University Field Station (Delta Marsh)

1994 personnel

Group photo

Regular Staff

Director: Gordon G.C. Robinson
Acting Assistant Director: L. Gordon Goldsborough
Manager: Russell Mead
Office Assistant: Pat Gutoski
Resident Maintenance Person: Dick Convery
Cooks/Housekeepers: Doreen Greening & Shirley Dinwoodie
Cook/Housekeeper Assistants: Ardith Hamilton & Heidi Mead

Summer Assistants

Biological Assistant: Curtis Horning
Maintenance Assistant: Kenneth Sandilands

Faculty

Dr. Mark Abrahams (Department of Zoology, University of Manitoba)
Dr. Dorothy Berner (Department of Biology, Temple University)
Dr. James Briskie (Department of Biology, Queen's University)
Dr. H. Lisle Gibbs (Department of Biology, McMaster University)
Dr. Gordon Goldsborough (Department of Botany, Brandon University)
Dr. Richard Gordon (Department of Botany, University of Manitoba)
Dr. Brenda Hann (Department of Zoology, University of Manitoba)
Dr. Keith Hobson (Canadian Wildlife Service, Saskatoon, Saskatchewan)
Dr. Norm Kenkel (Department of Botany, University of Manitoba)
Dr. Gordon Robinson (Botany, University of Manitoba)
Dr. Spencer Sealy (Department of Zoology, University of Manitoba)

Graduate Students

Gerry Alderson *(M.Sc. candidate*, Department of Biology, McMaster University)
Sharon Gill *(M.Sc. candidate*, Department of Zoology, University of Manitoba)
Paula Grieef *(M.Sc. candidate*, Department of Zoology, University of Manitoba)
Mike Kattenfeld *(M.Sc. candidate*, Department of Zoology, University of Manitoba)
Gabriela Lichtenstein *(Ph.D. candidate*, Department of Zoology, Cambridge University)
Glen McMaster *(M.Sc. candidate*, Department of Zoology, University of Manitoba)

Technicians & Research Assistants

Jennifer Barker (Co-op Workterm, Environmental Science, University of Manitoba)
Diane Beattie (Department of Zoology, University of Manitoba)
Kim Caldwell (Department of Zoology, University of Manitoba)
Doug Froese (Department of Zoology, University of Manitoba)
Kelly Graham (Summer Project Asst., Canada Trust / Friends of the Field Station / Botany, University of Manitoba)
Paula Grieef (Summer Project Asst., Canada Trust / Friends of the Field Station / Canadian Wildlife Service)
Heidi den Haan (Canadian Wildlife Service)
David Jones (NSERC summer student, Department of Biology, McMaster University)
Anke Kirch (Geography exchange student, Germany)
Mandy Lloyd (Co-op Workterm, Environmental Science Program, University of Manitoba)
Janice Lorenzana (Department of Zoology, University of Manitoba)
Rhonda McDougal (NSERC summer student, Department of Botany, Brandon University)
Philip Northover (Department of Botany, University of Manitoba)
Tom Pratt (Department of Zoology, University of Manitoba)
Graham Stinson (Co-op Workterm, Environmental Science Program, University of Manitoba)
Leanne Zrum (Department of Zoology, University of Manitoba)

Director's Report

Gordon Robinson
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1994 has been a year of substantial accomplishments, most of which are directly attributable to the University Field Station staff and the faithful users of the facility. I would, therefore, like to use this opportunity of thanking them all for their hard work and dedicated effort. I would particularly like to acknowledge Dr. Gordon Goldsborough for sacrificing so much of his time to Field Station administration. He acted very effectively as Director of the Station throughout the summer; he has again edited and formatted this report; he has, as 'Internet surfers' will know, established an impressive "Home Page" on the Worldwide Web; and he established the Station's first computer laboratory. For all of this and more, I thank him very much.

The support of the University through the Faculty of Science, the Faculty of Science Endowment Fund, the Office of the President and Physical Plant is gratefully acknowledged, as is the Natural Sciences and Engineering Research Council of Canada for the provision of an Infrastructure Grant. The efforts and support of the Fiends of the Field Station, and the financial support of Canada Trusts' Friends of the Environment Foundation are deeply appreciated as are the donations of many generous individuals.

Overall Use

The following table summarizes the overall use of the University Field Station since 1985.

	User Days				
Year	**Research**	**Courses**	**Schools**	**Other**	**Total**
1985	2002	927	630	257	3709
1986	1558	559	639	866	3622
1987	1186	298	585	1214	3283
1988	1565	626	465	1196	3852
1989	1754	397	574	1304	4029
1990	1251	787	747	1547	4337
1991	912	712	727	2104	4455
1992	914	1096	1008	1742	4760
1993	1067	994	1317	2241	5619
1994	1314	1026	2091	1890	6321

In 1994 use of the Field Station increased by 12.5% over the previous year, by 33% over 1992, by 42% over 1991 and by 64% over 1988. The trend is obvious. The Station is being increasingly used in essentially all categories.

Research

Research activities increased by 23% over 1993 and the following specific projects were either initiated or continued during 1994.

- **The effect of turbidity on predator-prey interactions in aquatic communities.** Dr. Mark Abrahams and Mike Kattenfeld, *Department of Zoology, University of Manitoba*

- **Biotic inventory and development of a low-impact self-guided trail in Oxbow Woods.** Jennifer Barker, Environmental Science Program and Dr. Norm Kenkel, *Department of Botany, University of Manitoba*
- **Sperm storage and the proximate mechanism of last-male sperm precedence in the Yellow-headed Blackbird.** Dr. James V. Briskie, *Department of Biology, Queen's University*
- **Patterns of frequency and abundance in parasite communities.** Dr. Albert Bush, *Department of Zoology, Brandon University*
- **Host-specificity in Brown-headed Cowbirds? A population-level approach.** Dr. H. Lisle Gibbs, *Department of Biology, McMaster University* and Dr. Spencer G. Sealy, *Department of Zoology, University of Manitoba*
- **The evolution and functions of Yellow Warbler alarm calls.** Sharon Gill and Dr. Spencer G. Sealy, *Department of Zoology, University of Manitoba*
- **Effects of pulsed and regular nutrient additions on algal, macrophyte and invertebrate communities in large littoral enclosures.** Dr. L. Gordon Goldsborough and Rhonda L. McDougal, *Department of Botany, Brandon University* Dr. Brenda J. Hann, *Department of Zoology, University of Manitoba* Mandy B. Lloyd, *Environmental Science Program, University of Manitoba*
- **Study of polyglycan secretions by benthic diatoms** Dr. Richard Gordon and Natalie K. Bjorklund, *Department of Botany, University of Manitoba*
- **Great Burdock (*Arctium lappa*) at Delta, Manitoba: demography and control measures.** Kelly Graham and Dr. Norm Kenkel, *Department of Botany, University of Manitoba*
- **Location and selection of Clay-colored Sparrow nests by Brown-headed Catbirds.** Paula Grieef and Dr. Spencer G. Sealy, *Department of Zoology, University of Manitoba*
- **Distribution of littoral Anomopoda in prairie potholes.** Dr. Brenda J. Hann, *Department of Zoology, University of Manitoba* and Dr. Dorothy B. Berner, *Department of Biology, Temple University*
- **An experimental determination of avian nest predation pressure in riparian habitats at Delta Marsh.** Dr. Keith A. Hobson, *Canadian Wildlife Service, Saskatoon, Saskatchewan*, Dr. Spencer G. Sealy and Douglas Froese, *Department of Zoology, University of Manitoba*
- **Neotropical migrant banding program at the University Field Station (Delta Marsh).** Dr. Keith A. Hobson, *Canadian Wildlife Service, Saskatoon, Saskatchewan*
- **Tree Swallows as bioindicators at Delta Marsh.** Dr. Keith A. Hobson, *Canadian Wildlife Service, Saskatoon, Saskatchewan*
- **Spatial and demographic patterns of a monodominant stand of Ostrich Fern (*Matteucia struthiopteris*).** Dr. Norm C. Kenkel, *Department of Botany, University of Manitoba*
- **Begging strategies of the parasitic cowbirds.** Gabriela Lichtenstein, *Department of Zoology, Cambridge University, England*
- **Manipulation of Yellow Warbler incubation behavior by cowbirds.** D. Glen McMaster and Dr. Spencer G. Sealy, *Department of Zoology, University of Manitoba*
- **Parasitism frequency on cowbird-egg ejectors, determined by direct observations.** Dr. Spencer G. Sealy, Glen McMaster and Sharon Gill, *Department of Zoology, University of Manitoba* Diane L. Neudorf, *Department of Biology, York University*
- **Behavioral reactions of some acceptor species to cowbird eggs added experimentally to their clutches.** Dr. Spencer G. Sealy and Janice Lorenzana, *Department of Zoology, University of Manitoba*
- **Do parasitic Brown-headed Cowbirds avoid already-parasitized nests?** Dr. Spencer G. Sealy and Diane Beattie, *Department of Zoology, University of Manitoba* Graham Stinson, *Environmental Science Program, University of Manitoba*
- **Temporal and spatial distribution of littoral invertebrate communities in Crescent Pond and Blind Channel.** Leanne Zrum and Dr. Brenda J. Hann, *Department of Zoology, University of Manitoba*

I would like to expand on two of these projects as they represent thrilling new prospects for the future of the Field Station:

Delta Marsh Bird Observatory (DMBO)

When birds start to disappear from our forests we know there is something seriously wrong with our environment. Recently there have been reports of population declines in a number of neotropical bird species.

Possible reasons probably include changes to factors in both wintering and breeding grounds. To develop conservation strategies for migrant birds, we first need to know their status, population trends and the causes of population change. Monitoring programs are required to detect and measure change. The best way to monitor these populations is to sample them as they migrate from within the boreal forest, taiga and tundra through southern Canada.

From 1992 to 1994, Dr. Keith Hobson, Paula Grieef, Heidi den Haan, acting for the Canadian Wildlife Service (C.W.S.), conducted a monitoring/banding program at the University Field Station (Delta Marsh), that was essentially a replication of a similar program conducted ten years earlier by Dr. Spencer Sealy and Heidi den Haan. In 1994 the Delta Marsh Bird Observatory (D.M.B.O.) was established at the Field Station. It is Manitoba's contribution to providing continued information on migratory songbirds. It is one of five working banding stations in Canada and part of the C.W.S. "Canadian Landbird Monitoring Strategy". D.M.B.O. is destined to become one of a network of 260 Monitoring Avian Productivity and Survivorship stations across North America. D.M.B.O. will operate as a non-profit organization and its board of directors are Paula Grieef, Heidi den Haan, Dr. Keith Hobson (C.W.S.), Dr. Bob Jones (Manitoba Natural Resources) and Dr. Spencer Sealy (Department of Zoology).

The University Field Station has a long established record in avian research and its new alliance with D.M.B.O. is an exciting and welcome development.

Prairie Wetland Ecology Team (PWET)

Canada is a nation of wetlands. Approximately 14% of the country's total land area is covered by shallow bodies of water that are home to diverse plant communities, abundant waterfowl and other aquatic life. Yet, these important resources are increasingly subject to damage from external influences. Over the past century many prairie wetlands were drained to support agricultural production. Those that remain are contaminated by nutrients, metals and acids and invaded by foreign animal and plant species.

The extent to which these external factors will upset the delicate natural balance of prairie wetlands is largely unknown. One way to gain further understanding is to conduct experiments in small areas of the wetland where these factors can be introduced in controlled quantities and the resulting response can be carefully monitored. This is being done in a series of experiments in channels of the Delta Marsh bordering the University Field Station. In 1991, large floating platforms (5 m x 5 m) were deployed in the Blind Channel. Each summer, plastic curtains are attached to the platforms and embedded in bottom sediments to isolate about 20,000 liters of marsh water. Enclosed within this volume is a subset of the marsh ecosystem, which includes submersed plants; algae suspended in the water column, attached to the plant surfaces and burrowing in the soft sediments; numerous swimming and attached invertebrates and several small fish species. These enclosures can be manipulated through controlled additions of chemicals to illustrate how sunlight energy flows from the photosynthesizing algae and plants to the grazing herbivores and ultimately to terrestrial species, such as birds, that depend on aquatic insects and fish for food.

Any project aimed at studying the responses of an entire ecosystem to experimentation is necessarily interdisciplinary, involving collaborators from several disciplines of biology. The current research team consists of Dr. Gordon Goldsborough (Department of Botany, Brandon University) and Dr. Brenda Hann (Department of Zoology), assisted by undergraduate students from the Environmental Science Program and graduate students in Botany and Zoology. Research funding is provided by research grants from the Natural Sciences and Engineering Research Council of Canada, the University Field Station, the University of Manitoba and Brandon University.

Since 1991, several controlled experiments have been carried out using the Delta Marsh enclosure complex. Early experiments involved adding chemical herbicides that block the growth of plants and, thereby, block energy flow to grazing animals. In 1993 and 1994 experiments were conducted using enrichment with nitrogen and phosphorus; two key nutrients found in human and animal wastes and in agricultural fertilizers and that are largely responsible for the greening of prairie lakes and rivers. One interesting response to fertilization was the

occurrence of thick floating carpets of algae. Species of invertebrates which use the floating algae to construct protective cases, and which were previously rare in the Delta Marsh, became abundant. This discovery received international media attention, as it indicated that the flora and fauna of polluted marshes may undergo significant changes. Upcoming experiments, to be done in collaboration with the Delta Waterfowl and Wetlands Research Station, will study the role of nutrients provided from ducks and geese that use the marsh as a stopover on their spring and autumn migrations through the area.

Expansion of the enclosure complex is planned to enable the simultaneous manipulation of several factors at once, in order to gain a better appreciation for the interactions that occur between environmental factors in a natural setting. The long-term goal of the project is to establish a large complex of enclosures that can be used for further study of energy flow through the Delta Marsh, so that the impact of environmental changes on this delicate and fundamentally important ecosystem can be predicted.

Five research papers have emanated from work done at the Station in 1994.

Teaching

The following credit courses were presented at the Field Station during 1994:

Vascular Flora of Manitoba *Instructor: Maria Zbigniewicz*	1.207	June 26 - July 9
Principles of Ecology Instructor: *Tom Booth*	1.237 / 22.237	July 10 - 23
Community Ecology Instructor: *Norm Kenkel*	1.354	July 24 - August 6
Field Ecology Instructors: *Isobel Waters & Jack Gee*	1.342 / 22.345	August 21 - Sept. 2
Landscape Architectural Field Ecology Instructor: *Jason Greenall*	31.712	August 21 - 26

Schools Program

Outreach activities with schools in Manitoba have again increased in 1994 (by 59% over 1993). I would like to commend the teachers and counselors for the enthusiasm and dedication which bring them and their students to the University Field Station.

New Building

Those who spend any time at the Field Station very quickly realize that the multiple use of Mallard Lodge as classroom, meeting room and library leads to congestion, and there is a clear need for a new classroom/library facility at the Station. This is increasingly obvious as facility use increases. I am happy to report that plans for such a new facility exist, and with the support of Friends of the Field Station, Canada Trust Friends of the Environment Foundation and private donators, it will hopefully be built in the next year.

Manager's Report

Russell G. Mead
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A busy schedule of research and undergraduate courses kept the station staff on their toes during the summer. Special thanks go to Gordon Goldsborough, who assumed the duties of the Director for these months; his help with the many day-to-day requirements was greatly appreciated. Extra responsibilities were also delegated to Ken Sandilands, who capably looked after the maintenance duties in the summer months. Curt Horning proved to be an excellent teacher and research assistant. Dick Convery was away during autumn; fortunately, the Andersons helped with many duties in his absence–thanks Rob and Trish. Last but not least, the kitchen and housekeeping staff had, without doubt, their busiest year yet and I sincerely thank Doreen, Shirley, Heidi and Ardith for their diligence and concern for the station.

Facility and Property Improvements

An air injector pump was added to the water system late in autumn. This alleviated the continuing water pressure problem experienced over the summer. Thanks are due to Physical Plant and Ray Goetz for their assistance in maintaining and repairing the facility. A backup generator was purchased and a building to house the unit is due to be built in 1995. Finally, Jennifer Barker and Anke Kirch established a low-impact, self-guiding interpretive trails in the Oxbow Woods (see elsewhere in this report for details).

Meteorological Station

The most notable change to the instrumentation was the establishment of a tilting anemometer tower (the second of its kind in the province) along the winter road in early autumn. Environment Canada relocated the tower a greater distance away from the beach ridge, thereby avoiding the air disturbance caused by the ridge trees in the upper air flow measured by the instruments. Two Li-Cor portable weather stations (daily mean air and soil temperature, precipitation, and solar irradiance) were installed in August, one at the marsh meteorological site and one at Oxbow Woods; many thanks to Gordon Goldsborough for installing these units. Monthly sampling of water from Lake Manitoba continued on behalf of Manitoba Environment, along with weekly reporting to the Crop Network program.

School Program

1994 was a distinct year in that it emphasized the station's ongoing commitment to education and research. The statistics show that all types of use, both in absolute numbers and diversity of offerings, increased over previous years. Junior High and Senior High students from many parts of the province were taught the peer counseling and student match curricula. Although not typical biology lessons, the opportunity for the students to experience a marsh and lake setting (albeit in winter) did provide enhanced awareness of these environments. These visits were in addition to existing programs; consequently, autumn was a particularly busy time at the station. Biological use groups were active at the station during most of the year; special thanks to the dedicated teachers: Mike James (St. James Collegiate), Brent Poole (Fort Richmond Collegiate), Lois Quesnell (St. Adolphe) and Catherine Fillis (Lord Selkirk). Twelve schools from Portage la Prairie and the surrounding area visited the station for day tours of the marsh, mostly in May and June.

Seminars, Workshops, and Elderhostels

The following six presentations were given during the annual summer seminar series:

Louis Lenz
Department of Plant Science, University of Manitoba
"From the wild to the garden"

Dr. Karen Johnson
Museum of Man and Nature, Winnipeg
"Typical plant communities of Manitoba"

Drs. Bill Preston & Brian McKillop
Museum of Man and Nature, Winnipeg
"Field studies of butterflies and moths"

Dr. Richard Staniforth
Department of Biology, University of Winnipeg
"Dynamics of plant populations in the high sub-arctic"

Dr. Jennifer Shay
Department of Botany, University of Manitoba
"Delta Marsh, then and now"

Dr. Jon Gerrard
Canadian Secretary of State for Science, Research, and Development
"The bald eagle: hunt and habit of a wilderness monarch"

The course on Arctic Lifestyles/Winter Survival, held in January, was a great success due, in no small part, to the enthusiasm generated by its instructors, Jill Oakes and Rick Riewe; many thanks for their great instruction and sharing.

A Photography Workshop was held in March with Mike Grandmaison and Dick Toews. A successful afternoon of public canoeing in the marsh, followed by a supper on the beach, was held in August in conjunction with the “International Year of the Family.” Jean Horton instructed an autumn birding workshop in September. Finally, the third Elderhostel offered at the station was held in May. Thanks to the support and assistance of Lorraine Rae and the Portage and District Chamber of Commerce, it was a tremendous success and everyone involved had a memorable experience.

Noteworthy Happenings

- The First Annual Delta Marsh fashion show was held in June; thanks to Rhonda McDougal and others, it was a real hoot!
- A successful summer picnic was held by the Friends of the Field Station.
- The t-shirt design contest was won by Mandy Lloyd and Leanne Zrum - well done!

Weather and water quality data summary (1994), University Field Station (Delta Marsh)

L. Gordon Goldsborough
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The following is a summary of meteorological and water quality data collected at the Field Station during 1994. The complete data are available as *Microsoft Excel* spreadsheets on Macintosh or PC diskettes, and on the Station's page on the World Wide Web (Delta Marsh Home Page) at http://www.umanitoba.ca/faculties/science/delta_marsh/ufshome.html. Wind velocity and direction data, pyrheliometer traces, barometer traces, and hygrothermograph traces are available on request.

Users are advised that the period represented by "daily" values differ between parameters: temperature, precipitation, and anemometer data are collected at 08:00 CST and represent the 24-hour period starting at 08:00 CST on the preceding day. This affects the interpretation of some parameters. For example, the maximum air temperature reported for 1 January (X°C) may the value for 31 December of the previous year if the maximum actually occurred prior to 24:00 or it may be the value for 1 January if the maximum occurred between 00:00 and 08:00. Other daily data, including photosynthetically available radiation and hours of sunshine, are accurate for the reported calendar day, being cumulative between 00:00 and 24:00 CST. Monthly summary statistics (total, mean, median, minimum and minimum) are calculated for the period starting on the first day of the month, without consideration for the above.

Data for daily photosynthetically available radiation (PAR) were found to underrepresent actual values due to drift in the calibration of the PAR sensor installed in December 1992. A method of correcting affected data is being developed; updated information will be available on the Delta Marsh Home Page.

Two Li-Cor Li-1200 Minimal Dataset Recorders were installed in August 1994, one at the existing meteorological station, and the other in Oxbow Woods by the Inkster Farm. Both recorders are maintained year-round and data for daily solar irradiance, precipitation, maximum, minimum and mean air temperature, and mean soil temperature (10 cm depth) are available.

Collection of weather data was made possible by instruments provided by the Atmospheric Environment Service of Environment Canada. Weather data were collected by Dick Convery, Shirley Dinwoodie, Doreen Greening, Gordon Goldsborough, Curt Horning, Russ Mead and Gordon Robinson.

