson and Cummins 1979, Butler 1984, Sweeney 1984, Hawkins 1986, Sweeney et al. 1986, Hogue and Hawkins 1991). The effect of predators on life history characteristics of aquatic insects is poorly understood, although the recent study by Feltmate and Williams (1991) is a notable

exception. Using enclosures they found that exposure of the stonefly, Paragnetina media, to rainbow trout, Oncorhynchus mykiss (Richardson), reduced larval size, and adult condition and fecundity. My results indicate that disturbance by a model R. cataractae altered growth trajectories of larval B. tricaudatus. Growth trajectories of B. tricaudatus in safe patches were significantly higher than in risky patches. In fact, the slope of the growth trajectory of larvae reared under risky, low food conditions was less than half that when larvae experienced safe, high food conditions. The reduction in growth rates under different food and predator regimes is consistent with the contention of Stearns and Koella (1986) that a common response for age at maturity is one in which organisms mature at a larger size when growth is rapid and later at a smaller size when growth is slow (i.e., they adopt a slow life style (Sih 1987)).

Analysis of development time measured as time from small larvae ($\bar{x} = 2.8$ mm) to adult and adult mass indicated both variables were phenotypically plastic. Variation in mayfly adult size and mass have been reported elsewhere (Butler 1984, Sweeney 1984, Hawkins 1986). However, the results from my study are amongst the first to indicate that life-history attributes of aquatic insects can be significantly affected by predation risk. The amount of variation in adult characteristics explained by predation

risk is unclear, but represents an important consideration for those attempting to understand life history dynamics. The selective advantage of large adult body size is often interpreted as resulting from the positive correlation between body size and fecundity, although other potential benefits can exist. For example, large adult body size could increase mating success if larger adults compete more intensely for higher quality mates in mating swarms (Allan and Flecker 1989) as shown by Flecker et al. (1988) adult male Epeorus longimanus Eaton (Heptageniidae) in a Rocky Mountain stream.

The relationship between egg size and fecundity has been addressed from both theoretical and empirical perspectives (Lack 1947, 1967, 1968, Smith and Fretwell 1974, Jennings and Calow 1975, Stearns 1976, Lloyd 1987, Wilbur 1977, Rohwer 1988, Godfray and Parker 1991, Sinervo and Licht 1991). The nature of this trade-off is thought to be the result of balancing the benefits of more fit offspring (i.e., larger offspring from larger eggs) against the reduction in number of offspring. A negative relationship between these variables has been commonly observed (Ware 1975, Harper 1977, Manning 1978, Stanton 1984, Mann and Mills 1985, Brodie and Ducey 1989, Cook et al. 1989, Ford and Seigel 1989, Sinervo and Licht 1991, Shipley and Dion 1992). Alternatively, several studies have found no relationship between these variables (Duncan 1987,

Rohwer 1988). However, few studies have shown egg size to be positively related with fecundity. Coleman and Whittall (1990) found a positive relationship between egg size and fecundity for Bengalese finch (Lonchura striata) (Eisner) when clutch size ranged from four to seven. Clifford (1970) observed positive relationships between body size and fecundity and body size and egg size for the leptophlebid mayfly, Leptophlebia cupida (Say). While Clifford did not show the relationship between fecundity and egg size, the strong non-linear relationships of body size with fecundity and egg size suggest that fecundity and egg size were also positively related.

My experiments showed a variable ($r^2 = 0.45$) yet significant ($P < 0.001$), positive relationship between egg size and body mass for B. tricaudatus. As large eggs can only be produced by a reduction in egg number the positive relationship between egg size and fecundity suggests that larger females sacrifice fecundity against producing larger eggs. The importance of this positive relationship is unclear and requires longer term study, but would have important consequences for larval fitness and population density if hatching success, larval growth rates and adult characteristics such as development time, biomass and survival are positively related to egg size.

Foraging behaviour is often investigated using short term experiments, the duration of which often span only

minutes to hours. Results from such studies are invariably interpreted by assuming that short-term behaviours have longer-term fitness consequences. However, there is little evidence directly linking foraging and reproductive success (Blanckenhorn 1991). The way in which foragers allocate foraging time among patches differing in risk and reward can be considered optimal for some foragers if time allocation patterns are concordant with fitness consequences associated with foraging in those patches. Blanckenhorn (1991) investigated the relationship between short-term patch choice by water striders (Gerris remigis Say) and long term fitness consequences, and showed that selection for higher food patches increased both foraging success and fecundity.

I have shown that patch use by larvae of B. tricaudatus is enhanced when patches contain high food compared to low food and when predators are absent (i.e., safe) compared to when predators are present (i.e., risky). Based on Fraser and Huntingford's trade-off models (Chapter 1) B. tricaudatus larvae are risk-adjusters, allocating a small proportion of time to feeding in risky patches although the reduction in the use of these patches is not inversely related to food reward.