Lake water samples were collected by Russ Mead at monthly intervals as part of an ongoing water quality monitoring program of Manitoba Environment. Station WQ666 is approximately 1 km offshore from the UFS. Curt Horning and Ken Sandilands collected marsh water samples at six sites (Fig. 7) on 15 July, and 15 August. Russ Mead collected marsh water samples on 13 September.

1994 Datasets:

- Daily photosynthetically available radiation (E/m²/d)
- Daily total sunshine
- Daily air temperature (°C)
- Daily precipitation (mm)
- Daily wind velocity (km/h)
- Daily wind direction (degrees)
- Water quality at station WQ666 (Lake Manitoba)
- Pesticide residues at station WQ666 (Lake Manitoba)
- Water quality in Delta Marsh

Figure 1. Uncorrected total daily photosynthetically available radiation (PAR - 400 to 700nm; E/m²/d) at the University Field Station (Delta Marsh) in 1994, as reported by miscalibrated PAR sensor Q11490. The smooth curve represents the maximum daily (cloudless) PAR at the station, as calculated using the SIMSOL computer program (Fee, E. J. 1990. Computer programs for calculating in situ phytoplankton photosynthesis. Can. Tech. Rep. Fish. Aquat. Sci. No. 1740, v + 27pp.).

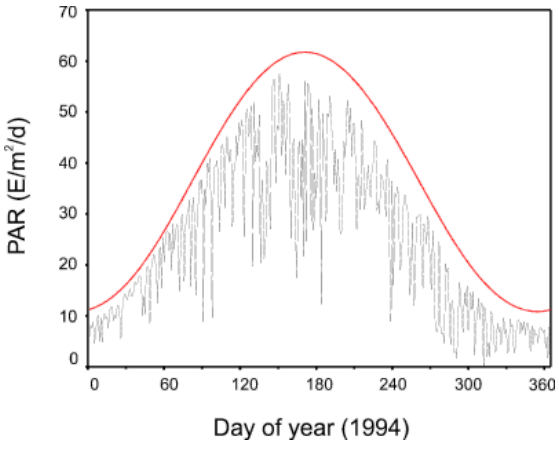

Figure 2. Daily hours of sunshine at the University Field Station (Delta Marsh) in 1994. The annual mean, denoted by the horizontal line, was 6.9 hours of sun per day. The range was 0 to 15 hours.

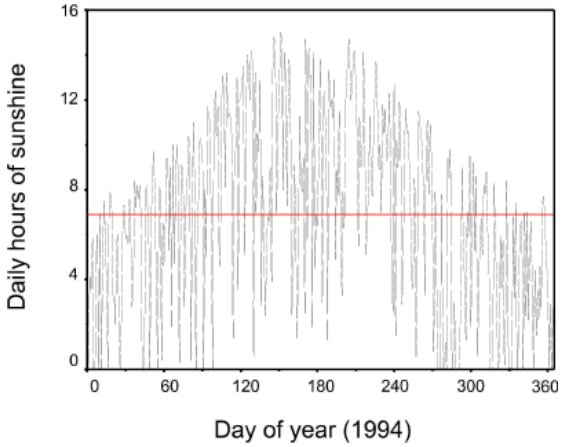

Figure 3. Daily mean air temperature (°C) at the University Field Station (Delta Marsh) in 1994. The smooth curve represents normal daily mean air temperature at the station, as calculated by R.McGinn (pers.comm. 1991). The annual mean daily temperature, denoted by the horizontal line, was 2.9°C. The minimum recorded temperature was -36.5°C and the maximum temperature was 31.5°C.

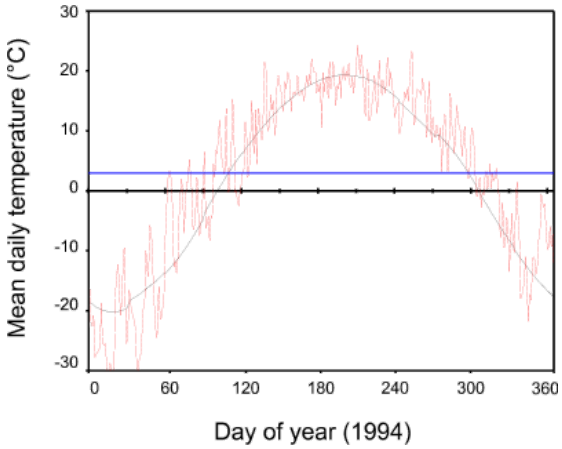

Figure 4. Daily total precipitation (water equivalents in mm) at the University Field Station (Delta Marsh) in 1994. The total annual precipitation was 469 mm, 85% of which fell as rain with the remainder as snow. The maximum amount of precipitation received in a single day was 27.4 mm (19 October).

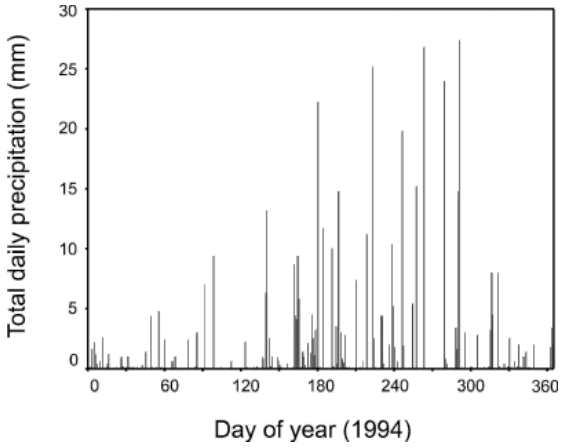

Figure 5. Daily mean wind velocity (km/h) at the University Field Station (Delta Marsh) in 1994. The annual mean wind velocity, denoted by the horizontal line, was 17 km/h.

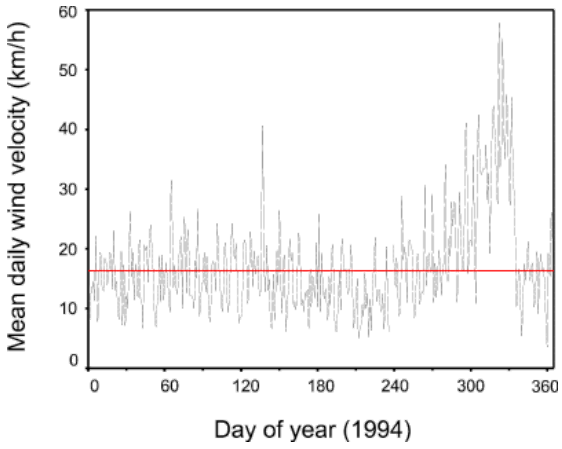

Figure 6. Daily mean wind direction (degrees) at the University Field Station (Delta Marsh) in 1994. North = 0°/360°, East = 90°, South = 180°, West = 270°. The annual mean wind direction, denoted by the horizontal line, was 198°.

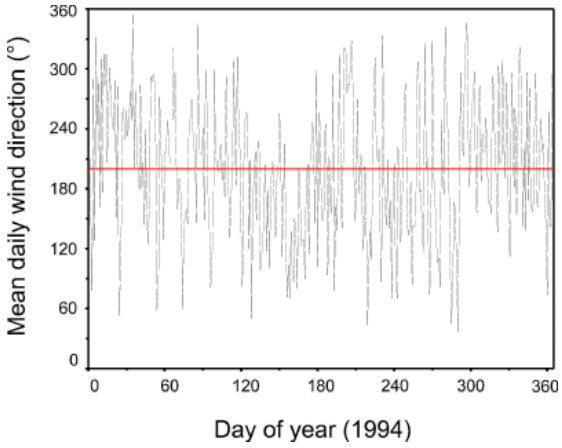

Table 1. Water quality at sampling site WQ666 located 1 km offshore from the University Field Station in Lake Manitoba (1994). Analyses were performed by the Manitoba Department of Environment. Date format: day/month. ns = no sample.

Date	25-Jan	15-Feb	15-Mar	12-Apr	24-May	14-Jun	12-Jul	15-Aug	12-Sep	*14-Sep	25-Oct	22-Nov	12-Dec
Sampling time (CST)	12:00	11:40	9:00	9:00	9:45	10:00	9:00	9:00	9:00	12:30	9:30	13:00	13:00
Water temp. (°C)	0	0	1	1.5	15.5	18.5	19.5	18.0	17.0	19.0	5.0	-1.0	0.25
Ice thickness (cm)	91	1	1	90	0	0	0	0	0	0	0	pack ice	43
Water depth (m)	3.6	3.5	3.1	3.2	3.1	3.6	3.55	3.62	3.3	n/a	3	0.65	3.5
Secchi depth (m)	1.55	0.8	0.6	1.8	0.65	0.65	0.34	0.45	0.45	n/a	0.2	0.35	0.5
Total coliforms (/mL)	< 10**	0	23	0	0	0	9	43	23	230	0	4	46000***
Conductivity (µS/cm)	2480	2660	1910	255	1930	1910	1860	1420	1810	786	1980	2100	2230
Total residue (mg/L)	1500	1600	1200	150	1100	1200	1300	930	1100	580	1300	1300	1400
Filter. residue (mg/L)	1500	1600	1200	150	1100	1200	1300	910	1100	570	1200	1300	1400
Non-filter. residue (mg/L)	8	< 5.0	7	< 5.0	< 5	13	34	16	21	7	77	19	< 5.0
pH	8.25	8.22	8.19	8.72	8.6	8.65	8.71	8.59	8.71	8.07	8.54	8.45	8.39
Total alkalinity (mg/L)	306	326	216	34.7	241	2.38	239	249	238	260	250	256	272
Bicarb. alkalinity (mg/L)	373	397	264	8.04	247	247	245	255	241	318	270	291	307
Carb. alkalinity (mg/L)	< 0.6	< 0.6	< 0.6	16.9	22.9	21.4	23.1	23.8	24.4	< 18	< 18	< 18.0	< 18.0
Hydrox. alkalinity (mg/L)	< 0.34	< 0.34	< 0.34	<.34	< 0.34	< 10.2	< 10.2	< 10.2	< 10.2	< 10.2	< 10.2	< 10.2	< 10.2
Dissolved oxygen (mg/L)	11.5	10.2	13.6	10.2	7.6	6.9	7.4	7.3	8.3	5	11.5	12.9	20.2
Total organic C (mg/L)	19.5	25	24	6	18	13	14	10.3	20.3	12.5	24.3	26.3	11.1
Total inorganic C (mg/L)	61	66	44	7	56	45	46.5	51.5	51.9	61.1	41.6	56.9	62.9
Total carbon (mg/L)	80.5	91	68	13	74	58	60.5	61.8	72.2	73.6	65.9	83.2	74
True color (Pt)	< 5.0	5	5	< 5	5	< 5	< 5	15	5	< 15	10	5	15
Turbidity (NTU)	3.5	2.6	7.4	2.1	9.6	10	28	13	17	6.2	79	20	8.3
Total Kjeldahl N (mg/L)	1.26	1.27	2.33	0.59	1.01	1.21	1.33	1.45	1.72	1.05	2.05	1.2	1.16

Ammonia-N (mg/L)	0.052	0.042	0.654	0.087	< 0.02	< 0.02	< 0.02	< 0.02	< 0.02	0.047	0.151	< 0.02	0.026
Nitrate/nitrite-N (mg/L)	0.04	0.03	2.56	0.05	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.01
Total phosphorus (mg/L)	0.024	0.03	0.071	0.029	0.033	0.037	0.047	0.083	0.05	0.347	0.092	0.037	0.032
Total diss. P (mg/L)													
Total partic. P (mg/L)													
Chlorophyll-a (µg/L)	2.5	2.5	2.5	5	3	6	8.5	5.5	7	5	32	5	1.5
Chloride (mg/L)	484			41			376				398		
Extr. aluminum (µg/L)	0.301			0.146			0.02				0.232		
Total arsenic (mg/L)	0.002			< 0.001			0.003				0.003		
Diss. boron (mg/L)	0.27			<0.05			0.23				0.25		
Extr. cadmium (mg/L)	0.003		< 0.001	< 0.001			< 0.001				< .001		
Hex. chromium (mg/L)	< 0.02			< 0.02			< 0.2				< 0.02		
Extra. calcium (mg/L)	53			6.68			35.4				36.8		
Extr. magnesium (mg/L)	87.6			8.44			64.2				66.2		
Hardness (mg/L)	493			51.4			353				364		
Extr. sodium (mg/L)	344			26			250				268		
Extr. potassium (mg/L)	20.3		13.8	< 5			18.5				18		
Extr. copper (mg/L)	< 0.01			< 0.01			< 0.01				< 0.01		
Extr. zinc (mg/L)	< 0.01			< 0.01			< 0.01				< 0.01		
Extr. iron (mg/L)	0.07			0.06			0.07				< .002		
Extr. manganese (mg/L)	< 0.02			< 0.02			< 0.02				< 0.02		
Extr. lead (mg/L)	< 0.002			< 0.002			< 0.002				< 0.002		
Extr. nickel (mg/L)	< 0.005			< 0.005			< 0.005				0.009		
Sulphate (mg/L)	260			18			181				202		
Total cations (meq)	25.3			2.22			18.4				19.4		
Total anions (meq)	25.2			2.24			19.5				20.5		
Ion balance error (%)	0.27			0.33			2.8				2.63		

Table 2. Pesticide residues at sampling site WQ666 located 1 km offshore from the University Field Station in Lake Manitoba (1994). Analyses were performed by the Manitoba Department of Environment. Date format: day/month.

Date	25-Jan	15-Feb	15-Mar	12-Apr	24-May	14-Jun	12-Jul	15-Aug	12-Sep	*14-Sep	25-Oct	22-Nov	12-Dec
Aldrin (ug/L)	< 0.01			< 0.01									
BHC- alpha (ug/L)	< 0.02			< 0.02									
BHC- beta (ug/L)	<0.03			< 0.03									
BHC- gamma/Lindane (ug/L)	< 0.02			< 0.02			< 0.02				> 0.02		
BHC- delta (ug/L)	< 0.01			< 0.01									
Chlordane-cis (ug/L)	< 0.01			< 0.01			< 0.01				< 0.01		
Chlordane-trans(ug/L)	< 0.01			< 0.01			< 0.01				< 0.01		
PP'-DDD (ug/L)	< 0.03			< 0.03									
PP'-DDE (ug/L)	< 0.01			< 0.01									
PP'-DDT (ug/L)	< 0.03			< 0.03									
Dichlofop-methyl (ug/L)	< 0.09			< 0.09			< 0.09				< 0.09		
Dieldrin (ug/L)	< 0.02			< 0.02									
Endosulfan I (ug/L)	< 0.01			< 0.01									
Endrin (ug/L)	< 0.02			< 0.02									
Heptachlor (ug/L)	< 0.02			< 0.02									
Heptachlor epoxide (ug/L)	< 0.01			< 0.01									
Methoxychlor (ug/L)	< 0.04			< 0.04			< 0.04				< 0.04		
Mirex (ug/L)	< 0.02			< 0.02									
Alachlor (ug/L)	< 2.0			< 2			< 2.0				< 2		
Atrazine (ug/L)	< 0.5			< 0.5			< 0.05				< 0.5		
Bromacil (ug/L)	< 1.0			< 1			< 1.0				< 1.0		

Metribuzin (ug/L)	< 1.0			< 1			< 1.0			< 1.0		
Propachlor (ug/L)	< 2.0			< 2								
Simazine (ug/L)	< 2.0			< 2			< 0.5			< 0.5		
Triallate (ug/L)	< 1.0			< 1			< 1.0			< 1		
Trifluralin (ug/L)	< 0.03			< 0.03			< 0.03			< 0.03		
Carbofuran (ug/L)	< 2.0			< 2			< 2.0			< 2.0		
Propoxur (ug/L)	< 2.0			< 2			< 2.0			< 2.0		
Bromoxynil (ug/L)	< 0.01			< 0.01			< 0.01			< 0.01		
2,4-D (ug/L)	0.06			< 0.05			< 0.05			0.06		
2.4-DB (ug/L)	< 0.2			< 0.2			< 0.2			< .2		
2,4-DP (ug/L)	< 0.1			< 0.1			< 0.1			< 0.1		
Dicamba (ug/L)	< 0.02			< 0.02			< 0.02			< 0.02		
Dinoseb (ug/L)	< 0.05											
MCPA (ug/L)	< 10.0			< 10			< 10			< 10.0		
2,4,5-T (ug/L)	< 0.01											
2,4,5 -TP (ug/L)	< 0.01											
Trichlopyr (ug/L)	< 0.02			< 0.02			< 0.02			< 0.02		
Picloram (ug/L)	< 0.2			< 0.2			< 0.2			< 0.2		
Azinphos methyl (ug/L)	< 1.5			< 1.5								
Chlorpyrifos -E (ug/L)	< 0.8			< 0.8			< 0.8			< 0.8		
Diazinon (ug/L)	< 0.5			< 0.5								
Dimethoate (ug/L)	< 1.0			< 1			< 1.0			< 1.0		
Malathion (ug/L)	<0 .9			< 0.9			< 0.9			< 0.9		
Parathion ethly (ug/L)	< 0.9			< 0.9								
Parathion methyl (ug/L)	< 0.6			< 0.6								
Terbufos (ug/L)	< 0.7			< 0.7						< 0.7		

Figure 7. Map of the area of Delta Marsh adjacent to the University Field Station where surface water samples were collected at six sites on 15 July, 15 August and 13 September, 1994. Site coordinates were determined using a portable Global Positioning System (GPS) receiver.

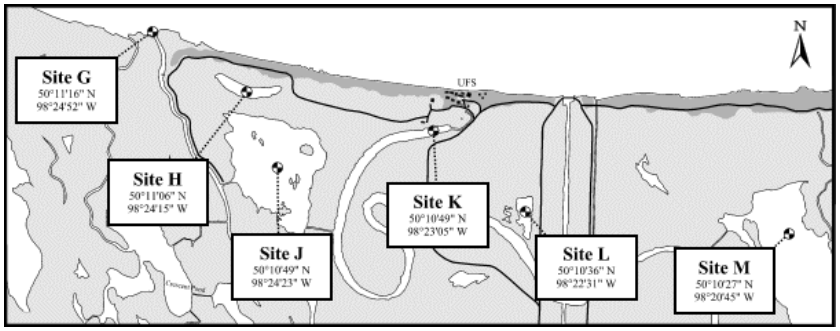

Table 3. Water chemistry determined at six sites in Delta Marsh in mid-July, August and September 1994. Most analyses, except for field measurements and total chlorophyll, were performed by Norwest Labs Inc. (Winnipeg).

	G	H	J	K	L	M
	Cram Creek mouth	Crescent Pond	Forster's Bay	West Blind Channel	West Dike Pond	School Bay
12-Jul-94						
Sample time (CST)	9:15	10:50	10:25	12:05	14:10	13:15
Water temperature (°C)	19.0	21.0	19.5	22.5	22.0	22.0
Water depth (m)	1.40	0.80	0.51	0.65	0.75	0.90
Secchi depth (m)	0.48	bottom	0.49	0.52	bottom	0.43
pH (field)	8.3	8.5	8.6	8.3	9.0	9.0
pH (lab)	8.4	8.5	8.6	8.2	9.0	8.8
Conductivity (µS/cm)	1950	943	2020	2250	4170	1590
Calcium (mg/L)	37.8	27.5	36.7	57.8	55.1	24.8
Magnesium (mg/L)	65.7	34.6	67.4	82.6	275.0	67.7

Sodium (mg/L)	249	110	264	316	498	194
Potassium (mg/L)	20.2	19.9	21.6	23.8	24.4	30.6
Manganese (mg/L)	<0.003	<0.003	<0.003	<0.003	<0.003	<0.003
Iron (mg/L)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Sulphate (mg/L)	149.0	43.2	147.0	138.0	468.0	86.9
Chloride (mg/L)	373	160	406	462	1030	281
Carbonate (mg/L)	4.59	6.77	11.70	nd	47.50	23.60
Bicarbonate (mg/L)	306	238	296	415	244	315
Nitrate+nitrite (mg/L)	<0.05	<0.05	0.3	0.16	<0.05	0.34
Fluoride (mg/L)	0.27	0.22	0.27	0.30	0.21	0.27
Alkalinity (mg/L)	259	206	262	340	279	297
Hardness (mg/L)	365	211	369	484	1270	341
TDS (mg/L)	1050	519	1100	1280	2520	863
Ionic balance (%)	98.5	99.1	97.5	105.0	107.0	101.0
Ammonia-N (mg/L)	0.171	0.013	0.015	<0.005	0.009	<0.005
TKN (mg/L)	1.37	1.47	1.67	2.29	1.57	3.00
Total phosphorus (mg/L)	0.39	<0.05	<0.05	<0.05	<0.05	<0.05
Total carbon (mg/L)	83.4	77.4	84.1	106	90.7	85.4
TOC (mg/L)	18.4	17.4	17.1	21.4	27.7	24.4
TIC (mg/L)	65.0	60.0	67.0	84.6	63.0	61.0
True color (Co units)	15	45	15	45	30	30
Turbidity (NTU)	18.0	1.5	13.0	2.0	2.2	15.0
Silicon (mg/L)	3.0	<1.0	2.0	3.0	<1.0	3.0
Total chlorophyll (µg/L)	14.6	2.2	15.5	10.2	2.3	8.9
15-Aug-94						
Sample time (CST)	9:10	10:15	9:50	10:30	12:00	12:35
Water temperature (°C)	19.0	19.5	19.0	19.0	20.5	21.0
Water depth (m)	1.38	0.67	0.60	0.66	0.77	0.81
Secchi depth (m)	0.17	bottom	0.32	0.43	bottom	0.44
pH (field)	nd	nd	nd	nd	nd	nd
pH (lab)	8.5	9.2	8.7	8.5	9.2	9.4
Conductivity (µS/cm)	1840	1120	1820	2110	4380	1780
Calcium (mg/L)	47.9	24.0	45.8	53.2	47.0	24.5
Magnesium (mg/L)	69.3	44.4	67.3	77.2	233.0	79.4
Sodium (mg/L)	232	143	233	272	509	226
Potassium (mg/L)	17.1	20.8	17.1	19.9	21.6	32.8
Manganese (mg/)	<0.050	<0.050	<0.050	<0.050	<0.050	<0.050
Iron (mg/L)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Sulphate (mg/L)	181.0	67.5	182.0	185.0	594.0	138.0
Chloride (mg/L)	332	199	331	396	1010	320
Carbonate (mg/L)	12	39	24	12	66	78
Bicarbonate (mg/L)	302	180	268	354	201	226
Nitrate+nitrite (mg/L)	<0.05	0.08	<0.05	0.1	<0.05	0.07
Fluoride (mg/L)	0.24	0.20	0.22	0.24	0.17	0.23
Alkalinity (mg/L)	268	213	260	310	275	315
Hardness (mg/L)	405	243	392	451	1080	388
TDS (mg/L)	1040	626	1030	1190	2580	1010
Ionic balance (%)	100.0	102.0	99.8	100.0	94.8	101.0
Ammonia-N (mg/L)	0.200	0.075	0.110	0.085	0.011	0.294
TKN (mg/L)	1.55	1.68	1.55	1.61	1.90	2.94
Total phosphorus (mg/L)	0.1	<0.05	<0.05	<0.05	<0.05	0.06
Total carbon (mg/L)	91.6	65.9	86.8	107.0	92.0	104.0

TOC (mg/L)	nd	nd	19.3	23.1	37.1	36.3
TIC (mg/L)	nd	nd	67.5	83.9	54.9	67.7
True color (Co units)	30	65	25	40	45	55
Turbidity (NTU)	53.1	0.5	14.9	6.0	1.0	5.7
Silicon (mg/L)	2.0	1.0	2.0	1.0	3.0	4.0
Total chlorophyll (µg/L)	21.7	2.3	15.9	16.1	3.6	24.6
13-Sep-94						
Sample time (CST)	14:49	15:09	14:30	10:05	9:45	9:15
Water temperature (°C)	17.0	21.5	18.0	16.0	15.0	15.0
Water depth (m)	0.62	0.60	0.56	0.60	0.66	0.60
Secchi depth (m)	0.39	0.60	0.38	0.58	0.66	0.56
pH (field)	8.4	9.2	8.5	8.1	9.2	9.5
pH (lab)	8.6	9.4	8.7	8.2	9.2	9.1
Conductivity (µS/cm)	1660	1200	1650	1910	5080	1930
Calcium (mg/L)	56.2	26.9	58.0	63.2	51.1	29.7
Magnesium (mg/L)	65.1	46.0	64.9	72.7	331.0	82.8
Sodium (mg/L)	211	161	207	240	614	257
Potassium (mg/L)	11.6	19.5	13.2	16.1	20.5	33.9
Manganese (mg/L)	0.145	0.034	0.135	0.371	0.081	0.114
Iron (mg/L)	0.11	<0.01	0.08	0.04	0.02	0.02
Sulphate (mg/L)	172.0	63.9	164.0	169.0	846.0	133.0
Chloride (mg/L)	276	221	280	331	1210	354
Carbonate (mg/L)	21	45	30	nd	75	51
Bicarbonate (mg/L)	320	186	412	418	159	305
Nitrate+nitrite (mg/L)	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Fluoride (mg/L)	0.22	0.21	0.22	0.26	0.16	0.28
Alkalinity (mg/L)	298	228	388	343	255	335
Hardness (mg/L)	408	257	412	457	1490	415
TDS (mg/L)	970	675	1020	1100	3230	1090
Ionic balance (%)	101.0	104.0	91.8	101.0	99.5	104.0
Ammonia-N (mg/L)	<0.050	0.110	0.089	0.075	<0.050	0.186
TKN (mg/L)	1.53	1.58	1.60	1.80	1.73	2.43
Total phosphorus (mg/L)	0.14	<0.05	0.14	0.13	<0.05	0.09
Total carbon (mg/L)	nd	nd	nd	nd	nd	nd
TOC (mg/L)	15.2	22.0	16.5	16.2	37.9	35.6
TIC (mg/L)	nd	nd	nd	nd	nd	nd
True color (Co units)	25	60	30	30	40	55
Turbidity (NTU)	13.9	0.8	13.3	6.9	1.3	7.0
Silicon (mg/L)	4.0	0.1	4.2	7.0	nd	nd
Total chlorophyll (µg/L)	nd	nd	nd	nd	nd	nd

Field evidence for multiple host contacts during blood feeding by *Culex tarsalis, Culex restuans* and *Culex nigripalpus* (Diptera: Culicidae)

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Introduction

Some mosquitoes attracted to bait hosts have ingested blood recently (Mitchell and Millian 1981; Trpis and Hausermann 1986). Though blood meal identification studies repeatedly have shown that many North American *Culex* vectors of encephalitis viruses ingest blood from more than one type of animal in a single gonotrophic cycle (Edman and Downe 1964; Cupp and Stokes 1976), no information is available with regard to multiple feeding by most species of *Culex* on conspecific avian hosts.

We use the term *multiple feeding* to describe the situation in which a mosquito ingests some blood from at least 2 hosts during a single gonotrophic cycle. This is distinct from the situation in which a mosquito is interrupted during blood uptake, but returns to the same host to complete the blood meal. Multiple feeding during a single gonotrophic cycle may occur for either of 2 distinct reasons. In 1 case, 2 or more hosts may be bitten if mosquitoes are prevented from acquiring sufficient blood from one host to induce neural and hormonal mechanisms which inhibit further blood feeding (Klowden 1988). Interruption of blood uptake before satiation is associated most commonly with defensive behavior by the hosts (Edman and Scott 1987, Davies 1990). This would be the prevalent situation for gonotrophically concordant species that require only 1 blood meal per reproductive cycle. Alternatively, species that require several blood meals for oogenesis or for metabolic reserves may continue to host seek (perhaps daily) between one oviposition event and the next. This is the case for some *Anopheles* (Klowden and Briegel 1994) and *Aedes aegypti* (Trpis and Hausermann 1986; Scott *et al.* 1993).

The objective of our study was to use a novel marking technique to determine if *Culex tarsalis* Coquillett, *Culex restuans* Theobald and *Culex nigripalpus* Theobald take multiple meals on conspecific avian hosts. Such information would provide insight as to whether multiple feeding on conspecific hosts is a behavioral phenomenon that has been overlooked in previous blood feeding studies based on serological methodology.

Materials and Methods

Following the preliminary work of Kimsey and Kimsey (1984), in which rubidium was used as a host-blood marker, Anderson *et al.* (1990) developed a blood-marking technique in which rubidium is injected into 1 of 2 hosts (such as quail) and cesium is injected into the other. Pairs of birds marked in this way are made available to host-seeking mosquitoes and the blood meals are assayed for the presence of both rubidium and cesium. This technique permits the identification of mosquitoes that have obtained blood from 1 or both birds in the pair, although interrupted meals resumed on the same host are not detectable.

Blood feeding by wild mosquitoes was studied in Manitoba, Canada, at Delta Marsh during 1991 and at Winnipeg during 1993. Delta Marsh is a large freshwater marsh (>20,000 ha) at the south end of Lake Manitoba. The Winnipeg site is located on the University of Manitoba campus along the Red River. Both sites provide extensive breeding habitat for passerine birds and mosquitoes such that large populations of both coincide during the summer.

Box traps (30 by 30 by 30 cm) (Fig. 1) with baffled, slotted entrances (narrowing from 30 by 8 cm to 30 by 2 cm) on the underside were used to capture mosquitoes attracted to the quail. The baffled entrances were

constructed of fine mesh to permit downward movement of host odors. Traps were suspended ≈ 1 m above the ground on the edge of wooded areas at each location in Manitoba. Traps were baited with pairs of numbered, Japanese quail (*Coturnix japonica* Temminck & Schlegel). Quail were 8-12 wks old and weighed, on average, 120 g. Overall, 102 pair of quail were used during 1991, and 40 pair of quail were used during 1993.

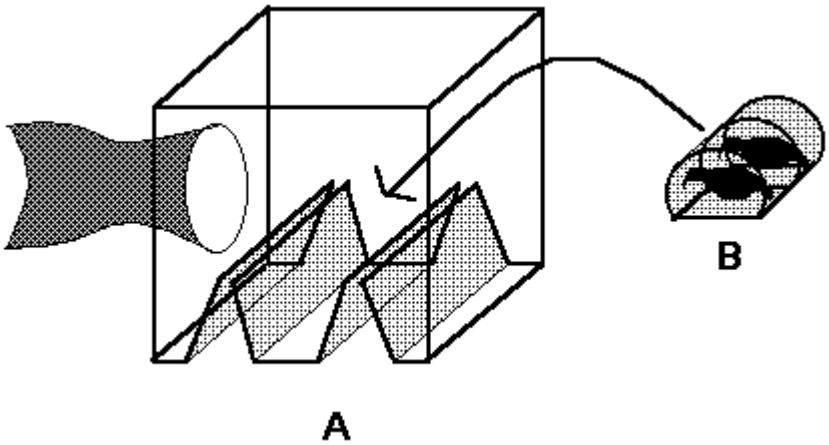

Figure 1. Box trap used to collect blood-fed mosquitoes attracted to marked quail. (A) Trap design. (B) Wire cage for quail. Arrow indicates the position of the wire cage within the trap

Quail were placed in cylindrical, wire cages (25 by 15 cm diameter, mesh size 1.3 by 1.3 cm) (Fig. 1) which were inserted through the stocking sleeve and placed between the baffles in the box traps (Fig. 1). (All experiments that involved the use of animals conformed to guidelines contained in the "Guide to the Care and Use of Experimental Animals", vol. 1., Canadian Council on Animal Care, and experimental protocol #C-91-46 was approved by the University of Manitoba Animal Care Committee.) These small cages restricted the quail from access to the inside surfaces of the box trap to prevent resting mosquitoes from being eaten; however, the quail had sufficient room to turn around, stretch and, groom themselves. One quail of each pair was injected with the alkali metal rubidium and the other with cesium. Rubidium and cesium circulate in the blood for several days, are assayed easily in blood fed mosquitoes, and permit the unequivocal determination of which bird was fed upon by each mosquito in a particular trap (Anderson *et al.* 1990). If both metals are present in a single mosquito, then that mosquito obtained blood from both hosts during the period of exposure.

Box traps were placed in their field locations ≈ 30 min before sunset and were collected within 30 min of sunrise. At collection, the no-return entrances were sealed with foam rubber plugs and the quail cages were removed through a sleeve of surgical stocking. Quail were returned to the flock cage and box traps were placed in a freezer at -20°C to kill the mosquitoes.

The same method was used to collect blood-fed *Cx. nigripalpus* in Florida in August of 1992, except that Northern Bob-white (*Colinus virginianus* L.) were used as bait animals to attract *Cx. nigripalpus* and to measure multiple feeding by this species. The average weight of the northern bob-white was 95 g. Twenty-six pairs of quail were used during this part of the study. All mosquitoes were collected in the hardwood hammock that surrounds the Florida Medical Entomology Laboratory at Vero Beach. Box traps were of similar design to those used in Manitoba, except that they were made from clear acrylic (plastic) rather than plywood. Exposure times also were from before sunset to after sunrise, but the number of hours exposure was not equivalent because of significant latitudinal differences between central Florida and Manitoba.

Mosquitoes collected from all quail-baited traps were identified and blood-fed individuals were retained for rubidium and cesium analysis by atomic emission flame spectrophotometry (Anderson *et al.* 1990). The mosquitoes collected in one box trap during a given sunset to sunrise collection period were defined as a sample. Thus, each sample provided a replicate measure of the frequency (expressed as percent) of multiple host contacts. Only blood-fed mosquitoes positive for either rubidium or cesium were included in the number blood fed per sample. The few blood-fed mosquitoes in some of the samples that were negative for both rubidium and cesium presumably obtained blood from other sources and were excluded from the calculation described above.

The frequency of multiple feeding per sample was calculated as the number of blood-fed mosquitoes with both rubidium and cesium, divided by the total, marked, blood-fed individuals of that species. Initially, all blood-fed *Cx. tarsalis* collected in 1991 were lumped together to calculate the overall frequency of multiple feeding by this species. The same approach was used for *Cx. nigripalpus* collected in 1992 and for *Cx. restuans* and *Cx. tarsalis* collected in 1993. Estimates of the range in frequency of multiple feeding were based on samples in which at least 17 mosquitoes blood fed on the quail. According to the binomial expansion, 17 is the minimum number of blood-fed mosquitoes per sample for which an increase of 1 multiple blood meal does not result in rejection of the null hypothesis that the true frequency of multiple feeding is 5%. In other words, samples smaller than 17 were considered unreliable. We initially estimated the overall frequency of multiple feeding by *Cx. tarsalis*, *Cx. restuans* and *Cx. nigripalpus* to be 5% based on combining the data for each species collection. The mean, standard error and confidence limits of the frequency of multiple feeding by species and year of collection were calculated directly from the quotients of number of 2-host meals divided by the number of quail-fed mosquitoes multiplied by 100.

In addition to the direct evidence of multiple feeding by double-marked mosquitoes described above, 2 sources of indirect evidence for other mosquitoes with high potential for refeeding are provided. First, blood meals were assigned to 1 of 4 size classes: trace, one-quarter full, one-half full, and full according to the criteria of Edman *et al.* (1975) to provide information on the extent of multiple feeding by partially and fully engorged mosquitoes. Edman *et al.* (1975) found that *Cx. nigripalpus* with half a full blood meal or less were more likely to refeed than were females with greater than a half full blood meal. In our study, mosquitoes with a half blood meal or less (partial meals) and both rubidium and cesium were individuals that had taken blood from 2 hosts and were considered likely to refeed again. The means of the percentages of multiple feeding for each species collection were compared by ANOVA (Statistix 1992). Confidence limits of the percentage of multiple feeding that resulted in partial blood meals were calculated from the binomial expansion (Sokal and Rohlf 1981).

Second, mosquitoes in the box traps that contained fresh blood, but negative for both markers were assumed to be host-seeking, although already engorged. Very few (<<1% of all mosquitoes collected in the box traps) were gravid or teneral females or males.

Results

In Manitoba in 1991, 13,857 female mosquitoes were collected in 165 trap-nights with pairs of marked quail as bait. Of these mosquitoes, 5,218 were *Cx. tarsalis* and 3,102 (59%) had ingested blood from at least 1 quail. In Manitoba in 1993, 4,141 female mosquitoes were collected in 40 trap-nights of which 2,027 were *Cx. restuans* and 1,764 were *Cx. tarsalis*. Overall, 1,409 (70%) of the *Cx. restuans* and 1,207 (68%) of the *Cx. tarsalis* ingested blood from at least 1 quail. In Florida in 1992, 2,110 female mosquitoes were collected, of which 2,041 (97%) were *Cx. nigripalpus*; 857 (42%) had ingested blood from at least 1 of the quail.

Overall, 331 of 6,575 (5.03%) engorged *Culex* took blood from 2 quail. The percentage and sample size of multiple host contacts by species were 5.09% of 3,102 engorged *Cx. tarsalis* collected in 1991, 4.14% of 1,207 engorged *Cx. tarsalis* collected in 1993, 5.39% of 1,409 engorged *Cx. restuans* collected in 1993, and 5.48% of 857 engorged *Cx. nigripalpus* collected in 1992. The range in frequency of patent multiple blood meals is given for samples with at least 17 marked, blood-fed mosquitoes in Table 1. The frequency of multiple blood feeding did not differ among the species studied.

Table 1. Variation in the frequency of multiple host contacts by *Culex tarsalis* and *Culex restuans* on Japanese quail and *Culex nigripalpus* on northern bob-white. There are no significant differences among the mean percentages (ANOVA, Analytical Software 1992). LCL, lower confidence limit; UCL, upper confidence limit; confidence interval = 95%. n, number of samples in which > 17 mosquitoes blood-fed on >1 quail.

		% Frequency			
Species		Mean±SE	LCL-UCL	Min-Max	*n*

Culex tarsalis	1991	5.5 ± 0.88	3.7 - 7.3	0 - 15.2	25
	1993	5.0 ± 1.34	2.2 - 7.8	0 - 18.5	20
Culex restuans		5.5 ± 2.00	1.4 - 9.6	0 - 33.3	18
Culex nigripalpus		6.2 ± 1.02	4.1 - 8.4	0 - 17.6	20

The number and frequency (expressed as percent) of mosquitoes that took blood from both quail, but for which the blood meals were graded as partial are given by species in Table 2. Multiple host contacts that resulted in partial meals by *Cx. nigripalpus* occurred at a significantly greater frequency than for *Cx. tarsalis* collected in 1991.

Table 2. Number and frequency of multiple blood meals that were partial (those for which the total volume was < ½). Percentages followed by the same letter are not significantly different (Sokal and Rohlf 1981).

Species		Partial/Multiple	%	LCL-UCL
Culex tarsalis	1991	21/158	13.3a	9.0 - 19.6
	1993	8/50	16.0ab	8.6 - 29.1
Culex restuans		13/76	17.1ab	10.4 - 27.5
Culex nigripalpus		15/47	31.9b	20.9 - 47.1

The number and frequency of blood-fed mosquitoes that had ingested blood before attraction to the quail (unmarked with either rubidium or cesium) are given in Table 3. These are minimum estimates, because previously engorged mosquitoes that obtained blood from either quail would not be included in this category. The frequency of unmarked blood meals was greatest for *Cx. nigripalpus* and the 1993 *Cx. tarsalis* collection. More than 85% of unmarked blood meals were partial according to the grading scheme of Edman *et al.* (1975) (Table 3).

Table 3. Number of blood-fed mosquitoes that acquired blood (unmarked with rubidium or cesium) before entering traps baited with quail. Numbers followed by the same letters are not significantly different (Sokal and Rohlf 1981). [a]Total blood-fed mosquitoes in which neither rubidium nor cesium was detected: defined as unmarked. [b]Marked + unmarked, blood-fed mosquitoes in quail baited traps. [c]Unmarked blood meals as a percentage of all blood-fed mosquitoes. [d]Percentage of unmarked, partial blood meals, according to the criteria of Edman et al. (1975). All percentages in this column are not significantly different (Sokal and Rohlf 1981).

Species		Total[a]/Blood-fed[b]	%[c]	Partial/Total[a]	%[d]
Culex tarsalis	1991	39/3141	1.2a	38/39	97.4
	1993	25/1232	2.0ab	24/25	96.0

Culex restuans		15/1424	1.0a	13/15	86.7
Culex nigripalpus		31/ 888	3.5b	27/31	87.1

Discussion

Blood from 2 or more hosts, distinguishable at the species or family level by serology, has been demonstrated many times in the guts of individual mosquitoes of many species (Edman and Downe 1964; Cupp and Stokes 1976). However, multiple feeding on individuals of the same species (cryptic meals) has been demonstrated only for a few anopheline and culicine species feeding on humans with distinct ABO blood groups or haptoglobins (Boreham *et al.* 1978; Boreham and Lenahan 1979; Burkot *et al*. 1988). Avians are important hosts for *Cx*. *tarsalis*, *Cx*. *restuans*, and *Cx*. *nigripalpus* (Washino and Tempelis 1983). Often, a few species of passerine birds are most important for virus amplification (Holden *et al.* 1973). Traditional serological methods are not adequate for detection of multiple feeding on conspecific hosts, but multiple feeding in this situation may be of importance in the enzootic transmission of virus.

Furthermore, many avian species often aggregate in colonial nesting areas, on the nest, at roosts, and at feeding sites (Weatherhead 1981, 1983). Behavioral studies of interactions between host-seeking mosquitoes and avian hosts have shown that birds may interrupt blood feeding such that mosquitoes potentially may contact more than one host of the same species in the course of obtaining a full blood meal (Kale *et al.* 1972; Webber and Edman 1972).

In our study, *Cx*. *tarsalis*, *Cx*. *restuans*, and *Cx*. *nigripalpus* took multiple meals from conspecific avian hosts. Although the overall frequencies were close to 5%, the maximum observed frequencies ranged from 13.6% for *Cx*. *tarsalis* to 33.3% for *Cx*. *restuans*. Edman (1974) recorded <1% multiple feeding by *Cx*. *nigripalpus* from Florida. Edman and Downe (1964) recorded overall percentages of multiple meals by 13 species of mosquitoes in 5 genera, including *Cx*. *tarsalis*, (21.5% multiple), *Cx*. *salinarius* Coquillett (36.7% multiple), and *Cx*. *pipiens* L.(20% multiple). Cupp and Stokes (1976) noted that 13% of 328 *Cx*. *salinarius* took multiple meals. Anderson et al. (1990) observed that 19% of *Cx*. *quinquefasciatus* Say ingested blood from 2 chickens in the laboratory. Additionally, multiple feeding by *Culex* mosquitoes on conspecific hosts is not restricted to ornithophagic species. For example, Boreham *et al*. (1978) found that from 7.5% to 19.8% of *Cx*. *quinquefasciatus* Say collected in Kisumu, Kenya, imbibed blood from 2 or more human hosts.