Allocation of foraging time by B. tricaudatus among patches can be ranked from high to low with time in safe, high food patches exceeding that in safe, low food patches exceeding that in risky high food patches exceeding that in

risky, low food patches. Similarly, fitness correlates can also be ranked from most beneficial to least beneficial. Comparison of rankings between time allocation patterns and fitness correlates were concordant for three (larval growth rates, adult mass, fecundity) of the five fitness measurements. Rankings between time allocation and fitness correlates for the remaining fitness correlates (time to adult, egg size) were concordant with the more general prediction of the risk-adjusting strategy, such that fitness consequences in safe patches exceeded those in risky patches. When taken together, these results suggest that the risk-adjusting trade-off is the optimal solution for B. tricaudatus when foraging patches vary in both predation risk and food reward. Whether fitness consequences of the risk-balancing strategy observed for schooling minnows by Pitcher et al. (1986), colonial ants (Nonacs and Dill 1990) and dipteran larvae (Macchiusi and Baker in press) are also optimal remains to be determined. The combination of short-term behavioural experiments and long-term studies of fitness consequences will undoubtedly be a useful approach to investigate the adaptive value of behavioural trade-offs.

CHAPTER 7

SUMMARY

Behavioural trade-offs are common in ecological systems (Sibley and Calow 1986, Dill 1990). Foraging patches often differ in foraging benefits (e.g., food reward) and costs (e.g., mortality risk due to predation). Thus, when balancing predation risk against food reward, natural selection must favour individuals which exhibit behaviours that maximize fitness.

Fraser and Huntingford (1986) provide a conceptual framework in which to examine the effects of predation risk and food reward on foraging patch selection. They identify risk-avoiding, risk-adjusting, risk-balancing and risk-reckless strategies. Several studies have used these models to investigate the predation risk - food reward trade-off and have shown that three-spined sticklebacks (Gasterosteus aculeatus) are risk-adjusters, whereas schooling minnows (Phoxinus), and colonial ants (Lasius pallitarsis) are risk-balancers (Fraser and Huntingford 1986, Pitcher et al. 1988, Nonacs and Dill 1990). Three important questions, however, remain unanswered. First, do different sized foragers allocate the same amount of time among feeding patches when they experience different levels of mortality risk? Second,

are time allocation patterns affected by predator species when the level of prey (i.e., forager) mortality risk differs between predators? If quantitative differences in time allocation patterns are sufficiently large they can produce a qualitatively different trade-off (e.g., risk-adjusting to risk-balancing). Third, do foraging patches differing in predation risk and food reward affect a foragers fitness and are such effects consistent with the behavioural trade-off strategy displayed by a forager?

The objectives of this thesis were: (1) to determine whether the trade-off between predation risk and food reward is affected by forager size, (2) to determine whether foragers adopt the same trade-off strategy to different predator species, (3) to determine whether selection of foraging patches, in terms of time allocation patterns, differing food reward and predation risk affect forager fitness, and (4) whether such fitness effects are consistent with time allocation patterns.

The ability to address these objectives is contingent upon finding a food web where: (1) a forager's mortality risk due to predation is related to its size; (2) mortality risk from two predator species is predator species-specific, and (3) where food reward levels display significant between patch variation. Thus, to determine whether the algal - B. tricaudatus - C. sabulosa and/or R. cataractae food web fulfilled these conditions, I determined spatial and

temporal overlap between B. tricaudatus and their predators, the level of mortality risk that each predator species imposed on B. tricaudatus larvae and whether food reward levels varied significantly among patches.

Analysis of diel activity patterns of B. tricaudatus indicated that small larvae fed throughout the day and night (i.e., aperiodic activity pattern) whereas large larvae were almost exclusively nocturnal foragers (Chapter 2). Stomach content analyses of C. sabulosa indicated they also fed during the hours of darkness and a nocturnal feeding periodicity has been reported for R. cataractae (Culp 1989). Gut content analyses of C. sabulosa and R. cataractae indicated that both predators consumed more small than large B. tricaudatus larvae but the level of mortality risk imposed by R. cataractae was almost twice that by C. sabulosa (Chapter 2). Lastly, algal biomass on upper stone surfaces from the Bow River was highly variable and represented significantly different rates of food intake among 25%, median and 75% biomass quartiles. When taken together, these results indicate that the algal - B. tricaudatus - C. sabulosa & R. cataractae is an appropriate food web to test hypotheses regarding forager size-specific trade-offs of food reward and predation risk forager size-specific trade-off as affected by predator species.

Allocation of foraging time by B. tricaudatus among patches differing in food reward and predation risk imposed

by R. cataractae was significantly affected by predation risk and food reward. These effects were observed for both small and large B. tricaudatus (Chapter 4). The majority of foraging time by larvae was spent in safe rather than in risky patches. For small larvae, the presence of a predator lowered patch occupation by a constant proportion irrespective of whether such patches contained low or high food reward. In contrast, time allocation in risky patches by large B. tricaudatus increased four-fold when risky patches contained high food reward. Increased time allocation in risky patches was associated with a food-dependent drift response. While small and large B. tricaudatus displayed quantitative differences in time allocation patterns among risky patches, both adopted a risk-adjusting trade-off strategy when risky patches contained R. cataractae (Chapter 4).