The box trap used in our study was designed to retain mosquitoes during and after blood feeding on the quail, and this may have resulted in unnaturally high multiple feeding by keeping the mosquitoes in close proximity to hosts. Also, our use of quail as model avian hosts may not reflect perfectly the response of mosquitoes to passerine birds. However, with one exception, the estimates of the frequency of multiple feeding on conspecific hosts by the species in our study accord well with estimates from other studies of multiple feeding by *Culex* mosquitoes on natural hosts (Edman and Downe 1964; Cupp and Stokes 1976).

Despite the potential bias presented by the trap design, we feel that the frequencies of multiple feeding observed in our study likely represent an underestimate of the frequency of host contacts that involve secretion of saliva. We measured only host contact based on blood uptake. Mosquitoes may salivate into a host without ingesting blood (Ribeiro 1987). Furthermore, many mosquitoes (up to 31.9% in our study, Table 2) that had made at least 2 host contacts and ingested detectable amounts of blood were likely to blood feed again because the total amount of blood obtained from 2 hosts probably was still not sufficient to inhibit further blood feeding (Edman et al. 1975). Additionally, we observed that up to 3.5% of blood-fed mosquitoes attracted to the quail had first ingested blood from other sources (Table 3).

Our data provide a basis for challenging the assumption of 1 host contact per mosquito per gonotrophic cycle for the purposes of modeling vectorial capacity (Smith 1987). Multiple host contacts may increase the number of opportunities for individual mosquitoes to both acquire and transmit virus. Contact between mosquitoes and vertebrate hosts appears twice in the vectorial capacity model as multiplied terms. Effectively, disease transmission increases as the square of the increase in frequency with which mosquito vectors feed on amplifying vertebrate hosts (Dye 1992). For example, 5% multiple feeding may result in more than a 10% increase in transmission (Fig. 2). Vectorial capacity may be underestimated if it is assumed that each mosquito bites 1 host each gonotrophic cycle. Our contention that transmission may increase as a result of multiple feeding rests on 2 assumptions. First, we assume that small meals taken during multiple feeding by uninfected mosquitoes produce infective vectors. Second, we assume that a single mosquito is capable of delivering virus to more than one host during serial probing. Once infected with Western Equie Encephalitis Virus or Saint Louis Encephalitis Virus, *Cx. tarsalis* generally are infected for life (Henderson *et al.* 1979; Mitchell *et al.* 1980; Hardy 1987). Multiple feeding by 3 species of North American *Culex* occurred in 2 geographically distinct locations. Clearly, more attention should be paid to the dynamics of interrupted and multiple blood feeding on similar and dissimilar hosts with regard to disease transmission.

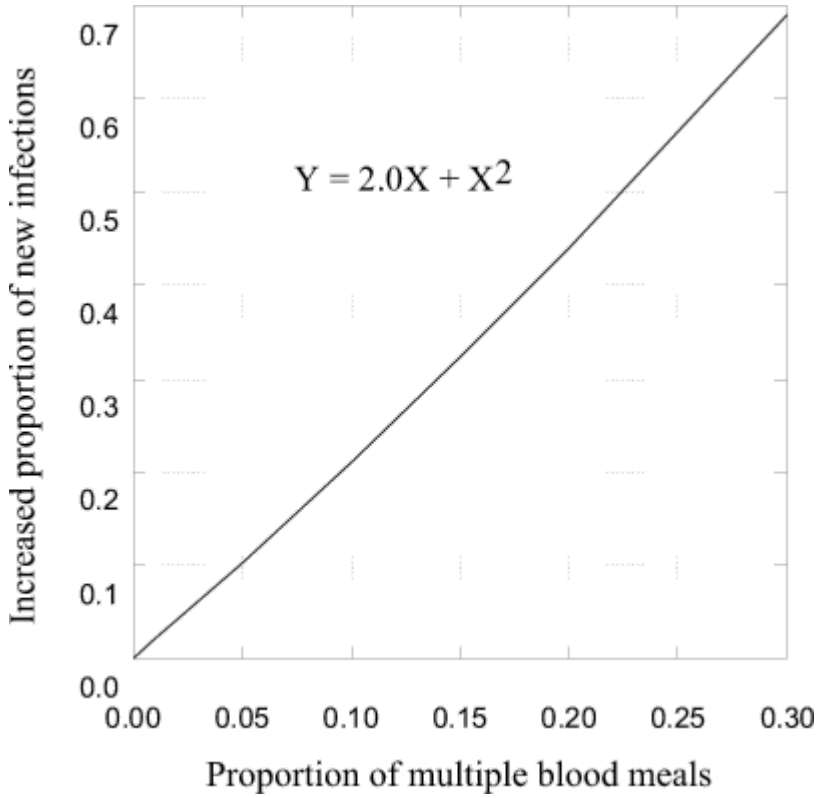

Figure 2. Relationship between increase in reproductive rate (R) of an arbovirus during amplification in an avian population and increase in vectorial capacity caused by multiple feeding of mosquitoes. The relationship is calculated for the range in multiple feeding (0-30%) observed in our study, and according to the formula advanced by Smith (1987). Increase in transmission is calculated relative to R = 1 for stable tranmsission. From Smith's model (1987), 2 parameters associated with mosquito-host contact, "M" (average number mosquitoes per host per day) and "B" (average number of blood meals per mosquito per day), have been increased by the proportion representative of multiple feeding such that the calculation yields a squared relationship between the increase in host contacts caused by multiple feeding and the increase in R.

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Interrupted and multiple blood feeding by natural populations of *Culex tarsalis*, *Culex restuans* and *Culex nigripalpus* (Diptera: Culicidae) in relation to differences in tolerance to mosquito attack among individual hosts

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Introduction

The frequency at which mosquitoes contact vertebrate hosts is an important aspect of the epidemiology of vector-borne disease (Dye 1992). In most models of disease transmission, it is assumed that there is only 1 host contact per mosquito per gonotrophic cycle, (de Moor and Steffens 1970; Smith 1987). This assumption often is violated because mosquitoes may feed more than once prior to the first batch, or during the period between egg batches. In so doing, they contact more than one host (Edman and Downe 1964; Boreham and Garrett-Jones 1973; Burkot *et al.* 1988; Anderson *et al.* 1990; Scott *et al.* 1993; Anderson and Brust, in press). Thus, it is important to understand factors that influence blood feeding frequency and to estimate accurately the rate of mosquito-host contact.

Multiple meals with blood from distinguishable hosts are defined as patent (Boreham and Garrett-Jones 1973), while those in which serial feeding attempts involve the same individual host or multiple hosts indistinguishable by conventional techniques are defined as cryptic. Boreham and Garrett-Jones (1973) estimated the frequency of cryptic multiple feeding by multiplying the ratio of the probability of a cryptic double meal (the probability of one host being fed on squared) to the probability of a patent double meal (the probability of one host being fed on times the probability of a second host being fed on) by the proportion of detected patent multiple meals. They assumed explicitly that the same hosts are available during both feeds and that the source of each feed is chosen randomly. Burkot *et al.* (1988) extended the model of Boreham and Garrett-Jones (1973) to include the probability of interruption on each of at least two possible hosts and assumed these probabilities to be equal. However, there is significant variation in defensive behavior of individual hosts, either of the same or different species (Edman *et al.* 1972; Kale *et al.* 1972). Consequently, the tendency of vertebrate hosts to interrupt blood feeding mosquitoes may be a more variable phenomenon than assumed by Burkot *et al.* (1988).

One objective of our paper is to examine the extent to which individual avian hosts vary relative to other individuals of the same species, sex, size and age in the frequency at which they are fed on by 3 species of ornithophilic *Culex*. Another objective of our paper is to use blood-meal size to estimate and compare the frequency of interrupted blood meals on individual hosts. Additionally, we examine the way in which the frequency of interrupted and multiple feeding by mosquitoes is related to variation in the degree to which individual hosts are fed on by mosquitoes.

Materials and Methods

Mosquitoes were collected in box traps (Anderson and Brust, in press) at Delta Marsh, Manitoba in 1991, at Vero Beach, Florida in 1992 and at Winnipeg, Manitoba in 1993. Each box trap was baited with two quail, one of which was injected with rubidium and the other with cesium (Anderson *et al.* 1990). (All experiments which involve the use of animals conform to guidelines contained in the Guide to the Care and Use of Experimental Animals, Vol. 1., Canadian Council on Animal Care and experimental protocol #C-91-46 has been approved by the University of Manitoba Animal Care Committee.) Rubidium and cesium can be used as host-blood markers to permit identification of hosts of mosquito blood meals and for detection of multiple feeding (Anderson *et al.*

1990). Two hosts were caged together, instead of singly, to determine if mosquitoes imbibe blood at equal frequencies from equally available sources. Additionally, the two host flock provided the opportunity for mosquitoes interrupted during feeding to resume, possibly on a second individual. With this experimental design, we were able to relate the frequency of multiple feeding to the joint probabilities of each host being fed on. Japanese quail (*Coturnix japonica* Temminck and Schlegel) were used in Manitoba and Northern Bob-white (*Colinus virginianus* L.) were used in Florida.

All mosquitoes collected in the box traps were identified, counted and sorted for engorged specimens. The size of blood meals was graded as ≤ ½ full or replete according to the criteria of Edman *et al.* (1975), who found that *Culex nigripalpus* Theobald with a partial blood meal ≤ ½ full were likely to continue blood feeding. In our study, mosquitoes with ≤ ½ of a blood meal and only one marker were assumed to have been interrupted at least once by the correspondingly-marked host before satiation (Edman *et al.* 1975). Multiple blood meals, or those with both markers were also assumed to have been interrupted and then resumed on the other host.

Blood-fed mosquitoes were analyzed individually for rubidium and cesium. A mosquito with only 1 marker was defined as having 1 blood meal. A mosquito with both markers was defined as having 2 blood meals. The probability of each quail being fed upon was calculated as the number of marked meals of one type divided by the total, marked meals of both types for each trap night. For the purposes of this calculation, each component of a multiple feeding is considered to be one meal. If there was no difference in tolerance to mosquito attack between the birds in a trap, we would expect that approximately equal numbers of blood meals during most trap-nights would be from each bird. The proportions of blood meals taken from each of the two possible hosts in each cage were plotted to illustrate the frequency with which blood feeding was distributed evenly or unevenly among the quail. For each sample size represented by the number of blood meals per trap night, confidence limits were calculated for the value 0.5 and for the proportion of blood meals that represented the split between rubidium-marked meals and cesium-marked meals. The difference between these proportion was considered significant if there was no overlap of the confidence intervals at $p = 0.05$ (2-tailed).

Only trap nights with at least 17 marked, engorged mosquitoes are presented, and estimates of the range in frequency of multiple feeding were based on these samples. According to the binomial expansion, 17 is the minimum number of blood-fed mosquitoes per sample for which an increase of one multiple blood meal does not result in rejection of the null hypothesis that the true frequency of multiple feeding is 5%. We initially estimated the overall frequency of multiple feeding by *Cx. tarsalis*, *Cx. restuans* and *Cx. nigripalpus* to be 5% based on combining the data for each species collection (Anderson and Brust, in press). The trap nights are sorted by magnitude of the proportion value that represents the split between the blood meals from the rubidium-injected quail and the cesium-injected quail. For the purposes of this paper, *Cx. restuans* and *Cx. tarsalis* collected in the same trap night in 1993 were combined as a single category, *Culex*. Both species are aviophilic and preliminary analysis indicated that feeding success of both species was approximately equal.

An index of interrupted feeding for the mosquitoes fed from each quail was calculated in the following way. For meals ≤ ½ full and only one marker, a probability of interruption of 1 was assigned to the correspondingly marked host for each meal. For multiple meals, a probability of interruption of 0.5 was assigned to each host for that particular blood meal (Burkot *et al.* 1988). The number of meals interrupted by a particular host equals the number of correspondingly-marked meals ≤ ½ full plus 0.5 X the number of multiple meals. The total number of blood meals originating on each quail equals the number of completely or partially fed female mosquitoes plus 0.5 X the number of multiple meals. The number of interrupted meals from one quail divided by the total number of blood meals originating on that quail is used as an index of the probability of interruption by that host. It is not an exact estimate because of cryptic meals. The indices of interruption for both quail in each pair were compared as a ratio of the greater to lesser probability of interruption for each trap night. The frequency distribution of this ratio was used to calculate the probability with which differences in the rate of interruption would occur for a given pair of quail. Only trap nights with at least 10 engorged mosquitoes from each quail were used for this analysis so that a difference in the proportion of interrupted meals due to 1 blood fed mosquito would not exceed 0.1. We examined the relationship between the probability of being fed on and the probability of interruption for each quail using regression analysis.

Burkot *et al.* (1988) showed mathematically that the highest frequencies of multiple feeding should occur in situations in which there is little or no difference in the probability of each of two hosts being fed upon. For a 2-host flock as in our experimental design, our null hypothesis is that the probability of feeding on each quail is 0.5. Therefore, as the proportion of blood meals from one bird deviates away from 0.5, we expect to see a corresponding decrease in the proportion of multiple meals. Accordingly, we examined the relationship between the probability of detecting multiple meals and the deviation from an even distribution of blood meals on each bird (0.5 rubidium and 0.5 cesium).

Results

A total of 70 box trap collections (trap nights) had at least 17 blood fed *Culex* in each (Anderson and Brust, in press). In 25 of these trap nights from the Delta Marsh site in 1991, *Cx. tarsalis* was the dominant species (> 80% of mosquitoes), both in terms of total number of mosquitoes and in terms of number of blood-fed mosquitoes. In 20 trap night collections with at least 17 blood fed mosquitoes from Vero Beach, *Cx. nigripalpus* comprised more than 95% of the total. In 25 trap nights collected at Winnipeg in 1993, *Cx. tarsalis* and *Cx. restuans* were represented in approximately equal proportions and combined, accounted for more than 90% of all mosquitoes.

For *Cx. tarsalis* collected in 1991, the proportion of blood meals taken from 1 of the 2 quail in each box trap ranged from 0.047 to 0.954 (Fig. 1A). In 9 of 25 samples, the distribution of blood meals was skewed significantly away from 0.5 on each of the 2 birds (Fig. 1B). Not all of the apparently skewed proportions deviated significantly from 0.5 because confidence limits of proportions increase with decreasing numbers of individuals counted (Fig. 1A). For *Cx. nigripalpus* collected in 1992, the proportion of blood meals taken from 1 of the 2 quail in each box trap ranged from 0.154 to 0.778 (Fig. 1B). The distribution of blood meals was skewed significantly from 0.5 on each bird in only 1 of 20 samples, partly because of the low numbers of mosquitoes per trap night (Fig. 1B). For *Cx. tarsalis/Cx. restuans* combined collections from 1993, the proportion of blood meals taken from 1 of the 2 quail in each box trap ranged from 0 to 1.0 (Fig. 1C). The distribution of blood meals was skewed significantly from 0.5 on each bird in 19 of 25 samples (Fig. 1C). The density of host-seeking *Cx. tarsalis* in 1991 and *Cx. tarsalis/Cx. restuans* in 1993 was higher than for *Cx. nigripalpus* collected in 1992 (Fig. 1).

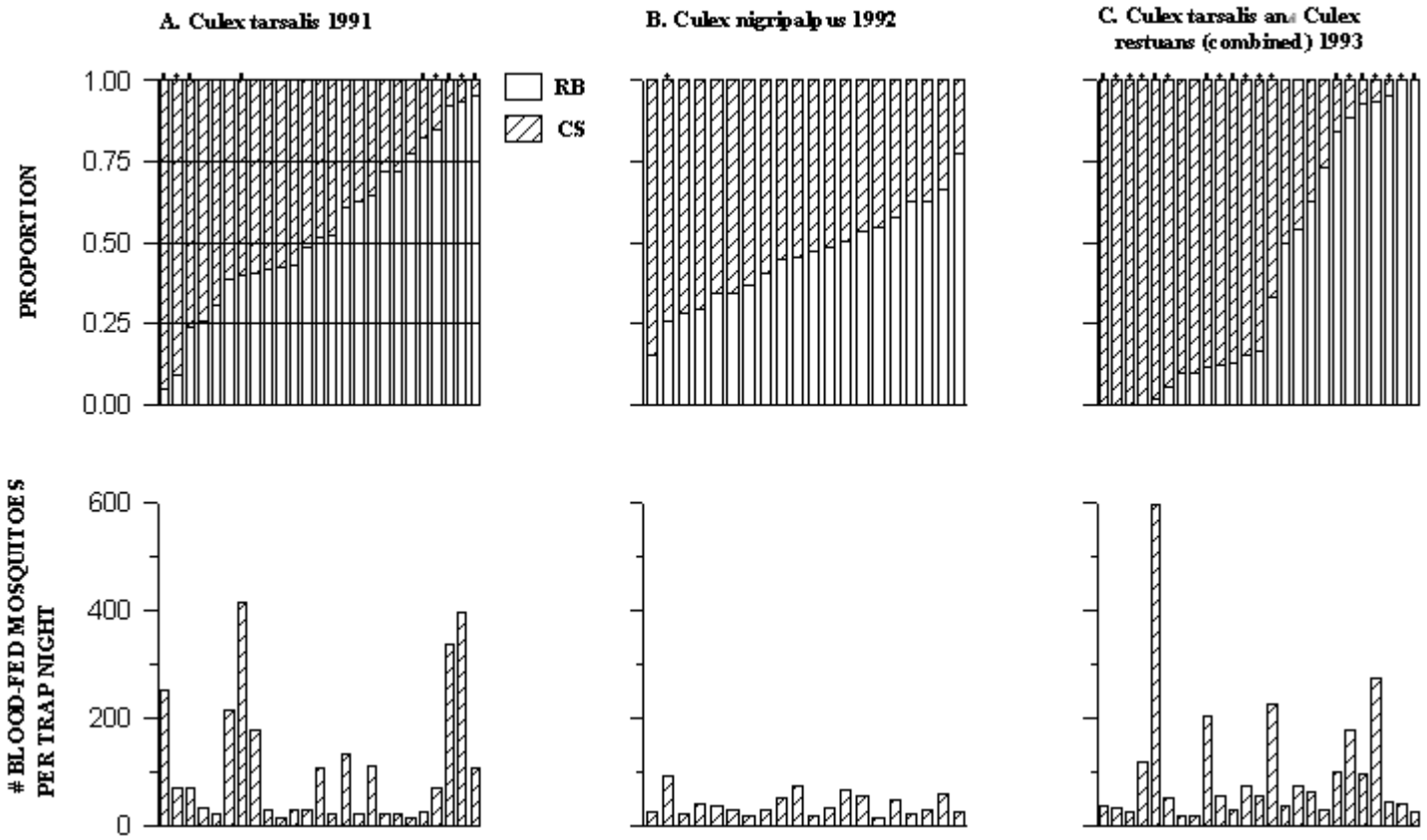

Figure 1. Distribution of mosquito blood feeding on each of two quail for each trap night with at least 17 blood fed, marked *Culex* mosquitoes. Each bar represents 1 trap night. Black bars represent the proportion of blood meals marked with rubidium. White bars represent the proportion of blood meals marked with cesium. Bars capped by filled circles denote proportions of blood meals significantly different from 0.5 on each bird. The number of marked mosquitoes for each trap night is given by the height of the crosshatched bar in the bottom graph. A) *Cx. tarsalis* collected in 1991 (25 trap nights), B) *Cx. nigripalpus* collected in 1992 (20 trap nights), C) *Cx. tarsalis* and *Cx. restuans* combined, collected in 1993 (25 trap nights)

A total of 40 trap night collections contained at least 10 blood fed mosquitoes marked with rubidium and 10 marked with cesium. For 15 trap night collections of *Cx. tarsalis* from 1991, the proportion of interrupted blood meals ranged from 0.032 to 0.583 for the rubidium-marked quail and from 0.053 to 0.727 for the cesium-marked quail (Fig. 2A). In 8 of 15 cases, interrupted blood meals were from 2 to 8.8 times more likely from 1 bird relative to the other in a given pair (Fig. 2A). For 14 trap night collections of *Cx. nigripalpus* from 1992, the proportion of interrupted blood meals ranged from 0.017 to 0.571 for the rubidium-marked quail and from 0.119 to 0.607 for the cesium-marked quail (Fig. 2B). In 5 of 14 cases, interrupted blood meals were from 2 to 6.9 times more likely from 1 bird relative to the other in a given pair (Fig. 2B). For 11 trap night collections of *Cx. tarsalis/Cx. restuans* from 1992, the proportion of interrupted blood meals ranged from 0.056 to 0.95 for the rubidium-marked quail and from 0.138 to 0.548 for the cesium-marked quail (Fig. 2C). In 5 of 11 cases, interrupted blood meals were from 2 to 4.7 times more likely from 1 bird relative to the other in a given pair (Fig. 2C).

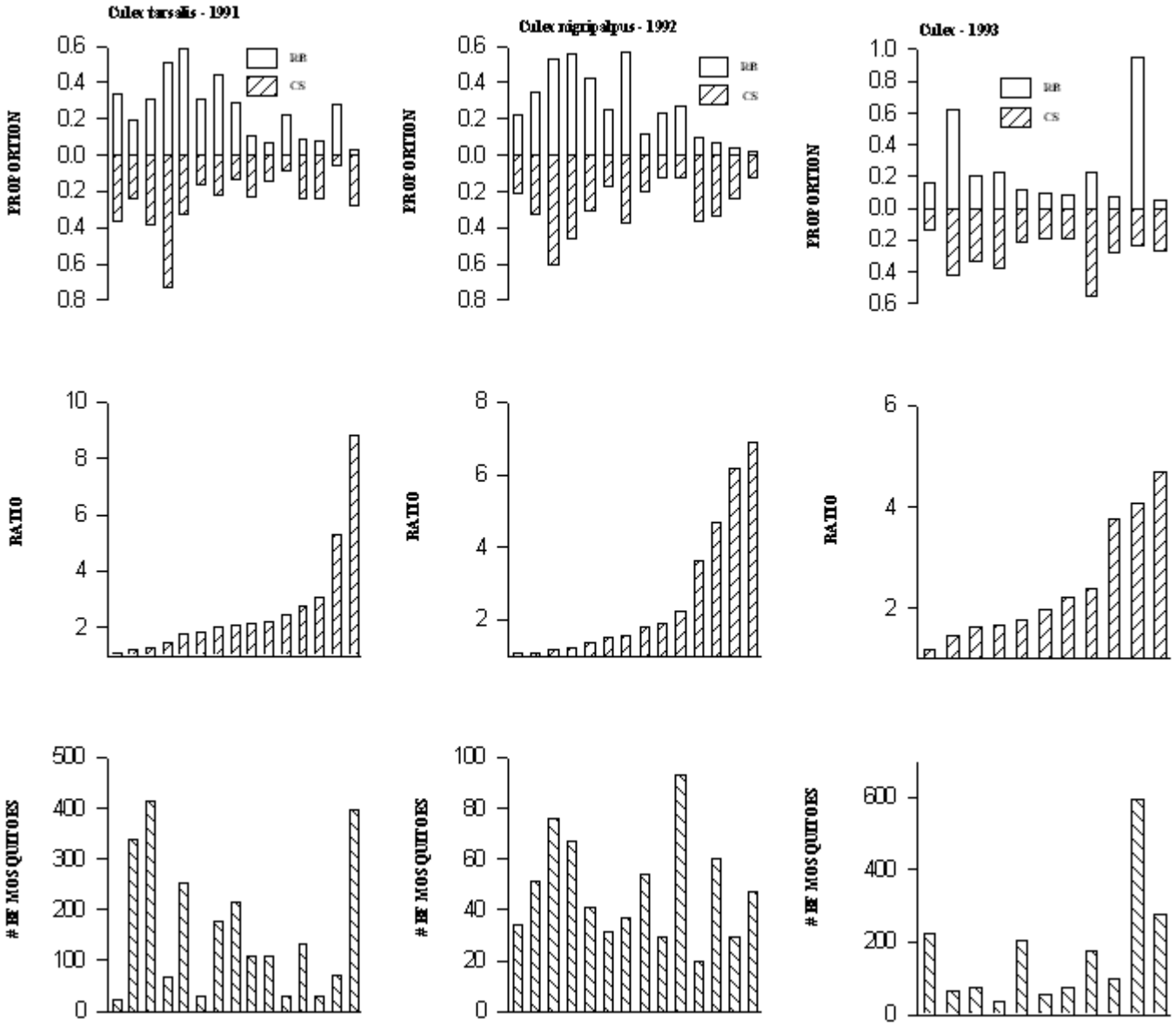

Figure 2. Proportions of interrupted blood meals (see text for definition) on each of rubidium and cesium marked quail for each trap night (top graphs). The middle graph contains the ratio of the larger proportion to the smaller from the top graph. The number of marked mosquitoes for each trap night is given by the height of the crosshatched bar in the bottom graph. Each bar represents a trap night. There are at least 10 rubidium-marked mosquitoes and 10 cesium-marked mosquitoes for each trap night represented. A) *Cx. tarsalis* collected in 1991 (15 trap nights), B) *Cx. nigripalpus* collected in 1992 (14 trap nights), C) *Cx. tarsalis* and *Cx. restuans* combined, collected in 1993 (11 trap nights)

The relationship between the probability that meals from a given bird would be ≤ ½ full and the probability of the same bird being fed upon is shown in Figure 3. The proportion of interrupted meals from a given quail was negatively correlated with the proportion of blood feeding on that quail ($p = 0.0026$) (Fig. 3). The proportion of detectable multiple meals was negatively correlated with the degree of skewness away from equal blood feeding success on each quail ($p < 0.0001$) (Fig.4).

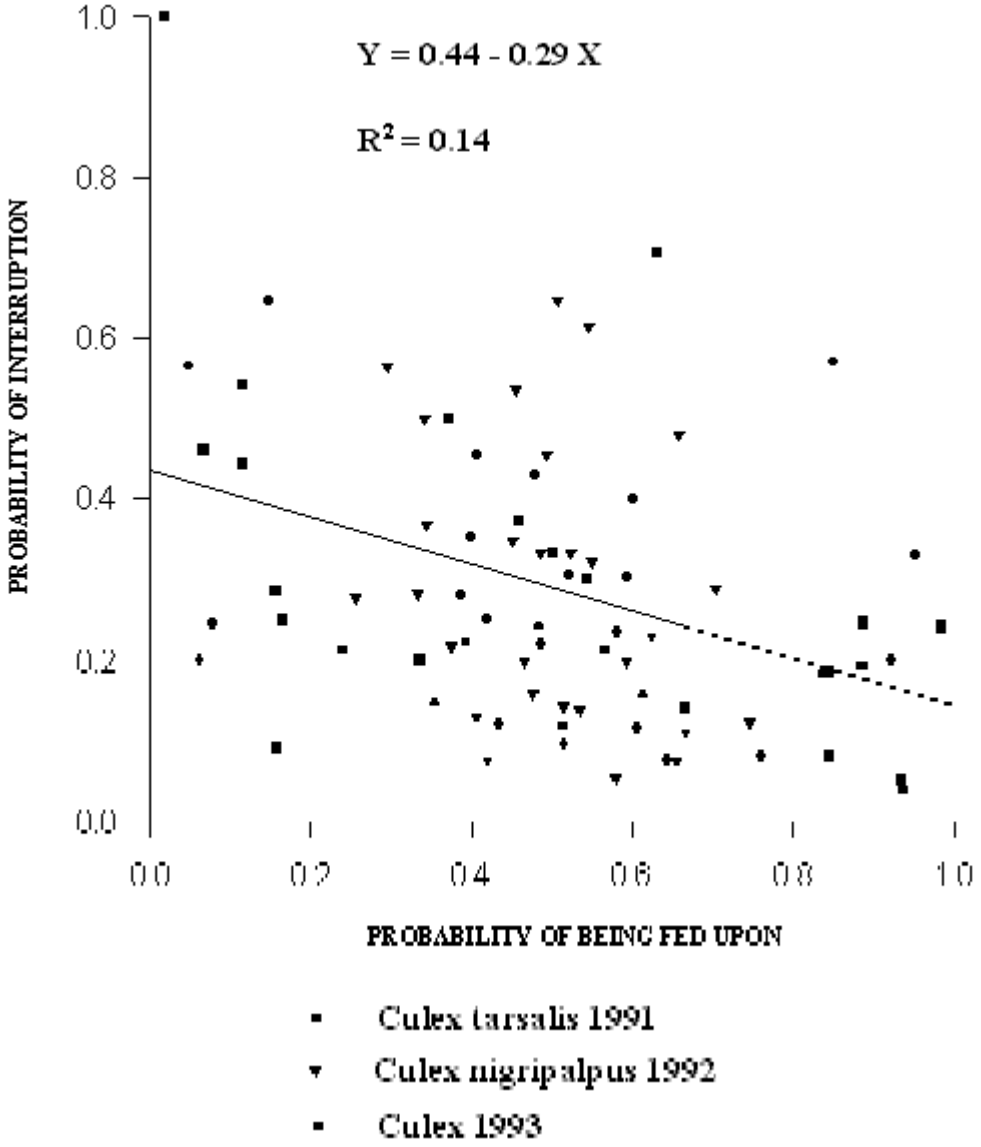

Figure 3. Relationship between the probability of a blood meal ≤ ½ full and the probability of being fed upon for each quail from trap nights with at least 10 each of rubidium-marked mosquitoes and cesium-marked mosquitoes. Symbol shapes denote the year of collection and species of *Culex* as in the figure legend. Regression is significant (p = 0.0026).

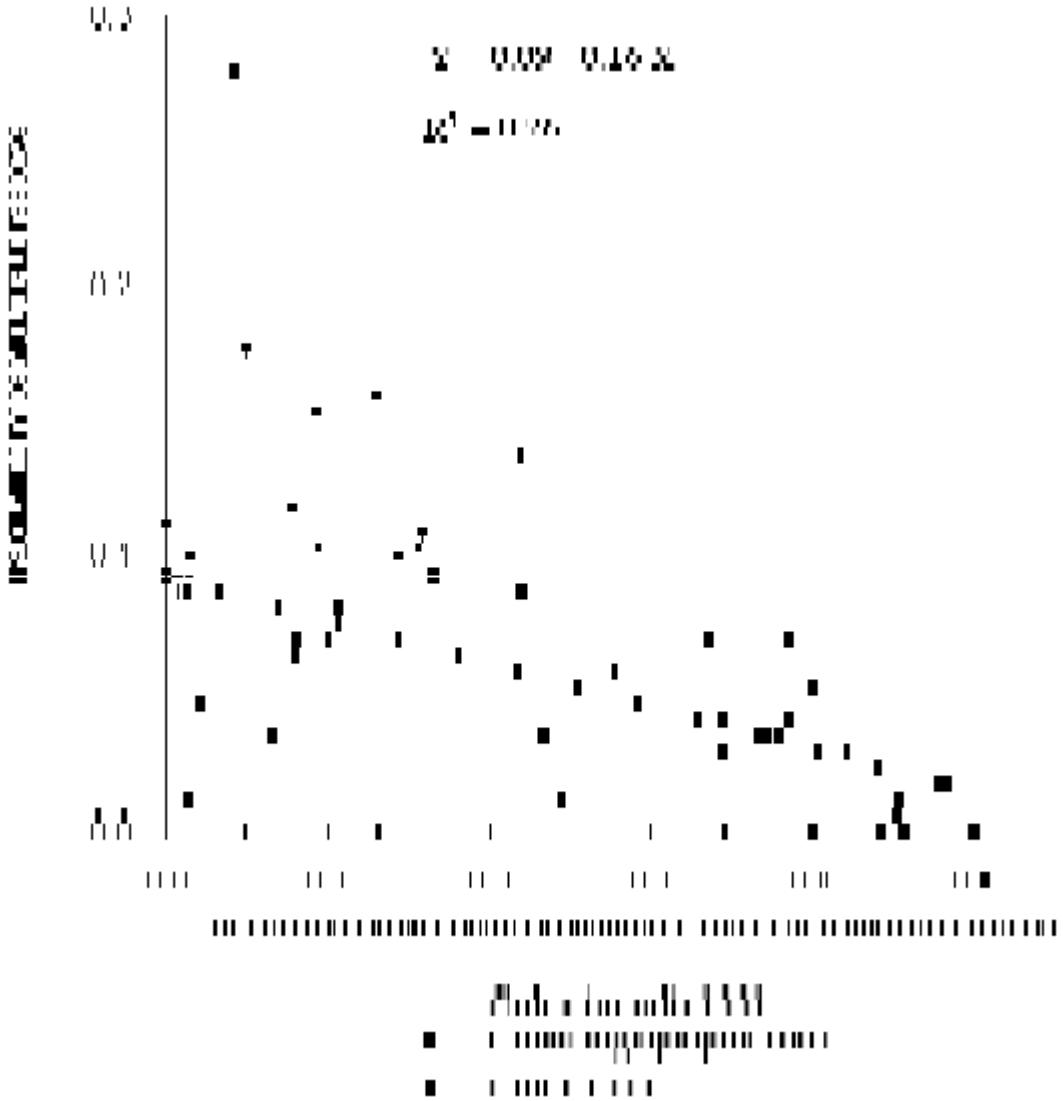

Figure 4. Relationship between probability of multiple feeding and the skewness away from equal probability of mosquitoes feeding on each bird. Each trap night has at least 17 blood-fed, marked mosquitoes. Regression is significant ($p < 0.0001$)

Discussion

Individual quail of the same species, size, sex and age vary considerably in the degree to which mosquitoes ingest blood from them (Fig. 1). The degree of skew in the distribution of blood meals between 2 possible hosts was greater for *Cx. tarsalis* collected in 1991 and for *Cx. tarsalis/Cx. restuans* collected in 1993 than for *Cx. nigripalpus* collected in 1992 (Fig. 1). This was likely due to the lower number of blood-fed mosquitoes per pair of birds in 1992 compared with the number of mosquitoes in 1993 (Fig. 1). Confidence limits of proportions increase as the number of individuals counted declines. Thus it is more difficult to reject a null hypothesis that the proportion of blood meals from each bird is equal to 0.5 for trap nights with small numbers of blood fed mosquitoes.

The proportion of mosquitoes with interrupted blood meals varied from 0.01 to 0.95 for individual quail in our study (Fig. 2). These estimates are based on physical criteria associated with blood meal size. It is difficult to compare them directly with estimates of interrupted feeding derived from the equation of Burkot *et al.* (1988) as used by Scott *et al.* (1993) for a different species of mosquito. However, in our study and in that of Scott *et al.* (1993), the estimates of the probability of interruption for blood-feeding mosquitoes varied from close to 0 to 1.0.

The often skewed patterns of blood feeding observed in our study were the result of differences in the intensity of defensive behavior exhibited by the individual hosts (Anderson and Brust, unpublished data). In other studies, feeding success of mosquitoes varied considerably from one individual to another of a particular host species (Dow *et al.* 1957, Kale *et al.* 1972), although Edman and Scott (1987) concluded that individual differences among hosts were not the most important factor that determined mosquito feeding success.

Interruption of blood feeding by quail is a trait which is negatively correlated with the probability that mosquitoes will obtain blood (Fig. 3). Our results are consistent with those of Edman *et al.* (1972), who showed that fewer mosquitoes overall, obtained blood and more took partial blood meals from the most defensive avian hosts. Although quail are not the most important avian hosts for wild populations of *Cx. tarsalis*, *Cx. restuans* and *Cx. nigripalpus*, variation among wild avian hosts exists (Dow *et al.* 1957, *Kale et al.* 1972) and is likely an important source of uncertainty and patchiness in the blood resource available to host seeking mosquitoes.

Variation in the degree to which individual hosts tolerate mosquito attack may be a significant factor that determines the average host contact rate of mosquitoes from one location to another because those interrupted during feeding may resume on other hosts (Anderson and Brust, in press). Serology may be used to measure multiple feeding by mosquitoes (Scott *et al.* 1993, Burkot *et al.* 1988), but it may not detect cryptic multiple meals. Boreham and Garrett-Jones (1973) recognized the potential importance of cryptic multiple feeding and developed a series of probabilities to account for the ways in which a mosquito might take one or two meals given that at least two types of hosts are available. They assumed that hosts are attacked randomly for each feeding attempt, although the probability of successful feeding is not necessarily equal among potential hosts and not necessarily equal even if both hosts are available during both blood feeding attempts.

Burkot *et al.* (1988) recognized that, to calculate the frequency of cryptic multiple feeding by the method of Boreham and Garrett-Jones (1973), and in the absence of specific information about the tendency of different hosts to interrupt blood feeding mosquitoes, one must assume that the probability of interruption on different hosts is equal. Burkot *et al.* (1988) used this implicit assumption to calculate the overall probability of interruption for three species of *Anopheles* in Papua New Guinea based on the observed proportion of patent, multiple meals and the probability of each host being fed on. The method of Burkot *et al.* (1988) was used by Scott *et al.* (1993) to calculate the probability of interruption for *Aedes aegypti* L. from serological data on host selection and patent multiple feeding. However, no data were presented in either study to confirm the assumption that different hosts interrupt blood feeding mosquitoes at the same frequency, even though the probabilities of each type of host being fed on varied considerably from location to location. In both of these studies, more than one type of host as well as more than one individual host of each type were involved with the attendant potential for variation among hosts operating at 2 levels. Based on our data, it is not valid to assume that individual hosts interrupt blood feeding mosquitoes at the same rate, especially when the probability of hosts being fed on varies (Fig. 3). In 18 of 40 cases in which we calculated the relative rate of interrupted blood feeding, 1 quail was from 2 to 8 times more likely to interrupt mosquitoes than was the other immediately available quail (Fig. 2). Additionally, Burkot *et al.* (1988) demonstrated graphically that the proportion of cryptic mixed feeding is significantly altered in situations in which the probability of interruption differs among potential hosts. Thus, calculations are suspect that depend on assuming homogeneity among hosts with respect to tendency to interrupt blood feeding mosquitoes.

The equation used by Burkot *et al.* (1988) provides an indirect means of estimating total interrupted feeding if the proportion of patent multiple meals is known. However, several authors (Scott *et al.* 1993; Burkot 1988; Burkot *et al.* 1988) considered such estimates to be equivalent to the probability of multiple feeding, even though the total proportion of feeding attempts that are interrupted during one feeding are actually estimated. Some, but not all interrupted feeds are completed on a second host and only this smaller proportion represents multiple host contacts. Some mosquitoes interrupted before satiation may not continue to blood feed or they may not successfully imbibe more blood during subsequent attempts. Thus, the value, 'I', estimated according to the method of Burkot *et al.* (1988) can not be considered an estimate of multiple host contacts.

We have shown that a significant amount of variation in observed frequencies of multiple feeding is correlated with relative differences in the degree to which individual quail are fed upon (Fig. 4). Burkot *et al.* (1988) calculated that patent multiple feeding is expected to be maximal when the probability of feeding on either of 2

hosts is equal (0.5). This calculation rests on the assumption that, for each feeding attempt, mosquitoes attack hosts of the same type at random with respect to their physical availability, but successfully blood feed depending on the tolerance of the host. Any given meal is most likely to come from the host most tolerant to attack. Consequently, if one host is very intolerant relative to the other, few mosquitoes will imbibe any blood from the intolerant host and most partial blood meals will have been interrupted and resumed on the same host. Alternatively, if both hosts are relatively equal in tolerance to mosquito attack, an interrupted meal is equally likely to be resumed on either of the two hosts. The total amount of multiple feeding would depend on the tendency of both hosts to interrupt blood feeding attempts. Thus, the proportion of patent multiple meals would be highest for situations in which many meals on both hosts are interrupted and the two hosts are very similar in terms of the probability of being fed on. Our data are consistent with this model (Fig. 4). One implication of this is that the host contact rate of mosquitoes may increase substantially in habitats in which the most available hosts are uniformly intolerant of mosquito attack.

Multiple feeding may occur by two fundamentally different mechanisms. *Ae. aegypti* (Scott *et al.* 1993) and many *Anopheles* (Klowden and Briegel 1994) may be gonotrophically discordant and thus blood feed several times between egg batches to supplement nutritional reserves. Alternatively, gonotrophically concordant species may contact more than one host because an earlier feed was interrupted before satiation (Klowden 1988), usually by host defensive behavior (Davies 1991). In the latter situation, serial feeding attempts are likely to occur during a short period of time such as a single night. Refeeding avidity tends to decrease as the delay between serial meals is increased (Edman *et al.* 1975). Our results with respect to interrupted and multiple feeding by *Cx. tarsalis*, *Cx. restuans* and *Cx. nigripalpus* are most consistent with the situation outlined for gonotrophically concordant species. In either situation, even relatively low frequencies of multiple host contacts may be important because of additional opportunities for the mosquito to acquire or transmit pathogens (Smith 1987).

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Biotic inventory and development of a low impact, self-guided trail in Oxbow Woods, Delta, Manitoba

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Introduction

The term 'gallery forest' (a fringe forest) is often used in reference to river bottom forests in the prairie regions of North America (e.g., Killingbeck and Wali 1978). Weaver (1960) offers an overview of these forests in the Missouri-Nebraska-Kansas-South Dakota region of the United States. A number of additional papers have described the structure and floristic composition of gallery forests in the midwestern United States (e.g., North Dakota: Wikum and Wali 1974, Killingbeck and Bares 1978, Keammerer *et al.* 1975, Johnson *et al.* 1976, Reily and Johnson 1982; South Dakota: Wilson 1970; Illinois: Bell and del Moral 1977, Hosner and Minckler 1963; Oklahoma: Ware and Penfound 1949; Wisconsin: Barnes 1985, Dunn and Stearns 1987; Kansas: Abrams 1986; Minnesota: Noble 1979; Nebraska: Weaver *et al.* 1925). In Canada, well-developed prairie gallery forests are restricted to the province of Manitoba. General descriptions of forests bordering the south shore of Lake Manitoba, which show a strong floristic affinity with riverine gallery forests, include Lšve and Löve (1954), MacKenzie (1982) and Kenkel (1986). Essenburg (1991) offers a floristic description of gallery forests in southern Manitoba.

Prairie gallery forests develop on eroded river sediments. Prairie rivers are continually changing their course, eroding sediments on the outside of a meander while depositing material on the inside. These accumulated nutrient-rich sediments provide a substrate for vegetation colonization. The first woody species to colonize on the moist sediments are willows (*Salix exigua, S. nigra, S. amygdaloides)* and the cottonwood (*Populus deltoides*). This vegetation stabilizes the substrate and allows later-successional species to establish and grow (Wilson 1970, Noble 1979, Barnes 1985). Mature gallery forests in North Dakota and Manitoba are generally dominated by *Fraxinus pennsylvanica* (green ash), *Acer negundo* (Manitoba maple, box elder), *Ulmus americana* (American elm) and *Tilia americana* (basswood) (Kenkel 1986, Killingbeck and Bares 1978). Flooding-intolerant species such as *Quercus macrocarpa* (bur oak), *Populus tremuloides* (trembling aspen), and *P. balsamifera* (balsam poplar) occur in areas less prone to spring flooding. Gallery forests further south generally have a higher tree diversity. *Celtis occidentalis* (hackberry), which also occurs along the south shore of Lake Manitoba, is common from South Dakota southward. Other tree species occurring further south include silver maple (*Acer saccharinum*), river birch (*Betula nigra*), various oak and ash species, and a number of others (for a complete list, see Abrams 1986, Hosner and Minckler 1963, Weaver 1960).