Numerous studies have shown that the intensity of a forager's response to a predator is positively related to its vulnerability (Stein and Magnuson 1976, Peckarsky 1980, Werner et al. 1983a, Power 1984). Thus, it is likely that the amount of time that a forager allocates to feeding in risky patches should differ when they contain different predators. A general prediction is that the amount of time spent in risky patches should be inversely related to the level of mortality risk. Field estimates of mortality risk on B. tricaudatus indicated that risk from R. cataractae

was higher than from C. sabulosa. Despite this difference, quantitative difference in time allocation patterns by B. tricaudatus among foraging patches were minor when risky patches contained R. cataractae and/or C. sabulosa. As a result, the trade-off between predation risk and food reward was not significantly affected by predator species.

Foraging theory is based on the assumption that natural selection favours individuals making foraging decisions which maximize fitness. Obtaining food often conflicts with avoiding predators. Thus, when balancing predation risk against food reward, selection should favour individuals which adopt the trade-off maximizing fitness. I have shown that B. tricaudatus are risk-adjusters and that the trade-off is not affected by B. tricaudatus size (Chapter 4) or whether risky patches contain a single R. cataractae and/or a single C. sabulosa (Chapter 5). Two unanswered questions remain. First, are fitness correlates affected by predation risk and food reward, and second, whether such effects are consistent with short-term time allocation patterns. A general prediction of the risk-adjusting trade-off is that fitness benefits in safe patches exceed those in risky patches. Additionally, because time allocated to feeding in high food patches exceeded that in low food patches, fitness benefits in high food patches should exceed those in low food patches.

Results of long-term growth trials under different

combinations of predation risk and food reward indicated that larval growth trajectories, time to adult, adult body mass, fecundity and egg size were significantly affected by predation risk and food reward. When fitness benefits were ranked from high to low, larval growth, adult body mass and fecundity were concordant with time allocation patterns such that fitness consequences in safe, high food patches > safe, low food patches > risky, high food patches > risky, low food patches. The remaining two fitness measurements (i.e., time to adult, egg size) were consistent with the more general prediction that fitness consequences in safe conditions should exceed those in risky conditions. The strong concordance between time allocation patterns and fitness consequences supports the hypothesis that the risk-adjusting trade-off is the optimal strategy for B. tricaudatus.

In summary, I have shown that when foraging patches vary in predation risk and food reward B. tricaudatus adopt a risk-adjusting trade-off strategy. This trade-off was unaffected by B. tricaudatus size or predator species, that is, when risk was imposed by R. cataractae and/or C. sabulosa. Additionally, long-term experiments indicate that predation risk and food reward significantly affect fitness correlates of B. tricaudatus. These effects are consistent with the risk-adjusting strategy suggesting that this trade-off strategy is the optimal solution for B. tricaudatus when

foraging patches differ in predation risk and food reward.

This research has raised a number of important questions associated with how a forager allocates feeding time and fitness consequences associated with those patterns. Here I pose a number of questions which warrant further study. First, what is the underlying basis for the food dependent drift response? The answer to this question requires size-specific information on the perceptual abilities of B. tricaudatus. Second, will subsequent studies on the behavioural trade-off between predation risk and food reward show strong concordance between short term patterns in time allocation and long-term fitness consequences as observed in this study? Third, what is the underlying fitness benefit of the positive relationship between fecundity and egg size? Further research to answer these questions will provide important information on behavioural trade-offs and increase our understanding of the proximate and ultimate factors producing spatial and temporal patterns in ecological systems.

REFERENCES

- Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70: 999-1007.
- Allan, J. D. 1978. Trout predation and the size composition of stream drift. *Limnology and Oceanography* 23: 1231-1237.
- Allan, J. D. 1982. Feeding habits and prey consumption of three setipalpiid stoneflies (Plecoptera) in a mountain stream. *Ecology* 63: 26-34.
- Allan, J. D. 1984. The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos* 42: 68-76.
- Allan, J. D., and A. S. Flecker. 1989. The mating biology of a mass swarming mayfly. *Animal Behaviour* 37: 361-371.
- Allan, J. D., Flecker, A. S., and N. C. McClintock. 1986. Diel epibenthic activity of mayfly nymphs, and its non-concordance with behavioural drift. *Limnology and Oceanography* 31: 1057-1065.
- Allan, J. D., Flecker, A. S., and N. L. McClintock. 1987. Prey size selection by carnivorous stoneflies. *Limnology and Oceanography* 32: 864-872.
- Anderson, N. H., and K. W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. *Journal of the Fisheries Research Board of Canada* 36: 335-342.
- Angradi, T. R. 1992. Effects of predation risk on foraging behavior of juvenile rainbow trout. *Canadian Journal of Zoology* 70: 355-360.
- Beers, C. B. and J. M. Culp. 1990. Plasticity in foraging behavior of a lotic minnow (*Rhinichthys cataractae*) in response to different light intensities. *Canadian Journal of Zoology* 68:101-105.
- Bence, J. R., and W. W. Murdoch. 1986. Prey size selection by the mosquitofish: relation to optimal diet theory. *Ecology* 67: 324-336.
- Blanckenhorn, W. V. 1991. Fitness consequences of foraging success in water striders (*Gerris remigis*; Heteroptera: Gerridae). *Behavioral Ecology* 2: 46-55.