In southern Manitoba, gallery forests occur in the valleys of the Red and Assiniboine rivers and their various tributaries. At the landscape level, these forests represent critical wildlife habitat and are important as corridors for the movement and dispersal of wildlife. Habitat fragmentation and degradation of these forests, the result of cutting for firewood and the clearing of land for agriculture and housing, is a serious problem in the province. In many areas river bottom forests have been completely destroyed, while the majority of the remaining gallery forest has been highly modified from excessive trampling and other human disturbances. These disturbances have resulted in a severe reduction in the floristic diversity of native species in these forests, while at the same time increasing the abundance of Eurasian invasive weedy species.

The objectives of this study were to: (a) complete a floristic inventory of Oxbow Woods, a large undisturbed gallery forest near Delta, Manitoba, and (b) develop an interpretive trail through this gallery forest, so as to provide cultural, natural and ecological information for educational use.

Study area

Location and Quaternary History

The Oxbow Woods gallery forest is located in southern Manitoba at 50_10'N, 98_20'W, at an elevation of approximately 250 m a.s.l. The forest is located on high ground adjacent to the Delta Marsh, about 2 km south of Lake Manitoba.

Approximately 13,500 years ago, glaciation in north-central Canada led to the formation of glacial Lake Agassiz, the result of water impoundment behind the northern ice sheet. Water levels subsided as the ice retreated northward, creating a flat landscape of clay soils on the former lake bottom. Between 9.5 and 6 thousand years ago the Lake Manitoba basin is thought to have alternately drained and filled in response to changing environmental conditions (Teller and Last 1981). All or part of the Assiniboine River system is thought to have drained into the south end of Lake Manitoba between 6,000-7,000 years ago and 3,000 years ago. Oxbow Wood occurs along one of three major drainage channels. Known as the Blind Channel, it drained the Assiniboine River into Lake Manitoba between about 4,500 to 3,000 years ago. After this time the river changed its course to drain into the Red River, as it does to this day (Rannie *et al.* 1989).

Climate

Southern Manitoba is characterized by a continental climate, with short warm summers and long, cold winters. Mean annual temperature is 1.9°C, with monthly means ranging from 19.2°C (July) to -18.1°C (January). Annual mean precipitation is ≈ 50 cm, about 60% of which falls between May and September (Environment Canada, means for the period 1967-1991, Delta University FS).

Dominant Vegetation and Floristic Affinities

The Oxbow Woods is strongly aligned floristically with the deciduous forests of eastern North America. The dominant tree species found in this forest, including bur oak, green ash and Manitoba maple, have an eastern deciduous forest affinity (Rudd 1951, Lšve 1959). Hackberry and basswood, which occurs sporadically in the Delta Marsh area, are also of eastern affinity.

Eastern deciduous forest understory species found in Oxbow Woods include *Smilacina racemosa, Trillium cernuum, Menispermum canadense, Rudbeckia laciniata, Phryma leptostachya, Amphicarpa bracteata* and *Celastrus scandens*. *Carex assiniboinensis*, which is often dominant in the understory of Oxbow Woods, is indigenous to continental North America (Manitoba and Saskatchewan, and south to northern Iowa and South Dakota). Eurasian invasive weedy species are uncommon, indicating minimal anthropogenic disturbance in Oxbow Woods.

In many parts of Oxbow Woods, woody shrubs form a major component of the biomass. Important species include American hazelnut (*Corylus americana*), choke cherry (*Prunus virginiana*), saskatoon (*Amelanchier alnifolia*) and nannyberry (*Viburnum lentago*).

A number of species common to Oxbow Woods reach their North American northern and/or western distributional limits in southern Manitoba (Löve 1959). The threatened gallery forests of southern Manitoba thus represent a unique community assemblage deserving of protection.

Disturbance History

Fire

Fire is a natural part of the history of southern Manitoba. Evidence of lightning strikes are apparent throughout Oxbow Woods. Most of these strikes take out a single large oak or ash tree. On occasion, lightning strikes may start localized ground fires which kill trees in larger patches.

Prairie fires may also burn into the forest, as happened during an accidental fire in April 1991. This fire burned into the extreme northern section of Oxbow Woods, killing a number of trees in the transitional forest-grassland region adjacent to the closed forest.

Herbivory

Porcupines are occasionally seen in Oxbow Woods, and may open the forest canopy by pruning the upper branches of large trees. Browsing by rabbits and white-tailed deer, both of which are abundant in Oxbow Woods, is expected to affect the distribution and abundance of tree, shrub and herbaceous species in the forest. *Osmorrhiza longistylis* (sweet-scented cicely) is most commonly found along the deer trails in the forest, suggesting that the sticky seeds of this species are dispersed by deer. Pocket gophers are important herbivores in the forest, eating both above and below-ground plant parts and turning up fresh mounds of soil. These mounds are nutrient rich and may provide temporary habitat 'islands' for ruderal plant species.

Methods

Historical Information

Old and recent maps and aerial photographs were consulted to determine recent changes in land use in the area. Interviews with field station staff and local residents provided information on the activities of the previous owners of the properties. Studies conducted at Oxbow Woods were also consulted. European settlement patterns were found in a book on the history of the Westbourne region.

A preliminary archaeological study was conducted in the north meadow of the Oxbow Woods to determine whether the area was used in pre-European contact times.

Floristic Inventory

Floristic information was acquired from herbarium records and previously compiled species lists (Löve and Löve 1954, Walker 1959, Tande and See 1977). The main inventory was conducted by plant collection, sight identification and the ground truthing survey. Dr. Bruce Ford (Department of Botany, University of Manitoba) helped identify a number of *Carex* species in the forest.

Ground Truthing Survey

The forest was gridded with five north-south transects and seven east-west transects using compass-to-compass measurements. Intersections and end points were marked with flagging tape. In areas with high shrub cover, it was necessary to flag the transects every 50 m. These reference points were used for navigational purposes and for trail mapping.

Vegetation Types

Vegetation types were delineated based on species dominance. Only areas distinguishable on aerial photographs, and of sufficient spatial scale to appear on the vegetation map, were considered. The following general type delineation was used:

- Meadow: No tree cover. Dominated by low shrubs, herbs and grasses.
- Meadow/shrub: Low tree cover. Meadow interspersed with shrub/tree clumps.

- Fern stands: Tree canopy (ash-oak), with an understory dominated by ostrich fern.
- Balsam poplar forest: Tree canopy, balsam poplar dominant.
- Forest/Herb: Closed-canopy ash-oak forest, with a diverse herb layer and a sparse shrub layer.
- Forest/Open Shrub: Open to closed-canopy ash-oak forest, with shrub patches.
- Forest/Shrub: Semi-closed ash-oak forest, with a dense shrub layer.

Other unique features of the area were also noted, such as the location of the only basswood tree found in the forest, and the location of the elm trees.

Mapping With Geographical Information Systems

Provincial topographic maps (1:50,000 scale) and recent aerial photographs were consulted to determine the scale and alignment of the transects. A contour map of the Delta Marsh region (Ducks Unlimited, 1980) was also consulted.

Infrared aerial photographs from 1988 of Oxbow Woods were scanned and exported into the Macintosh program Map II™. After processing, the image was then imported into Canvas™ 3.05 to produce the final vegetation and trail maps and figures.

Trail Implementation

1. Reconnaissance

Reconnaissance helped determine criteria for sighting the trail. It was decided to utilize previously established deer trails to minimize anthropogenic disturbance to the forest. Since deer trails meander through the forest, a systematic approach was necessary to determine which trails to utilize. The transects established for the ground truthing survey were also used in sighting the trail and obtaining a floristic inventory.

It was decided to establish a trail system consisting of two loops (short and long trails) beginning and ending in the same place. The longer trail was established so as to traverse the entire forest perimeter, and to exit into the ecotone between the marsh and the forest. The short trail encompasses the beginning and end of the long trail, but cuts across the central region. Interpretive stops along the trails highlight the major ecological communities and other interesting features in Oxbow Woods. The trail avoids particularly sensitive areas (e.g., Ostrich Fern stands) and areas where excessive clearing of vegetation would have been required.

2. Trail Marking

Preliminary paths were temporarily flagged and various trail options 'tested' by walking along the deer trails and noting landscape and floristic features. Areas of the forest particularly susceptible to trampling were avoided.

Parks Canada and Manitoba Provincial Parks personnel were contacted to determine how to best mark hiking trails. From the various options suggested, a low-impact approach was felt most appropriate. After visiting several provincial trails, it was decided to use corrugated plastic signs attached to trees (as used in Duck Mountain Provincial Park) to mark the Oxbow trail. We utilized triangular markers (20 x 15 cm) cut from commercially-obtained sheets of bright orange corrugated plastic. Interpretive stop numbers were stenciled onto markers with automotive spray paint. Markers were fastened to trees at eye level, using galvanized metal nails.

3. Trail Clearing

In some areas, a small amount of clearing was necessary to remove trail hazards. Most hidden logs were removed from the path, and shrub branches at eye and ground level were trimmed. In a few areas, branches obscuring the visibility of markers were trimmed. It was not felt appropriate to 'pave' the trail with wood chips or other material, since a minimal impact result was desired.

Results

Historical Information

The Assiniboine River flowed into Lake Manitoba via the Blind Channel between 4,520 and 3,000 years before present (Rannie *et al.* 1989). Old maps indicate that several additional former channels of the Assiniboine River occur in the area, but most have been drained and cleared for cultivation.

Cultural material recovered from the archaeological survey suggests that the Oxbow Woods area may have been used as a temporary camp by the indigenous peoples. La Verendrye was the first European to visit the region, building Fort La Reine north of present-day Portage la Prairie in 1738. Permanent European settlement in the region began after 1851 with the establishment of a mission by Reverend Cockran.

The Inkster family built their original homestead on the west side of the Blind Channel, in the small copse to the north-west of the Oxbow Woods. Remnants of this settlement can still be seen today. There was a small native settlement on the east side of the Blind Channel (north of Oxbow Woods). For a period of time the Insksters raised their cattle on this land, with the natives tending the herds, but this relationship soured. The next generation of Inksters built a successful farm east of the southern portion of Oxbow Woods. Sheriff Inkster had built a home on the south-west side of the channel, but no evidence of it remains (he perished in the fire that burned the structure to the ground). Donald Bain purchased the property which became the University Field Station (including the Inkster farm) in the 1920s, building the hunting lodge and outbuildings along the Lake Manitoba shore. The Inksters became his tenants for a time, but they eventually abandoned the farm after rents became unreasonable. The remaining farm buildings are used today for storage.

Anthropogenic Effects

There is evidence that the Delta Marsh area was an important encampment and hunting area for North American indigenous tribes. Early Europeans camped and hunted in the area after the La Verendrye explorations. Cattle from the Inkster farm grazed the grasslands in the area, and may have grazed the forest understory as well. Donald Bain apparently used the Oxbow Woods for deer hunting, but it appears to have been otherwise undisturbed. There is some very limited evidence of selective logging, but the stumps are only about the size of fence posts.

The University of Manitoba acquired the property in 1966, but Oxbow Woods was not used intensively for research purposes because of poor access. The Assiniboine River diversion, constructed between the University Field Station and Oxbow Woods, was completed in 1976. Today access to Oxbow Woods is most easily made by crossing the diversion and proceeding along the east dike road.

In 1988, the Province of Manitoba established Oxbow Woods and surrounding area as an Ecologically Significant Area. It is rumored that illegal hunting still occurs in Oxbow Wood, but the area is otherwise undisturbed.

Floristic Inventory

The floristic inventory of Oxbow Woods (Appendix A) includes several species not previously listed for the region. Of particular interest is the discovery of a large basswood (*Tilia americana*) tree in the forest. This specimen represents a slight northern extension for the species (the species occurs along the current Assiniboine River at Portage la Prairie and as far west as Spirit Sands, south of Carberry).

Dominant species in Oxbow Woods have mainly an eastern deciduous forest floristic affinity (Löve 1959). *Rudbeckia laciniata* often dominates the ground cover of open forest stands in mid to late summer. *Amphicarpa bractaeata* often forms a 'carpet' in well-shaded areas beginning in mid-June. In other areas the boreal species *Aralia nudicaulis* dominates the ground cover in early summer. *Ozmorrhiza longistylis*, *Zizia aurea* and *Galium*

sp. are common understory components in the spring. *Carex* sp. (mostly *C. assiniboinensis*) are also very common. They are practically 'evergreen', and as a result are most conspicuous in the early spring and late fall. *Matteuccia struthiopteris* (ostrich fern) is locally abundant, forming large monodominant clonal populations in open forest. Showy spring ephemeral species include *Trillium cernuum*, *Aquilegia canadensis, Viola pubescens* and *Cypripedium calceolus*.

Tall shrubs are commonly encountered in many regions of Oxbow Woods. *Corylus americana* (hazelnut, sometimes found with *C. cornuta*) is often the dominant shrub. *Amelanchier alnifolia* (saskatoon) and *Prunus virginiana* (chokecherry) occur in more open areas of the forest. *Viburnum lentago* (nannyberry) and *Crataegus rotundifolia*(hawthorn) are less abundant, and generally occur along forest margins. *Symphoricarpos occidentalis*, *Rubus idaeus* and *Rosa* sp. are common low shrubs in open meadows and glades. Other shrub species occasionally encountered include *Salix discolor* (pussy willow), *Ribes* sp. (gooseberries), *Prunus pennsylvanica* (pin cherry), *P. americana* (wild plum), *Cornus stolonifera* (red-osier dogwood), *Alnus rugosa* (speckled alder), *Sambucus pubens* (elderberry), various species of *Viburnum* (including *V. trilobum* (highbush cranberry), *V. rafinesquianum* (downy arrow-wood) and *V. edule* (lowbush cranberry)).

Dutch Elm Disease has killed most of the American elm in Oxbow Woods, but a few mature trees have survived. Some of the largest oaks occur at the extreme south end of the forest, along high banks near the Blind Channel. These may reach 150 years of age, though the mean age of the mature oaks in the area is about 100 years. The oaks typically grow on the higher, drier ground, while the Manitoba maple and green ash are more common in lower, wetter areas. The largest Manitoba maples are no more than about 80 years in age, while most mature green ash are between 70 and 100 years old (though some of the largest ash are about 120 years old).

In the balsam poplar stand, trees average about 60 years in age. The species is successfully regenerating in the area, though there is some evidence of invasion by green ash. This stand is surrounded on three sides by meadow vegetation, and the humus layer is not as well developed as in the mature oak/maple/ash forests.

Very old, dying specimens of trembling aspen (*Populus tremuloides*) are occasionally encountered in the forest, particularly in open forest areas dominated by green ash and sedges. These trees are not regenerating.

Vegetation Types

Meadow

Meadow areas occur at the north end of the forest. Grass species include *Poa pratensis*, *Agrostis stolonifera* and *Elymus virginicus*. The dominant shrubs are snowberry, rose and raspberry. A number of herb species also occur, including *Equisetum pratense* (meadow horsetail), *Thalictrum dasycarpum* (tall meadow rue), *Glycyrrhiza lepidota* (wild licorice), *Convolvulus sepium* (morning glory) and *Circium arvense* (Canada thistle). The few scattered trees and tall shrubs in these meadows were killed by a fire that burned through the area in 1991.

Meadow/Shrub

This vegetation represents a transition zone between the open meadows and closed forests. These areas have typical meadow vegetation interspersed with forested patches. The shrubs associated with the forested patches are primarily *Prunus virginiana* (chokecherry) and *Corylus americana* (hazelnut). Small tree species such as *Salix petiolaris* and *Crataegus rotundifolia* are found here as well.

Fern Stands

Stands of *Matteuccia struthiopteris* occur as two large colonies and a few smaller ones mainly on the west side of Oxbow Woods, in open forest areas. This species almost completely dominates the ground cover beginning in June. These stands are easily trampled and should be enjoyed from a distance.

Balsam Poplar Stand

Populus balsamifera almost completely dominates the canopy in this small area. The ground cover is not as diverse as the ash/maple/oak forest, and there is limited soil organic matter accumulation. On the south and east sides of this stand, a transition zone dominated by *Salix* species occurs adjacent to the open meadows.

Forest/Herb

These areas occur mainly in the north-central part of the forest. The forest consists of a closed canopy of bur oak and green ash and a subcanopy of Manitoba maple. The shrub layer is poorly developed, and this has resulted in a diverse herb layer. Common understory species include *Carex assiniboinensis*, *Amphicarpa bractaeata* (hog peanut), *Viola pubescens* (yellow violet), *Maianthemum canadense* (wild lily-of-the-valley), *Arenaria laterifolia* (grove sandwort), *Corydalis aurea* (golden corydalis), *Aralia nudicaulis* (wild sarsparilla), *Zizia aurea* (golden alexanders) and *Scutellaria galericulata* (skullcap mint). A few tall shrubs such as *Prunus americana* (wild plum) and *Viburnum lentago* (nannyberry) are occasionally encountered. The fern stands are occasional in these open forests.

Forest/Open Shrub

These areas occur mainly in the central portion of the Oxbow Woods. The open wooded areas are dominated by species typical of the open forest area, but scattered clumps of shrub (mostly hazelnut) are also common.

Forest/Shrub

These areas are found mainly along forest edges and at the south end of Oxbow Woods. The canopy is often dominated by bur oaks, while tall shrub stands form a dense subcanopy. Low light levels result in a poorly developed understory. The dominant shrubs are *Corylus americana*, *Amelanchier alnifolia* and *Prunus virginiana*.

Basswood Tree

In the spring of 1994 we discovered a single mature specimen of basswood (*Tilia americana*) in Oxbow Woods. It appears to be the only specimen of the species in this forest, and does not seem to be successfully regenerating. This is the furthest north that naturally-occurring basswood has been found in North America. The trail passes by the tree near the north-west edge of the forest (stop 3).

Mapping With Geographical Information Systems

Appendix C is the map of the trail system and interpretive stops. Appendix D is a map of the major vegetation types described above. These maps are available from at the field station office, or from Dr. Norm Kenkel (Department of Botany, University of Manitoba).

Trail Implementation

Appendix C shows the trail system (short and long trails) and the locations of interpretive stops. The trail begins at the north meadow and continues south into the transition between forest and meadow. The next highlighted feature is the basswood tree, followed by the fern stands. The trail continues past a stand of American elms, where the short trail splits off to the north-east and the long trail continues south into the more shrubby areas of the forest. The long path loops around at the south end of the forest, exits into the marsh-forest ecotone on the south-east edge, then continues along the east edge of the forest. The path turns north to meet up with the short trail just before entering the balsam poplar stand. Both trails go through the poplar stand and continue to the meadow-forest transition, where the loops are completed.

Discussion

A major concern in citing and utilizing the trails was to minimize present and future environmental impacts, specifically impacts related to trampling of the vegetation. Dale and Weaver (1974) demonstrated that both woody plants and certain 'delicate' species (e.g., *Aquilegia, Thalictrum*) are brittle and therefore do not tolerate trampling. They also noted that trailside species receive more light and rainfall, and have less root competition from trees. In an earlier study, Bates (1934) found the cover of genera such as *Galium*, *Viola* and *Agrostis* are unaffected by trampling except in wet conditions. Liddle (1975) found that monocots are generally more resistant to trampling than dicots, but that most dicots can survive moderate trampling. It should be noted that these studies were conducted under trampling intensity levels of >1,000 people per season, which is well above the anticipated use of the Oxbow Wood trails. Even so, the following precautionary measures should be followed to maintain ecosystem and trail integrity:

1. Before walking the trail, users should carefully remove all bur-like seeds from clothing. Shoes should also be carefully cleaned. This will minimize the invasion of weedy species into the forest.
2. Users are encouraged to keep to the marked trails to avoid unnecessary trampling.
3. The picking of any flowers should be discouraged. Capture plants on film instead.
4. The eating of fruits (e.g., berries) should also be discouraged, as the forest fauna depends on these resources for their survival.
5. Much damage can be done to the trailside species if they are wet. Avoid using the trails immediately following a rainfall.

To facilitate further study of the effects of trampling and trail use, it is recommended that records be kept of the number of persons using the trail each season. The following procedures for continued monitoring of trail use is recommended:

1. Set up permanent transects or plots along the trail to monitor changes in floristic composition.
2. Look for changes in species diversity, and invasion by invasive Eurasian weedy species, along the trail.
3. If necessary, implement a management plan to immediately combat problems so as to allow the area to recover. Such plans could include restricting trail access for a time, or the physical removal of invasive Eurasian species.

While the trail has been designed to be 'low-maintenance', limited seasonal clearing of obstructions and undergrowth may be required. In the future, markers will require replacement as they are damaged or lost.

The goal of the interpretive trail is to provide cultural, natural and ecological information on Manitoba gallery forests, primarily for educational use. The information provided by this study will be useful to naturalists, educational groups, summer university courses, elementary, secondary and post-secondary students, and researchers.

The interpretive trail pamphlets are a compilation of information gathered over the course of this study. The short pamphlet is designed for general use, as a handy guide through the forest trail and the interpretive stops (Appendix E). It should be useful to various school and naturalist groups. The long pamphlet includes detailed maps, and provides a more in-depth discussion of the interpretive stops and historical information (Appendix F). Both pamphlets are intended for educational use, and to raise public awareness of the status of gallery forests in Manitoba.

From this study, it is clear that a number of additional studies in the Oxbow Woods could be undertaken. Forest tree regeneration is a particularly interesting area of research. What is the fate of basswood in the forest, if the species fails to regenerate? Is secondary succession occurring in the forest, particularly in the balsam poplar stand? Why are some areas of the forest almost shrub-free, while others have a very dense shrub cover? What role does herbivory play in determining floristic composition and species abundance? How important are fire and lightning strikes?

Additional information on the fauna of Oxbow Woods is also required. Bird and mammal species lists (Appendix B) were compiled from information provided by Drs. Spencer Sealy and Rick Riewe (Zoology, University of Manitoba) and from The Manitoba Naturalists Society, but a more detailed survey is required. The invertebrates, mosses and fungi are also deserving of greater study.

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Lack of sperm storage by female migrant birds and the significance of copulations en route

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Introduction

Female birds store sperm in specialized sperm storage tubules (SSTs) located at the junction of the uterus and vagina (e.g., Fujii 1963, Shugart 1988, Birkhead et al. 1990, Briskie and Montgomerie 1993). SSTs appear necessary for the long-term survival of spermatozoa within the female reproductive tract because sperm not stored within SSTs soon die or are displaced (Lorenz 1966). The length of time that sperm can remain viable in storage varies from species to species but ranges from about 10 days in the Zebra Finch (*Taeniopygia guttata*; Birkhead et al. 1989) to over 72 days in the domestic Turkey (Lorenz 1950). Why sperm storage duration varies among species is not clear but may be related to the proximity of males and females during pre-laying (Birkhead and Møller 1992a). For example, sperm storage durations are particularly long in seabirds, in which females are separated from their mates for prolonged periods prior to laying. In contrast, males in many passerine birds typically remain close to females throughout pre-laying and these species have correspondingly shorter durations of sperm storage.

In most birds, copulations are generally restricted to a brief prelaying period, with the greatest frequency just prior to the laying of the first egg. For migratory species, pairing and mating are thought to take place largely on the breeding grounds and after the end of spring migration. However, by using lavages to census sperm within the cloacae of male and female migrant passerines, Quay (1985a, 1989) found that many Tennessee Warbler (*Vermivora peregrina*) females and possibly some Blackpoll Warbler (*Dendroica striata*) females had been inseminated while on migration and south of their nearest breeding grounds. In the Tennessee Warbler, about 25% of females contained sperm in their cloaca, indicating that copulatory behavior during migration may be widespread (Quay 1989). Recently, Moore and McDonald (1993) suggested that en route copulations may have an adaptive function, such as minimizing the time and costs of mate choice or ensuring females have an adequate supply of sperm should they not find a mate on the breeding grounds. Unfortunately, the role that en route inseminations play in the eventual fertilization of eggs remains unknown.

If copulations during migration play a role in the fertilization of eggs, then females must be able to store sperm acquired en route and to arrive on the breeding grounds with this sperm still viable (Quay 1989, Moore and McDonald 1993). Since sperm can remain viable for extended periods only if stored within the SSTs, migratory birds must have active and developed SSTs if en route copulations are to have any functional significance. In this study, I examined the reproductive tracts and SSTs of four species of migratory passerines, including Tennessee and Blackpoll warblers, to determine if females can store sperm prior to their arrival on the breeding grounds. My results suggest that sperm are unlikely to remain viable from inseminations occurring en route and that such behavior may be simply an epiphenomenon of the recrudescence of the reproductive organs during migration.

Methods

Six female Tennessee Warblers and three female Blackpoll Warblers were collected during the last week of May in 1992 and 1994 at Delta Marsh, Manitoba, Canada. Both species are common migrants in this area and were moving through in large numbers on the days they were collected. Neither species nests at Delta Marsh; the southernmost breeding location for Tennessee Warblers is about 100 km north of the collecting site while the

nearest record for Blackpoll Warblers lies about 450 km farther north (Godfrey 1986). I also salvaged one female Black and White Warbler (*Mniotilta varia*) on 14 May 1992 and one female Ovenbird (*Seiurus aurocapillus*) on 22 May 1992 from windowkills in the south end of the city of Winnipeg, Manitoba. The salvage site for these species lies within their respective breeding ranges, but it is likely that both were migrants because of the early date and the unsuitability of the salvage site (parking lot and apartment complexes) for breeding. For comparison with migrants, I collected one additional Blackpoll Warbler in breeding condition at Churchill, Manitoba on 10 June 1994. This female had an egg in the oviduct and several enlarged follicles in the ovary. All birds were collected or salvaged under permit from the Canadian Wildlife Service.

Within an hour of obtaining the specimens, the oviduct was removed, pinned straight to a cork board, and then immersed in 10% formalin. After fixing for 24 h, the tissue was transferred to a labelled vial and stored in 10% formalin for a further 4 to 6 months before processing. The method used for preparing oviduct tissue for the examination of SSTs has been described in detail by Briskie and Birkhead (1993). Briefly, I first exposed the oviductal lumen by making a longitudinal incision through the vagina and uterus and pinning the tissue flat onto a cork dissecting tray. The folds at the uterovaginal junction were counted, and a random sample of three folds was removed. Each fold was then cut along the mid-ridge, and each half was laid flat onto a glass slide with the lumenal surface facing down. A drop of phosphate-buffered saline was added, and the tissue was covered with a glass cover slip.

Sperm storage tissue was examined at high magnification (X 400) with a light microscope. For each fold, I counted the SSTs; the mean number of SSTs from the three folds was then multiplied by the total number of folds to estimate the total number of SSTs for that individual. Next, I measured the outside length of 30 SSTs per individual (10 SSTs/fold) with a calibrated ocular micrometer. SSTs for measuring were selected by running a transect across the fold from the uterine to vaginal end. This ensured that about equal proportions of SSTs from all regions of the uterovaginal junction were sampled. Finally, I examined each SST for the presence or absence of sperm. Passerine spermatozoa have a characteristic spiral-shaped head and thus are readily recognizable within the lumen of a SST (see Briskie and Montgomerie 1993).

Results and Discussion

SSTs were observed in all individuals of each species examined. The estimated number of SSTs varied from an average of 327 ± 39 (n = 6 females) in the Tennessee Warbler to 492 SSTs (n = 1 female) in the Black and White Warbler (Table 1). The number of SSTs in each of the four species of warblers studied here was less than half that expected for their body mass (Birkhead and Møller 1992b, Briskie and Montgomerie 1992, 1993). The reason for this difference is not known but could be either a characteristic of parulid warblers in general or the result of a seasonal change in the number of SSTs as egg laying approaches (all birds in the other studies were in breeding condition). Since all SSTs in migrating birds were typically small (see below), it is also possible that some of the very small SSTs were missed in my census. However, seasonal increases or small size are unlikely to explain the low number of SSTs in Blackpoll Warblers, as the number of SSTs in the single female collected on the breeding grounds (368 SSTs) was very similar to that observed in migrants of this species (331 ± 56 SSTs, n = 3 females; Table 1).

Table 1. Number and size of sperm storage tubules (SSTs) in individuals of four species of migrant passerines collected in southern Manitoba, Canada. SST length calculated from 30 SSTs per bird.

		SST length (µm)	
Species	**Number of SSTs**	**Mean ± SE**	**Range**
Tennessee Warbler	256	118.3 ± 6.9	47.5 - 180.0
	476	96.9 ± 5.3	42.5 - 167.5
	380	143.0 ± 6.0	82.5 - 217.5
	360	123.0 ± 5.9	57.5 - 187.5

	260	148.8 ± 8.1	52.5 - 275.0
	232	96.6 ± 3.6	52.5 - 132.5
Blackpoll Warbler	415	140.5 ± 7.6	67.5 - 210.0
	292	75.8 ± 3.4	42.5 - 110.0
	225	74.4 ± 4.1	40.0 - 137.5
Black and White Warbler	492	57.1 ± 4.3	22.5 - 102.5
Ovenbird	377	58.1 ± 3.2	27.5 - 102.5

Despite the presence of SSTs, no spermatozoa were observed in any migrating female of the four species examined (Figure 1). SST length ranged from an average of 121.2 ± 9.0 µm (n = 6 females) in the Tennessee Warbler to only 57.1 µm (n = 1 female) in the Black and White Warbler (Table 1). SST length for migrating Blackpoll Warblers (96.9 ± 21.8 µm, n = 3 females) was less than one-seventh that observed during the breeding season (725.8 ± 45.8 µm, n = 1 female). Although I was unable to measure the length of SSTs in breeding Tennessee Warblers, Black and White Warblers, and Ovenbirds, SSTs in these species on migration were generally much smaller than those measured by Briskie and Montgomerie (1993) in other passerine species collected during the breeding season. This suggests that SSTs in all the migrants I sampled were not developed nor potentially capable of storing sperm if inseminated. This is particularly evident when SST length is compared against sperm length. In the Tennessee Warbler, sperm length averages 187.8 µm (n = 2 males; unpubl. data) or about 55% greater than the average length of the SSTs during migration (121.2 µm; Table 1). Of the 180 SSTs measured in the 6 Tennessee Warbler females, only 7 (3.9%) SSTs were sufficiently large enough to accomodate the entire length of a spermatozoa. Since sperm not completely protected within a SST are unlikely to survive (Lorenz 1966), it appears that most SSTs are too short and undeveloped to store sperm during spring migration. The same pattern was evident in the three Blackpoll Warblers examined. In this species, sperm length (269.5 µm, n = 1 male; unpubl. data) was almost three times the average length of the SSTs (96.9 µm; Table 1) and none of the 90 SSTs examined in the three migrating females were large enough to accomodate even a single spermatozoa. No information is available on the length of sperm in either Black and White Warblers or Ovenbirds; however, both species also had very short SSTs, suggesting that they too would not be able to store sperm if inseminated at this stage.

The lack of sperm storage by female migrants is not a product of the lack of sperm production in males. Two male Tennessee Warblers collected on migration were estimated to have approximately 1.3 and 5.8 million sperm, respectively, in their seminal glomera (i.e., the site of sperm storage in male birds; unpubl. data). The seminal glomera of a single Blackpoll Warbler salvaged from a window kill also contained numerous sperm, although the exact number was not estimated. In a more extensive survey of sperm production by migratory birds, Quay (1985a, b, 1986a, b) found that males in a wide variety of passerines initiated sperm production while on migration and far south of their nearest breeding grounds. Thus, if copulations do occur en route in some migratory passerines, it is likely that males are capable of inseminating females with viable sperm, even though these inseminations do not appear to lead to subsequent sperm storage.

In a study of seasonal changes in SST morphology in the Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), I found that SSTs were present in all females and in roughly equal number throughout the season (Briskie 1994). As with the migratory warblers examined in this study, SSTs in blackbirds collected on the day they arrived on the breeding grounds (and thus at the end of their spring migration) were small and regressed and did not contain any sperm. After females arrived on the breeding grounds, their SSTs rapidly doubled in size and reached maximum length in about 8 - 14 days, although sperm were not observed within SSTs until 2 - 5 days before clutch initiation (Briskie 1994). However, it is interesting to note that SSTs in newly arrived birds were almost double the length of those found in post-breeding birds (Briskie 1994). This suggests that some development of the SSTs must occur while on migration, although not nearly enough to allow for sperm storage.

It is clear that none of the females on migration that I examined stored sperm or appeared capable of storing sperm if inseminated. Why then do some species copulate en route to their breeding grounds if such behavior

does not lead to the subsequent fertilization of eggs? Quay (1989) suggested that en route copulations may provide some physiological or behavioral advantage to the individual in a kind of "inseminatory practise run" before the breeding territory is reached. It is also possible that en route copulations may function in pair formation, although it seems unlikely that pairing occurs during migration in most species of passerines because of the differential timing of migration between the sexes (Francis and Cooke 1986). Perhaps the most parsimonious explanation is that en route copulation may simply result from migration occurring during the recrudescence of reproductive tissues. In other words, the hormonal system necessary to stimulate the re-growth of the genitals may also inadvertently trigger the corresponding sexual behaviors, such as singing or copulations. This may be especially true for northern birds, which face a relatively short window of favorable conditions in which to pair, mate, and raise offspring and therefore would be selected to arrive on the breeding grounds ready to breed. Indeed, the two species in which females are known to copulate en route (Tennessee and Blackpoll warblers) are two of the most northerly breeding species of warblers. Thus, en route copulations are most likely an epiphenomenon of the need for both males and females to arrive on the breeding grounds in reproductive condition and not as an adaptation to fertilize eggs.

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The evolution of Yellow Warbler alarm calls

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Introduction

Studies comparing the responses of populations sympatric with brood parasites to populations allopatric with brood parasites have provided insight into evolutionary processes involving brood parasites and their hosts (e.g., Cruz and Wiley 1989; Davies and Brooke 1989; Soler 1990; Soler and Møller 1990; Briskie *et al.* 1992). Similar studies have focused on evolutionary processes between predators and their prey (e.g., Giles and Huntingford 1984; Goldthwaite *et al.* 1990; Towers and Coss 1990; Foster 1994). These studies have inferred the loss of an adaptive behaviour in the absence of a selection pressure (e.g., Cruz and Wiley 1989; Goldthwaite *et al.* 1990; Foster 1994), the maintenance of a behaviour due to phylogenetic constraints (e.g., Towers and Coss 1990), and the presumptive evolution of a behaviour in the presence of a selection pressure (e.g., Briskie *et al.* 1992). These studies contribute to our understanding of the evolution of behaviour, but few have permitted the inference of the direction of evolutionary change (but see Bolles 1988; Cruz and Wiley 1989; Goldthwaite *et al.* 1990; Towers and Coss 1990; Foster 1994), or considered the influence of multiple selection pressures on a behavioural repertoire (but see Giles and Huntingford 1984; Goldthwaite *et al.* 1990; Towers and Coss 1990).

Yellow warblers (*Dendroica petechia*) have a complex alarm call system consisting of four calls that they utter during nest defence (Ficken and Ficken 1965; Hobson *et al.* 1988; Hobson and Sealy 1989; Gill and Sealy, ms). Chip and metallic chip calls grade into each other and are given in response to mammalian and avian predators (Hobson *et al.* 1988; Gill and Sealy, ms), but also in a wide variety of non-threatening contexts (Ficken and Ficken 1965; Spector 1991; pers. obs.). Seet calls are uttered preferentially to brown-headed cowbirds (*Molothrus ater*) and usually uttered in conjuction with nest-protection behaviour (Hobson and Sealy 1989; Neudorf *et al.*, ms.; Gill and Sealy, ms). The fourth call, the warble call, is given in tandem with distraction displays in response to nest predators (Gill and Sealy, ms).

Given that the seet call is uttered in such a restrictive context, Briskie *et al.* (1992) speculated that this call and the associated nest-protection behaviour evolved under the pressure of cowbird parasitism. To test this hypothesis, they compared the responses to a female cowbird model of a population sympatric with cowbirds to a population allopatric with cowbirds. They found that individuals in the population allopatric with cowbirds rarely uttered seet calls and never performed nest-protection behaviour in response to the cowbird, which supports their hypothesis (Briskie *et al.* 1992). However, they did not consider the responses of this population to an avian nest predator. Thus, these behaviours may have evolved in response to avian nest predation, but now are used in response to cowbirds (i.e. exaptation, Gould and Vrba 1982). In this scenario, avian nest predators and playbacks of seet calls, but not cowbird models, would elicit seet calls and nest-protection behaviour in the population allopatric with cowbirds. By contrast, if these behaviours evolved due to cowbird parasitism, seet calls and nest-protection behaviour should not be elicited by any stimuli in that population.

I tested the hypothesis that seet calls evolved due to cowbird parasitism by (1) presenting cowbird and predator models, and playbacks of alarm calls to a population allopatric with cowbirds (at Churchill, Manitoba), and (2) comparing the responses of that population to a population sympatric with cowbirds (Delta Marsh, Manitoba; Chapter 1). I predicted that (1) yellow warblers in the population allopatric with cowbirds would not respond with seet calls or nest-protection behaviour to any stimuli, and (2) that the populations would differ in their responses to the models and playbacks.

Methods

Study sites

I conducted research from 18 May to 7 July 1993 and 19 May to 16 June 1994 on property of the University of Manitoba Field Station (Delta Marsh) and Portage Country Club (PCC), west of the Assiniboine River diversion, and east of the diversion in the town of Delta. All sites are located at the south end of Lake Manitoba (see map in Sealy 1980, see MacKenzie 1982, Mackenzie *et al.* 1982 for description of study site). West of the diversion, yellow warblers nested in the forested dune-ridge that separates Lake Manitoba from the surrounding marsh. In the town of Delta, yellow warblers nested in sandbar willow groves situated along roads.

From 17 June to 7 July 1994, I studied a population of yellow warblers allopatric with cowbirds near the town of Churchill, MB (see Figure 1 in Briskie *et al.* 1992). Yellow warblers nested in willow-birch thickets that lined gravel ridges, streams, and ice ridges around lake and pond shores (Jehl and Smith 1970; Briskie, ms; see Johnson 1987 for description of habitat). The dominant shrubs in these areas are dwarf birch (*Betula glandulosa*), short-capsuled willow (*Salix brachycarpa*), hoary willow (*S. candida*), flat-leaved willow (*S. planifolia*), and green alder (*Alnus crispa*; Johnson 1987). Most warblers built their nests in flat-leaved willows, usually towards the centre of the thicket (Briskie, ms; pers. obs.).

Nest monitoring

At both study sites, I located nests during building, egg-laying and incubation stages, and flagged them from at least 2 m away. Nests were checked daily during nest-building and egg-laying periods until clutch completion, and after clutch completion, nests were monitored irregularly until the eggs hatched.

Model Presentation

At Delta Marsh, I presented taxidermic mounts of a fox sparrow, common grackle and female brown-headed cowbird near yellow warbler nests. Fox sparrows are a semi-novel stimulus to yellow warblers because they migrate through the study area (see Hobson and Sealy 1989a). Common grackles (female: 100 g, male: 127 g) are considerably larger than warblers, but at Delta Marsh, grackles are the smallest known avian predator of both eggs and nestlings (Sealy 1994). Furthermore, responses of some species are not influenced by model size (Robertson and Norman 1977; Neudorf and Sealy 1992). Common grackles have been observed preying on adult passerine birds the size of yellow warblers (Davidson 1994). Although Davidson (1994) observed only one grackle taking adult passerines during migration, her observations call into question my assumptions that grackles are solely egg and nestling predators and that nest owners do not perceive the models as threats to themselves.

At Churchill, I presented models of a fox sparrow, gray jay and female cowbird. Cowbirds occur only accidently in the Churchill area, with the nearest breeding record is approximately 600 km SW of Churchill (Allen 1945; Jehl and Smith 1970; Godfrey 1986; Figure 6). Fox sparrows nest uncommonly at Churchill (Godfrey 1986), but they were heard singing in areas in which yellow warblers nested (pers. obs.). I did not present a common grackle to nesting yellow warblers because grackles occur infrequently in the Churchill area (Godfrey 1986), although there are several breeding records (Jehl and Smith 1970). Instead, I presented to yellow warblers a study skin of a gray jay (*Perisoreus canadensis*) attached to a wire clip. Gray jays are common egg and nestling predators of passerine nests (Strickland and Ouellet 1993), and they occur in the boreal forests adjacent to the nesting habitat of yellow warblers (Godfrey 1986; pers. obs.). Briskie (ms) speculated that gray jays may prey upon yellow warbler nests, but that the major predators of warbler nests were arctic fox (*Alopex lagopus*) and red fox (*Vulpes fulva*). Previous studies have found that yellow warblers respond differently to mammalian nest predators than avian nest predators (compare Hobson *et al.* 1988 and Gill and Sealy, ms; see also Buitron 1983; Knight and Temple 1988). American crows (*Corvus brachyrhynchos*) are the other common avian nest predator on warbler nests (Briskie, ms). Because of the crow's large size, warblers may respond to them as a predator on themselves (e.g., Buitron 1983). Thus, neither crows nor foxes would be appropriate stimuli for a population comparison of the alarm calls towards an avian nest predator.

I tested nests at the egg-laying (2 to 5 days) stage. To avoid habituation or positive reinforcement, I tested each nest once with the models (Knight and Temple 1986a,b). I tested nests after 0700 (Central Standard Time) by which time yellow warblers had finished laying (S. G. Sealy and D. L. Neudorf, unpubl. data), and continued testing nests up to 1800. Observations were made from a blind positioned 5 - 10 m from the nest set up 15 min prior to testing to allow nest owners to habituate to the blind. Occasionally, I did not use a blind, but was positioned as far back as possible while maintaining a clear view of the nest.

After 15 min and if the nest owners were out of the area, I quickly positioned the model approximately 0.5 m from the nest, clipped to vegetation and facing the nest. If the nest owners were in the area after the 15-min period, I waited to present the model until both left the area. I presented the models in random order and separated successive tests by at least 15 min to reduce carry-over aggression (Knight and Temple 1986a, b). The 5-min testing interval began when a nest owner arrived within 5 m of the nest. As none of the birds tested was colour-banded, I assumed that when two individuals responded, they were the nest owners. Occasionally other yellow warblers responded, however, these individuals neither approached the model as closely nor responded as intensely to it as did the presumed nest owners. I recorded whether 1 or 2 birds responded, and the sex and behaviours elicited for the entire 5-min trial.