- Borror, D. J., D. M. DeLong, and C. A. Triplehorn. 1981. An introduction to the study of aquatic insects. 5th edition. Saunders College Publishing, Philadelphia, Pennsylvania, USA.
- Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. *Ecology* 71: 2343-2344.
- Brittain. J. E. 1982. The biology of mayflies. Annual review of Entomology 27: 119-147.
- Brodie, E. D., and P. K. Ducey. 1989. Allocation of reproductive investment in the redbelly snake Storeria occipitomaculata. *American Midland Naturalist* 122: 51-58.
- Butler, M. G. 1984. Life histories of aquatic insects. Pages 24-55 in V. H. Resh and D. M. Rosenberg (eds). The ecology of aquatic insects. Praeger, New York, New York, USA.
- Cerri, R. D., and D. F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *American Naturalist* 121: 552-561.
- Charnov, E. L., Orians, G. H., and K. Hyatt. 1976. ecological implications of resource depression. *American Naturalist* 110: 247-259.
- Clifford, H. F. 1970. Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size. *Canadian Journal of Zoology* 48: 305-316.
- Clifford, H. F. 1991. Aquatic invertebrates of Alberta. University of Alberta Press, Alberta, Canada. 538 pp.
- Coleman, R. M., and R. D. Whittall. 1990. Variation in egg weight in the Bengalese finch (Lonchura striata var. domestica). *Canadian Journal of Zoology* 68: 272-275.
- Colletti, P. J., Blinn, D. W., Pickart, A., and V. T. Wagner. 1987. Influence of different densities of the mayfly grazer Heptagenia criddlei on lotic diatom communities. *Journal of the North American Benthological Society* 6: 270-280.

- Cook, W. J., B. P. Smith and R. J. Brooks. 1989. Allocation of reproductive effort in female Arrenurus spp. water mites (Acari: Hydrachnidia; Arrenuridae). *Oecologia* 79: 184-188.
- Cooper, S. D. 1984. The effects of trout on water striders in stream pools. *Oecologia* 63: 376-379.
- Cowan, C. A. and B. L. Peckarsky. in press. Diel feeding and positioning periodicity of a grazing mayfly nymph in a trout stream and a fishless stream. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Crowl, T. A. , and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* 247: 949-951.
- Culp, J. M. 1989. Nocturnally constrained foraging of a lotic minnow (Rhinichthys cataractae). *Canadian Journal of Zoology* 67: 2008-2012.
- Culp, J. M., Boyd, I and N. E. Glozier. 1988. An improved method for obtaining gut contents from small, live fishes by anal and stomach flushing. *Copeia* 1988: 1079-1082.
- Culp, J. M., N. E. Glozier, and G. J. Scrimgeour. 1991. Reduction of predation risk under the cover of darkness: Avoidance responses of mayfly larvae to a benthic fish. *Oecologia* 85: 163-169.
- Culp, J. M., H. Hamilton, A. Sosiak and R. W. Davies. in press. Longitudinal zonation of the biota and water quality of a northern temperate river system in Alberta, Canada. In C. D. Becker and D. A. Neitzel (eds). *Water Quality of North American River Systems*. Batell Press.
- Diamant, A. and M. Shpigel. 1985. Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels. *Environmental Biology of Fishes* 13: 153-159.
- Dill, L. M. 1987. Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Canadian Journal of Zoology* 65: 803-811.
- Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish, Melanchromis chipokae. *Environmental Biology of Fishes* 27: 147-152.

- Dill, L. M. and A. H. G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (Oncorhynchus kisutch). Behavioural Ecology and Sociobiology 16: 65-71.
- Dill, L. M. and R. Houtman. 1989. The influence of distance of refuge on flight initiation distance in the gray squirrel (Sciurus carolinensis). Canadian Journal of Zoology 67: 233-235.
- Dill, L. M., and R. C. Ydenberg. 1987. The group size flight distance in water striders (Gerris remigis). Canadian Journal of Zoology 65: 223-226.
- Dixon, S.M., and R. L. Baker. 1988. Effects of fish feeding and growth of larval Ischnura verticalis. Canadian Journal of Zoology 65: 2276-2279.
- Downing, J. A. 1981. In situ foraging responses of three species of littoral cladocerans. Ecological Monographs 51: 85-103.
- Dudley, T. L. and C. M. D'Antonio. 1991. The effects of substrate texture, grazing and disturbance on macroalgal establishment in streams. Ecology 72: 297-309.
- Duncan, D. C. 1987. Variation and heritability in egg size of the Northern Pintail. Canadian Journal of Zoology 65: 992-996.
- Edmunds, G. F., S. L. Jensen, and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis, USA.
- Elliott, J. M. 1968. The daily activity patterns of mayfly nymphs (Ephemeroptera). Journal of Zoology 155: 201-222.
- Feltmate, B. W. and D. D. Williams. 1991. Evaluation of predator-induced stress on field populations of stoneflies (Plecoptera). Ecology 72: 1800-1806.
- Fisher, S. G., L. J. Gray, N. B. Grimm and D. E. Busch. 1982. Temporal variation in a desert stream ecosystem following a flash flooding. Ecological Monographs 52: 93-110.
- Flecker, A. S. in press. Fish predation and the evolution of diel drift periodicity in aquatic insects: evidence from neotropical streams. Ecology.

- Flecker, A. S., J. D. Allan and N. L. McClintock. 1988. Swarming and sexual selection in a Rocky Mountain mayfly. *Holarctic Ecology* 11: 280-285.
- Ford, N. B. and R. A. Seigel. 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica* 45: 75-83.
- Fraser, D. F., and E. E. Emmons. 1984. Behavioral response of blacknose dace (Rhinichthys atratulus) to varying densities of predatory creek chub (Semotilus atromaculatus). *Canadian Journal of Fisheries and Aquatic Sciences* 41: 364-370.
- Fraser, D. F., and F. A. Huntingford. 1986. Feeding and avoiding predation hazard: the behavioral response of the prey. *Ethology* 73: 56-68.
- Fretwell, S. D., and H. L. Jr. Lucas. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*. I. Theoretical Development 19: 16-36.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection when foraging under predation hazard: a model and a test with stream-dwelling minnows. *Ecology* 68: 1856-1862.
- Glozier, N. E. 1989. The effects of biotic and abiotic factors on the foraging success of a lotic minnow, Rhinichthys cataractae. M. Sc thesis, University of Calgary, Calgary, Alberta, Canada, 151 pp.
- Godfray, H. C. J., and G. A. Parker. 1991. Clutch size, fecundity and parent-offspring conflict. *Transactions of the Royal Society (London)* 332: 67-79.
- Graesser, A. and P. S. Lake. 1984. Diel changes in the benthos of stones and of drift in a southern Australian stream. *Hydrobiologia* 111: 153-160.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Hart, D. D. 1985. Grazing insects mediate algal interactions in a stream benthic community. *Oikos* 44: 40-46.
- Harvey, B. C., Cashner, R. C., and W. J. Mathews. 1988. Differential effects of largemouth and smallmouth bass on habitat use by stoneroller minnows in stream pools. *Journal of Fish Biology* 33: 481-487.

- Hassell, M. P. and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43: 567-594.
- Hatto, J. and J. L. Harper. 1969. The control of slugs and snails in British cropping systems, specially grassland. *International Copper Research Association Project 115(A)*: 1-25.
- Hawkins, C. P. 1986. Variation in individual growth rates and population densities of ephemereid mayflies. *Ecology* 67: 1384-1395.
- Helfman, G. S. and D. L. Winkelman. 1991. Energy trade-offs and foraging mode choice in American eels. *Ecology* 72: 310-318.
- Hill, W. R. and A. W. Knight. 1987. Experimental analysis of the grazing interaction between a mayfly and stream algae. *Ecology* 68: 1955-1965.
- Hogue, J. N., and Hawkins, C. P. 1991. Morphological variation in adult aquatic insects: associations with developmental temperature and seasonal growth patterns. *Journal of the North American Benthological Society* 10: 309-321.
- Holbrook, S. J., and R. J. Schmitt. 1988. The combined effects of predation risk and food reward on patch selection. *Ecology* 69: 125-134.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 295-320.
- Holmes, W. G. 1984. Predation risk and foraging behavior. *Behavioural Ecology and Sociobiology* 15: 293-301.
- Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology* 67: 737-748.

- Holomuzki, J. R. and T. M. Short. 1988. Habitat use and fish avoidance behaviours by the stream-dwelling isopod Lirceus fontinalis. *Oikos* 52: 79-86.
- Holomuzki, J. R. and T. M. Short. 1990. Ontogenetic shifts in habitat use and activity in a stream-dwelling isopod. *Holarctic Ecology* 13: 300-307.
- Jennings, J. B. and P. Calow. 1975. The relationship between fecundity and the evolution of entoparasitism. *Oecologia* 21: 109-115.
- Johnson, J. H., 1981. Food habits and dietary overlap of perlid stoneflies (Plecoptera) in a tributary of Lake Ontario. *Canadian Journal of Zoology* 59: 2030-2037.
- Johnson, J. H., 1983. Diel food habits of two species of setipalpi stoneflies (Plecoptera) in tributaries of the Clearwater River, Idaho. *Freshwater Biology* 13: 105-111.
- Kohler, S. L. 1983. Positioning on substrates, positioning changes, and diel drift periodicities of mayflies. *Canadian Journal of Zoology* 61: 1362-1368.
- Kohler, S. L. 1984. Search mechanism of a stream grazer in patchy environments: the role of food abundance. *Oecologia* 62: 209-218.
- Kohler, S. L. 1985. Identification of stream drift mechanisms: an experimental and observational approach. *Ecology* 66: 1749-1761.
- Kohler, S. L., and M. A. McPeck. 1989. Predation risk and the foraging behavior of competing stream insects. *Ecology* 70: 1811-1825.
- Kovalak, W. P. 1979. Day-night changes in stream benthos density in relation to current velocity. *Archives fur Hydrobiologie* 87: 1-18.
- Krebs, J. R. 1979. Foraging strategies and their social significance. pp 225-270. In Marler, P. and Vandenberg, J. G. (eds). *Handbook of behavioral neurobiology*. Vol 3. Social behavior and communication. Plenum Press, New York, USA.

- Krebs, J. R., and N. B. Davies 1978. Behavioural Ecology: An Evolutionary approach, 1st edition (eds). Blackwell Scientific Publications, Oxford.
- Krebs, J. R., and N. B. Davies. 1984. Behavioural Ecology: An Evolutionary approach, 2nd edition (eds). Blackwell Scientific Publications, Oxford.
- Krebs, J. R., and N. B. Davies. 1991. Behavioural Ecology: An Evolutionary approach, 3rd edition (eds). Blackwell Scientific Publications, Oxford.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89: 309-352.
- Lack, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18: 125-128.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.
- Lamberti, G. A., Ashkensas, L. R., Gregory, S. V. and A. D. Steinman. 1987. Effects of three herbivores on periphyton communities in laboratory streams. *Journal of the North American Benthological Society* 6: 92-104.
- Lang, H. H. 1980. Surface wave discrimination between prey and non-prey by the backswimmer Notonecta glauca L. (Hemiptera, Heteroptera). *Behavioural Ecology and Sociobiology* 6: 233-246.
- Lehman, J. T. and C. G. Sandgren. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnology and Oceanography* 30: 34-46.
- Lehmkuhl, D. M. 1976. Mayflies. *Blue Jay* 34: 70-81.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* 66: 60-67.
- Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Lima, S. L., T. L. Valone, and T. Caraco. 1985. Foraging - efficiency - predation - risk trade-off in the grey squirrel. *Animal Behaviour* 33: 155-165.

- Lloyd, D. G. 1987. Selection of offspring size at interdependence and other size-versus-number strategies. *American Naturalist* 129: 800-817.
- Ludwig, D. and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* 135: 686-707.
- Macchiusi, F. and R. L. Baker. in press. Effects of predators and food availability on activity and growth of Chironomus tentans (Chironomidae: Diptera). *Freshwater Biology*.
- Malmqvist, B. 1988. Downstream drift in Madieran levadas: tests of hypotheses relating to the influence of predators on the drift of insects. *Aquatic Insects* 10: 141-152.
- Malmqvist, B., and P. Sjostrom. 1980. Prey size and feeding patterns in Dinocras cephalotes (Perlidae). *Oikos* 35: 311-316.
- Malmqvist, B., and P. Sjostrom. 1988. Stream drift as a consequence of disturbance by invertebrate predators. *Oecologia* 74: 396-403.
- Mann, R. H. K. and C. A. Mills. 1985. Variations in the sizes of gonads, eggs and larvae of the dace, Leuciscus. *Environmental Biology of Fishes* 13: 277-287.
- Manning, T. H. 1978. Measurements and weights of eggs of the Canadian Goose, Branta canadensis, analysed and compared with those of other species. *Canadian Journal of Zoology* 56: 676-687.
- Milinski, M. and R. W. Heller. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (Gasterosteus aculeatus). *Nature* 275: 642-644.
- Milinski, M. 1985. The patch choice model: no alternative to balancing. *American Naturalist* 125: 317-320.
- Minshall, G. W. 1978. Autotrophy in stream ecosystems. *Bioscience* 28: 767-771.
- Morikawa, K. 1988. Differences in plating efficiency of bacteria from river epilithon sampled from upper and lower surfaces of artificial substrata. *Microbiological Ecology* 15: 217-225.

- Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models. Third edition. Irwin, USA.
- Newman, J. A., G. M. Recer, S. M. Zwicker, and T. Caraco. 1988. Effects of predation hazard on foraging "constraints": patch use strategies in grey squirrels. *Oikos* 53: 93-97.
- Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microfauna. *Ecology* 58: 1020-1032.
- Nonacs, P., and L. M. Dill. 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. *Ecology* 71: 1886-1892.
- Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free distributions. *Animal Behaviour* 34: 1222-1242.
- Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology* 61: 932-943.
- Peckarsky, B. L. 1991. Habitat selection by stream-dwelling stoneflies. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1069-1076.
- Peckarsky, B. L. 1987. Mayfly cerci as defense against stonefly predation: deflection and detection. *Oikos* 48: 161-170.
- Peckarsky, B. L. and M. A. Penton. 1989a. Mechanisms of prey selection by stream-dwelling stoneflies. *Ecology* 70: 1203-1218.
- Peckarsky, B. L. and M. A. Penton. 1989b. Early warning lowers risk of stonefly predation for a vulnerable mayfly. *Oikos* 54: 301-309.
- Peckarsky, B. L. and R. S. Wilcox. 1989. Stonefly nymphs use hydrodynamic cues to between prey. *Oecologia* 54: 301-309.

- Pennak, R. W. 1978. Freshwater invertebrates of the United States. John Wiley and Sons, Toronto, Ontario, Canada. 803 pp.
- Pierce, C. L. 1988. Predator avoidance, microhabitat shift, and risk-sensitive foraging in larval dragonflies. *Oecologia* 77: 81-90.
- Pierce, G. J. and J. G. Ollason. 1991. Eight reasons why optimal foraging is a complete waste of time. *Oikos* 49: 111-118.
- Pitcher, T. J., S. H. Lang, and J. A. Turner. 1988. A risk-balancing trade off between foraging rewards and predation hazard in a shoaling fish. *Behavioral Ecology and Sociobiology* 22: 225-228.
- Ploskey, G. R., and A. V. Brown, 1980. Downstream drift of the mayfly Baetis flavistriga as a passive phenomenon. *American Midland Naturalist* 104: 405-409.
- Power, M. E. 1984. Depth distribution of armoured catfish: predator induced resource avoidance. *Ecology* 65: 523-528.
- Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: the importance of stream depth and prey size. In: *Predation: direct and indirect impacts on aquatic communities*. Edited by W. C. Kerfoot and A. Sih. University Press of New England, Hanover, USA. pp 333-351.
- Pyke, G. H. 1978. Optimal foraging: movement patterns of bumblebees between inflorescences. *Journal of Theoretical Population Biology* 13: 72-98.
- Pyke, G. H. 1981. Optimal foraging in hummingbirds: rule of movement between inflorescences. *Animal Behaviour* 29: 889-896.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15: 523-571.
- Rader, R. R. and J. V. Ward. 1990. Diel migration and microhabitat distribution of a benthic stream assemblage. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 711-718.

- Rahel, F. J., and R. A. Stein. 1988. Complex predator-prey interactions and predator intimidation among crayfish, piscivorous fish, and small benthic fish. *Oecologia* 75: 94-98.
- Rankin, E. T. 1986. Habitat selection by smallmouth bass in relation to physical characteristics in a natural system. *Transaction of the American Fisheries Society* 115: 322-334.
- Rapport, D. J. 1991. Myths in the foundations of economics and ecology. *Biological Journal of the Linnaean Society* 44: 185-202.
- Richards, C. and G. W. Minshall. 1988. The influence of periphyton abundance on Baetis bicaudatus distribution and colonization in a small stream. *Journal of the North American Benthological Society* 7: 77-86.
- Ringler, N. H. 1979. Selective predation by drift feeding brown trout. *Journal of the Fisheries Research Board of Canada* 36: 392-403.
- Rohwer, F. C. 1988. Inter-and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105: 161-176.
- Rounick, J. S. and M. J. Winterbourn. 1983. The formation, structure and utilization of stone surface organic layers in two New Zealand streams. *Freshwater Biology* 13: 57-72.
- Rowe, L. and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. *Ecology* 72: 413-427.
- SAS. 1988. SAS/STAT users guide. Release 6.03 edition. SAS Institute, Cary, North Carolina, USA.
- Scott, W. B. and E. J. Crossman. 1973. *Freshwater Fishes of Canada*. Fisheries Research Board of Canada Bulletin 184. 966 pp.
- Scrimgeour, G. J. 1986. Prey selection by torrentfish, Cheimarrichthys fosteri Haast, in the Ashley River, North Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 20: 29-35.

- Scrimgeour, G. J., J. M. Culp, M. L. Bothwell, F. J. Wrona, and M. H. McKee. 1991. Mechanisms of algal patch depletion: importance of consumptive and non-consumptive losses in mayfly-diatom systems. *Oecologia* 85: 343-348.
- Scrimgeour, G. J., Davidson, R. J., and J. M. Davidson. 1988. Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 22: 337-344.
- Scrimgeour, G. J. and M. J. Winterbourn 1987. Diet, food resource partitioning and feeding periodicity of two riffle-dwelling fish species in a New Zealand river. *Journal of Fish Biology* 31: 309-324.
- Scrimgeour, G. J. and M. J. Winterbourn. 1989. Effects of flood events on epilithon and macroinvertebrate communities in a flood prone New Zealand river. *Hydrobiologia* 171: 33-44.
- Shipley, B., and J. Dion. 1992. The allometry of seed production in herbaceous angiosperms. *American Naturalist* 139: 467-483.
- Sibley, R. M., and P. Calow. 1986. *Physiological ecology of animals*. Blackwell Scientific Publications, Oxford, England, UK.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210: 1041-1043.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* 63: 786-796.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 In: W. C. Kerfoot and A. Sih, editors. *Predation*. University Press of New England, Hanover, New Hampshire, USA.
- Sinervo, B., and P. Licht. 1991. Proximate constraints on the evolution of egg size, number, and total clutch mass in lizards. *Science* 252: 1300-1302.
- Skelly, D. K. 1991. Field evidence for a cost of behavioural antipredator response in a larval amphibian. *Ecology* 73: 704-708.

- Skelly, D. K. and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71: 2313-2322.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108: 499-506.
- Smith, J. N. M. 1974. The food searching behaviour of two European thrushes. I. Description and analysis of search paths. *Behaviour* 48: 276-302.
- Soluk, D. A., and N. C. Collins. 1988. Balancing risks? Responses and non-responses of mayfly larvae to fish and stonefly predators. *Oecologia* 77: 370-374.
- Soluk, D. A., and N. C. Collins. 1989. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52: 94-100.
- Stamps, J. A. 1983. The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behavioural Ecology and Sociobiology* 12: 19-33.
- Stanton, M. L. 1984. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). *American Journal of Botany* 7: 1090-1098
- Statzner, B. and R. Mogel. 1985. An example showing that drift net catches of stream mayflies (*Baetis* sp. Ephemeroptera, Insecta) do not increase during periods of higher substrate surface densities of the larvae. *Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 22: 3238-3243.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3-47.
- Stearns, S. C. 1980. A review of life-history evolution. *Oikos* 35: 266-281.
- Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40: 893-913.

- Stein, R. A. 1979. Behavioral response of prey to fish predators. Pages 343-353 In: R. H. Stroud and H. Clepper (eds). Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C., USA.
- Stein, R. A., and J. J. Magnuson. 1976. Behavioral response of crayfish to a fish predator. *Ecology* 57: 751-761.
- Steinman, A. D. McIntire, C. D., Gregory, S. V., Lamberti, G. A. and L. R. Ashkensas. 1987. Effects of herbivore type on taxonomic structure and physiognomy of algal assemblages in laboratory streams. *Journal of the North American Benthological Society* 6: 175-188.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.
- Sumner, W. T. and C. D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. *Archiv fur Hydrobiologie* 93: 135-157.
- Sweeney, B. W. 1978. Bioenergetic and developmental response of a mayfly to thermal variation. *Limnology and Oceanography* 23: 461-477.
- Sweeney, B. W. 1984. Factors influencing life-history patterns of aquatic insects. Pages 56-100 in V. H. Resh and D. M. Rosenberg (eds). *The ecology of aquatic insects*. Praeger, New York, New York, USA.
- Sweeney, B. W., and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science* 200: 444-446.
- Sweeney, B. W., Vannote, R. L. and P. J. Dodds. 1986. Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 12-18.
- Tautz, J. 1987. Water vibration elicits active antennal movements in the crayfish, *Orconectes limosus*. *Animal Behaviour* 35: 748-754.
- Travers, S. E. and A. Sih. 1991. The influence of starvation and predators on the mating behaviour of a semiaquatic insect. *Ecology* 72: 2123-2136.
- Trexler, J. C., McCulloch, C. E. and J. Travis. 1988. How can the functional response best be determined. *Oecologia* 76: 206-214.

- Turner, A. M. and G. G. Mittlebach. 1990. Predator avoidance and community structure: invertebrates among piscivores, planktivores, and plankton. *Ecology* 71: 2241-2254.
- Vaught, G. L. and K. W. Stewart. 1974. The life history and ecology of the stonefly Neoperla clymene (Newman) (Plecoptera: Perlidae). *Annals of the Entomological Society of America* 67: 167-178.
- Walde, S. J., and R. W. Davies. 1984. The effect of intra-specific interference on Kogotus nonus (Plecoptera) foraging behaviour. *Canadian Journal of Zoology* 62: 2221-2226.
- Walde, S. J., and R. W. Davies. 1985. Diel feeding periodicity of two predatory stoneflies (Plecoptera). *Canadian Journal of Zoology* 63: 883-887.
- Ware, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. *Journal of Fisheries Research Board of Canada* 32: 2503-2512.
- Werner, E. E. and D. J. Hall. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *Journal of the Fisheries Research Board of Canada* 31: 1531-1536.
- Werner, E. E., J. F. Gilliam., D. J. Hall and G. G. Mittlebach. 1983a. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.
- Werner, E. E., Mittlebach, G. G., Hall, D. L., and J. F. Gilliam. 1983b. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64: 1525-1539.
- Wilbur, H. M. 1977. Propagule size, number, and dispersion pattern in Ambystoma and Asclepias. *American Naturalist* 111: 43-67.
- Wiley, M. J., and S. L. Kohler. 1980. Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. *Canadian Journal of Zoology* 58: 618-622.
- Wiley, M. J., and S. L. Kohler. 1984. Behavioral adaptations of aquatic insects. In: Resh, V. H. and D. M. Rosenberg (eds). *The ecology of aquatic insects*. Praeger Scientific Publications, New York pp 101-133.

- Wilkinson, L. 1988. SYSTAT: the system for statistics. SYSTAT Inc., Evanston, Illinois, USA.
- Williams, F. M. and S. A. Juliano. 1985. Further difficulties in the analysis of functional-response experiments and a resolution. Canadian Entomologist 117: 631-640.
- Wilzbach, M. A. 1990. Non-concordance of drift and benthic activity in Baetis. Limnology and Oceanography 35: 945-952.
- Winterbourn, M. J., Hildrew, A. G. and A. Box. 1985. Structure and grazing of stone surface organic layers in some acid streams of southern England. Freshwater Biology 15: 363-374.
- Wrona, F. J., P. Calow, I. Ford, D. J. Baird and L. Maltby. 1986. Estimating the abundance of stone-dwelling organisms: a new method. Canadian Journal of Fisheries and Aquatic Research 43: 2025-2035.
- Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16: 229-249.
- Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ, USA.