Once one of the nest owners responded, I quantified responses using the method of Smith *et al.* (1984) and Hobson and Sealy (1989a). I recorded the following responses displayed by both male and female nest owners: (a) alarm calls: seet and chip calls (Hobson and Sealy 1989a), metallic chip (Ficken and Ficken 1965), warble calls that have not been previously recorded (see Results) and zeep calls (Ficken and Ficken 1965); (b) silent watching; (c) distance of nest owner from model (< 2 m, 2-5 m, > 5 m); (d) distraction displays (see description in Hobson and Sealy 1989a); (e) close passes; (f) hovers; (g) strikes; (h) perch changes; (i) nest-protection behaviour, or sitting in the nest; (j) displacement activities such as preening, bill wiping, foraging, feeding female and/or nestlings; (k) singing by male and begging by female; and (l) nest owners out of area. Categories b, c, d, i, and l were recorded as the number of 10-second intervals in which they occurred (maximum value = 30 intervals), while the remaining categories were recorded as the number of times they occurred in the 5-minute trial. If both nest owners called during the model trial I could not assign vocalizations to a particular sex. Therefore, I combined male and female calling for all nests. I recorded observations using a hand-held tape recorder and transcribed the tapes later. Details on the non-vocal responses of yellow warblers (categories c - l) are provided in Gill and Sealy (ms) and Gill (unpubl. data).

Recordings during model presentation

During model presentations, I recorded the first 2 min of alarm calls elicited by the models using a Uher 4000 Report-L, Sennheiser ME 88 microphone with fixed windscreen and K3 low frequency filter, and Ampex Precision magnetic tapes. Tape speed was always set at 19 cm / sec to make the best quality recording possible (Spector 1991). The Sennheiser microphone is highly directional, and suitable when the microphone cannot be positioned close to the sound source, as was the case during model trials.

Playbacks

From the recordings, I made 1-min playback tapes of seet or chip calling for each nest. The 1-min length of playback is appropriate to prevent habituation of the receivers (Falls 1982). Moreover, parasitism by cowbirds (Sealy *et al.* 1995) and predation (Sealy 1994) occur within 1-2 mins. I selected a section of tape 2-30 sec long from which I made a 1-min playback using the Uher Report-L recorder, a Sony TCM-5000EV recorder and Sony Metal SR tapes. The template varied considerably in length because nest owners varied the length of time they spent calling. I recorded the section used to make the playback in all cases. I could not control for call rate in the playbacks because I made the tapes in the field, and the nature of yellow warbler alarm calling behaviour is such that they usually give more than one call per second. Thus, call rate varied between call types (seet = 114.8 ± 11.0 per min playback, chip = 37.9 ± 3.6). Call rate has been shown to influence responsiveness in some species (Leger and Owings 1978; Leger *et al.* 1979; Weary and Kramer 1995), but not others (Harris *et al.* 1983).

I performed the playback experiment one or two days after model testing, at the same nests at which model testing was done. Playbacks were delayed by two days only in cases of rain. Fifteen minutes prior to testing I set out a blind and placed an Audio-Technica amplified speaker 1 m below the nest, either on the ground or in a crotch of a tree. The speaker positions were appropriate as yellow warblers vocalized from the ground and from perches (pers. obs.). The speaker was connected by a 10-m cord to the Sony TCM-5000EV recorder. Although I did not measure the loudness of the calls, I played back the calls at what appeared to be their typical level. Loudness does not affect the responses of several species to playbacks of their alarm calls (e.g., Seyfarth *et al.* 1980a; Weary and Kramer 1995; but see Leger *et al.* 1979). I randomized the order of the playbacks.

Each playback trial consisted of observations made one min before and during the playback, and five mins of behavioural observation after the playback. The comparison of behaviours before, during and after playback is necessary to show that nest owners changed their behaviours in response to the playbacks. I recorded behaviours directly into a field notebook in which I had delineated 7 min into 10-sec intervals. I recorded the same behaviours as in the model presentation (see above). I also recorded the proportion of nest owners that moved closer to the speaker during the trial, because the distance categories used in model presentation do not necessarily show if this occurred.

At Churchill, I played back seet and chip alarm calls and a control playback of tape noise to yellow warblers at egg-laying and early incubation stages. I did not expect warblers at Churchill to seet call, therefore, I played seet calls recorded from warblers at Delta Marsh to warblers at Churchill. At one nest I played a chip call loop also recorded from Delta Marsh. However, this loop contained considerable background noise. Background noise was not obvious during playbacks at Delta Marsh where noise in the environment, especially wind, masked most noise on the tape loop (pers. obs.). At Churchill, however, this noise was clearly audible to me, and thus, presumably to the warblers. Therefore, I made a playback chip tape from Churchill warblers.

Statistical Analyses

I used nonparametric statistics to analyze the results because the data were not normally distributed. To determine whether model type (sparrow, grackle or cowbird) or call type (seet, chip or noise) influenced the vocal and nest defence responses elicited, I used FriedmanÕs tests blocked by nests. Blocking by nests reduces variance because secondary variables characteristic of the nest owners (e.g., age, experience) are held constant among stimuli (Kamil 1988). The Friedman test is equivalent to a parametric two-way analysis of variance on the ranked data (Conover and Iman 1981). When significant differences resulted ($p < 0.05$), I used Fisher's protected least significant difference (FPLSD) test on the ranks to determine which stimuli elicited significantly different responses. The FPLSD test is equivalent to non-parametric multiple comparisons (Conover and Iman 1981). To determine whether the proportion of nest owners that uttered alarm calls differed among models or call types I used chi-square tests. I used Wilcoxon two-sample tests to determine whether responses to the models or calls differed between Churchill warblers and Delta Marsh warblers.

Results

Model Presentation (Delta Marsh)

Yellow warblers, especially females, frequently vocalized during model presentation at the egg-laying stage (Table 1). They gave significantly more seet calls to the cowbird model than the sparrow or grackle. Most females (62.9 %) uttered seet calls as they performed nest-protection behaviour (Hobson and Sealy 1989a; Gill and Sealy, ms), but after entering their nests females usually stopped calling. Yellow warblers uttered significantly more chip calls in response to the grackle model than the other models, and more to the sparrow than the cowbird model. Yellow warblers gave metallic chip calls (Ficken and Ficken 1965) to cowbird and grackle models only, although this was not significant. Metallic chips were uttered intermittently during bouts of chip calling, although one male uttered metallic chips throughout the grackle trial. Warble calls were elicited only by the grackle model. One male nest owner uttered warble calls when he performed distraction displays. Females were silent most frequently during cowbird trials, whereas males were silent equally during all trials.

Model Presentation (Churchill)

At Churchill, female yellow warblers responded similarly regardless of model type (Table 2). Three nest owners uttered seet calls in response to the models. One female uttered seet calls to all the models, and also performed nest-protection behaviour in response to the cowbird. Once in the nest the female was silent for the remainder of the trial. The male at this nest did not appear during the trials. One male uttered seet calls in response to the cowbird model, and changed perches within 1 m of the nest during the entire trial. The female of this nest did not respond aggressively to the cowbird model, but she was in the nesting area during the trial. A third female apparently seet called in response to the jay model. This female gave 'zeep' calls to the cowbird and sparrow, which appeared to grade into the seet calls recorded in response to the jay. Females uttered chip calls more frequently in response to the jay model than the cowbird or sparrow model, but this was not significant. Females chipped intermittently throughout the trials, while changing perches. Metallic chip calls were uttered by only one nest owner each in response to the cowbird and jay models. The jay model elicited warble calls at one nest. The cowbird and jay models elicited zeep calls at five nests, and the sparrow elicited zeep calls at four nests. While uttering zeep calls, females changed perches. The greatest part of the trial was spent silently watching the models or ignoring the models and returning to the nest to resume incubation. Only one female showed true nest-protection behaviour in response to the cowbird, although up to six females returned to their nests and incubated during the trials.

Playbacks (Delta Marsh)

Females uttered significantly more seet calls in response to the seet playback than the chip or control playback (Table 3). Yellow warblers uttered more chip calls to the chip and noise playbacks than the seet playback, although this relationship was not significant. Warblers uttered metallic chip calls only in response to the control playback, but this was not significant. No warbles were recorded in response to any of the playbacks. Females spent a similar amount of time silent during all playbacks. Females performed nest-protection behaviour significantly more in response to the seet playback than chip and control playbacks.

Playbacks (Churchill)

The responses of female yellow warblers differed slightly among models (Table 4). Nest owners gave more chip calls during the chip playback than the seet or control playback but this was not significant. One female nest owner seet called and performed nest-protection behaviour in response to the seet playback. No other birds uttered seet calls or performed nest-protection behaviour during the playbacks. Metallic chip and warble calls were not uttered during any playback. Nest owners uttered zeep calls in response to the chip and control playback, but this was not significant. Females tended to be silent more during the seet and control playback than the chip playback, but this was not significant. Females tended to incubate more frequently during the control playback.

Population comparisons (Model presentation)

Overall, Delta warblers uttered more alarm calls than Churchill warblers during model trials (Tables 1 and 2). Delta warblers uttered significantly more seet calls to all models than Churchill warblers (Wilcoxon two-sample test, t_R = - 5.07, df = 1, P = 0.0001; t_R = - 1.99, df = 1, P = 0.0466; and t_R = - 3.00, df = 1, P = 0.0027, for cowbird, predator and sparrow models, respectively) . Delta warblers uttered significantly more chip calls to the predator than Churchill warblers (t_R = -2.41, df = 1, P = 0.0158). Warblers in both populations rarely uttered metallic chip and warble calls to any model (t_R < 0.53, df = 1, P > 0.50). Delta warblers never uttered zeep calls during model testing. Therefore, Churchill warblers uttered more zeep calls to cowbird and predator models (t_R = 3.32, df = 1, P = 0.0009; t_R = -3.32, df = 1, P = 0.0009, and t_R = -2.93, df = 1, P = 0.0033) for cowbird, predator and sparrow models, respectively). Churchill warblers were silent significantly more to the sparrow than Delta warblers (t_R = 2.13, df = 1, P = 0.0335). Females at Delta performed nest-protection behaviour significantly more in response to cowbird than Churchill females (t_R = -2.31, df = 1, P = 0.0211).

Population comparisons (Playbacks)

Delta warblers uttered significantly more seet calls (t_R = - 2.06, df = 1, P = 0.0396) and more frequently performed nest-protection behaviour (t_R = - 2.51, df = 1, P = 0.0121) to the seet playback than Churchill warblers (Tables 3 and 4). By contrast, Churchill warblers uttered significantly more chip calls in response to the chip playback than Delta warblers (t_R = 1.94, df = 1, P = 0.0522). Females at Churchill were silent more than Delta females during the control playback (t_R = 2.28, df = 1, P = 0.0228). The remaining behaviours did not differ significantly between populations for any playback (t_R < 1.45, df = 1, P > 0.10)

Discussion

Yellow warblers allopatric with cowbirds rarely uttered seet calls or performed nest-protection behaviour in response to cowbird and jay models, and seet and chip playbacks. These results do not support the hypothesis that these behaviours evolved in response to avian nest predation, and are currently used in the context of brood parasitism (i.e. Gould and Vrba 1982). Instead, the results support Briskie *et al.*'s (1992) hypothesis that seet calls and nest-protection behaviour evolved in response to cowbird parasitism. Interestingly, Robertson and Norman (1977) found that the aggressive responses of several species, including yellow warblers, towards cowbirds did not vary between populations in recent (Ontario) and ancient (Manitoba) sympatry with cowbirds (Mayfield 1965; see also Burgham and Picman 1989). Whether the population in recent sympatry gave seet calls and nest-protection behaviour is unknown because these authors used a subjective scoring index that did not provide details on yellow warbler responses. Burgham and Picman (1989) in another Ontario population found that yellow warblers performed nest-protection (although they misidentified this behaviour as premature incubation), but they did not describe alarm calls that were uttered. Nevertheless, Robertson and Norman's (1977) and Burgham and Picman's (1989) findings suggest that yellow warblers in recent sympatry have evolved a level of aggression within 200 years equal to that of yellow warblers in ancient sympatry with cowbirds. Thus, brood parasitism is an important selective pressure that influenced the evolution of nest-defence behaviours in yellow warblers (Robertson and Norman 1977; Briskie *et al.* 1992; this study).

Brood parasitism has driven the evolution of parasitic egg rejection by cowbird and cuckoo (*Cuculus* spp.) hosts. Several host species in areas of ancient sympatry with brood parasites eject parasitic eggs naturally or artifically introduced into their nests, whereas populations allopatric or recently sympatric with brood parasites rarely eject these eggs (Davies and Brooke 1989; Brown *et al.* 1990; Soler 1990; Soler and Møller 1990; Rothstein 1990; Briskie *et al.* 1992; but see Zuñiga and Redondo 1992). Briskie *et al.* (1992) further showed American robins (*Turdus migratorius*) do not eject conspecific eggs indicating that it is cowbird parasitism rather than conspecific brood parasitism that selected egg ejection in this species (see also Sealy *et al.* 1989; Sealy and Bazin, in press). By contrast, although eastern phoebes (*Sayornis phoebe*) and clay-colored sparrows (*Spizella pallida*) sometimes desert parasitized nests, they do so in response to partial clutch reduction associated ocasionally with parasitism, rather than in response to parasitism per se (Rothstein 1986; Hill and Sealy 1994; but see Davies and Brooke 1988; Moksnes and Roskaft 1989). These authors concluded that not all apparently adaptive behaviours evolved under in response to brood parasitism (Rothstein 1986; Hill and Sealy 1994).

Given that seet calls and nest-protection behaviour (hereafter anti-cowbird behaviours; Gill and Sealy, ms) evolved in response to cowbird parasitism (Briskie *et al.* 1992; this study), the expression of these behaviours was not expected in the Churchill population. However, three yellow warblers uttered seet calls and one female performed nest-protection behaviour in response to the models, and one of these females performed these behaviours in response to the seet call playback. Briskie *et al.* (1992) never recorded nest-protection behaviour in response to a cowbird model in this population, although one (n = 15) female uttered seet calls. Similarly, low levels of egg rejection have been documented in populations that are not parasitized (Davies and Brooke 1989; Briskie *et al.* 1992) or that have been parasitized only recently (Soler 1990; Soler and Møller 1990; but see Zuñiga and Redondo 1992).

Briskie *et al.* (1992) proposed two possible mechanisms for the presence of anti-cowbird behaviours in the Churchill population. First, Briskie *et al.* (1992) suggested that gene flow may be responsible for the presence of

anti-cowbird behaviour in the Chuchill population. Gene flow refers to the incorporation of genes from one population into another (Futuyma 1986), and hence this hypothesis assumes that the Churchill population is distinct from populations that are parasitized. Yellow warblers range continuously from Delta Marsh to Churchill (AOU 1983; Godfrey 1986), but morphological evidence suggests that these two populations are separate subspecies, *D.p. aestiva* and *D. p . amnicola*, respectively (Raveling and Warner 1976; Godfrey 1986). Browning (1994) suggested that yellow warblers in Manitoba are comprised of three subspecies, a northern population (*parkesi*, which includes Churchill), a central population (*amnicola*), and a southern population (*aestiva*, which includes Delta Marsh). Subspecies were assigned on plumage differences among populations (Raveling and Warner 1976; AOU 1983; Godfrey 1986; Browning 1994). Recently, Klein (1992) found that yellow warblers are more phenotypically variable than genotypically variable, therefore, subspecies classification should be viewed cautiously until genetic analysis is performed.

Gene flow among populations results from dispersal of individuals from one population to another, either in the hatch year, i.e. natal dispersal, or after breeding, i.e. breeding dispersal (reviewed by Gauthreaux 1982; Greenwood and Harvey 1982). Breeding dispersal of male yellow warblers is low in an Ontario population as over 70% of males returned to the territory in which they nested the previous year (Studd and Robertson 1989). The extent of breeding dispersal in female yellow warblers is unknown, however, females birds generally disperse farther than males (Gauthreaux 1982; Greenwood and Harvey 1982). The return of individuals to the area in which they were hatched (Gauthreaux 1982) is low in all passerines even when post-fledgling mortality is taken into account (reviewed in Weatherhead and Forbes 1994). Yellow warblers from the Delta Marsh population have a relatively higher natal philopatry (11.3 % of 1152 fledglings banded; J. V. Briskie in Weatherhead and Forbes 1994) compared with a second population (none of 81 nestlings banded returned to unstated location; R. J. Robertson in Weatherhead and Forbes 1994). Although the extent of dispersal is unknown for the Churchill population, Browning (1994) noted that plumage characteristics intergraded between the *amnicola* (*aestiva* ?) and *parkesi* (*amnicola* ?) populations. Therefore, it is likely that anti-cowbird behaviours are maintained in the Churchill population through gene flow from the central population (see also Soler and Møller 1990; but see Zuñiga and Redondo 1992). By contrast, Davies and Brooke (1989) indicated that the maintenance of egg rejection in Iceland birds could not result from gene flow due to the large barrier (Atlantic Ocean) separating populations allopatric and sympatric with cuckoos.

Second, Briskie *et al.* (1992) suggested that a founder effect may be responsible for the presence of the behaviours, which are presumably maintained because of low costs (e.g., Cruz *et al.* 1985; Cruz and Wiley 1989). Founder effect is the principle that individuals founding a new and isolated colony carry only a fraction of the total genetic variation present in the source population (Futuyma 1986). However, there is no evidence to suggest that the Churchill warblers formed an isolated colony at any time during their evolutionary history (*c.f.* Pielou 1991; Dawson 1992). Rather, the radiation of yellow warblers may have followed receding ice as has been suggested for other wood warblers (Mengel 1964). Thus, founder effect does not adequately explain the presence of anti-cowbird behaviours in the Churchill population.

Invoking founder effect to explain the rare occurence of anti-cowbird behaviours in the Churchill population contradicts the argument that the absence of these behaviours is plesiomorphic (i.e. the primitive condition). As applied by Briskie *et al.* (1992), this hypothesis implies that all individuals in the founding Churchill population displayed these behaviours at one time in evolutionary history and, over time most descendents of these founders secondarily lost the behaviours. Accordingly, the absence of anti-cowbird behaviours in the Churchill population is apomorphic (i.e. the derived condition; e.g., Foster 1994), and not plesiomorphic as suggested by Briskie *et al.* (1992). If the Churchill population was descended from a parasitized population during the radiation of yellow warblers, Churchill warblers may have inherited these behaviours (e.g., Davies and Brooke 1989), in which case the absence of the anti-cowbird behaviours is apomorphic.

Authors have incorrectly assumed that by showing differences in behaviour between populations that experience different selection pressures, they can infer the direction of evolutionary change (e.g., Davies and Brooke 1989; Soler 1990; Soler and Moller 1990; Briskie *et al.* 1992; but see Bolles 1988; Cruz and Wiley 1989; Goldthwaite *et al.* 1990; Towers and Coss 1990; Foster 1994). This clearly is not true, as this type of study cannot resolve whether a population has secondarily lost the behaviour (i.e. absence is apomorphic) or whether a population

originally lacked the behaviour (i.e. absence is plesiomorphic; see above). This question can be resolved only by mapping the behaviour of interest onto independently derived cladograms that show the phylogenetic relationships among populations (Brooks and McLennan 1991; but see Frumhoff and Reeve 1994). Foster (1994) recently used this method to study the diversionary display of three-spined sticklebacks in six freshwater populations and two marine forms. Foster (1994) found that the absence of diversionary displays was the apomorphic condition, a finding that is contradictory to the assumption of many authors that the expression of complex behaviours is apomorphic. Model presentation and playback experiments on other yellow warbler populations and an outgroup to control for phylogeny (Harvey and Pagel 1991), in conjuction with cladistic methods (Brooks and McLennan 1991), must be performed to assess whether seet calls and nest-protection behaviour represent a plesiomorphic or apomorphic condition.

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Cues used by brood parasites and predators to locate nests

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Introduction

Both predators and cowbirds must locate nests and choose a suitable one from among those found. They may use similar cues, as brood parasites can be considered a type of predator (Wiley 1982). Very little is known about how predators locate nests (Smith *et al.* 1974, Collias and Collias 1984). Few studies have looked at the predator/prey interaction from the point of view of the predator. Much of the literature describes tactics used to avoid being eaten or what occurs after food has been found or procured (but see Bell 1991). There is a large body of literature on optimal foraging that discusses what happens once the prey has been found (reviews in Krebs and McCleery 1984, Pyke 1984), indicating that predators should choose the most profitable prey given their current condition.

Andersson (1981) described three general methods of searching by predators: (1) continuous movement, (2) sit and wait, and (3) pause and travel. Different animals use different techniques. Many avian predators often use the sit and wait and the pause and travel techniques. Birds have been documented perching and scanning, hovering and soaring in search of food (Carlson 1985, Viitala *et al.* 1995). Avian predators that hunt on the ground and mammalian predators are believed to find prey using directional, systematic searching or random search movements (Zach and Smith 1981, Benhamou 1992).

Three methods of searching, in this case for nests to parasitize, have also been documented for Brown-headed Cowbirds: (1) watching hosts at their nests, (2) silently searching for nests, and (3) flushing hosts off nests (Norman and Robertson 1975, Wiley 1988). The most common method is watching hosts (Friedmann 1929, Hann 1941, Payne 1973).

Two behaviours predators and cowbirds could cue in on are activity and aggression of nest owners, which may indicate that there is an active nest in the area and draw the predator or parasite to the nest. Some other cues that might be used, include song rates of adults and host aggression to indicate the bird's quality (Smith 1981, Arcese and Smith 1988), activity around the nest to indicate nesting stage, nest placement (e.g., height, supporting vegetation, concealment), and nest type (Thompson and Gottfried 1981, Fleischer 1986, Orians *et al.* 1989, Briskie *et al.* 1990, Colwell 1992). These cues may lead predators or cowbirds to the location of nests, may help them select nests and perhaps even provide information on the fitness of the adults (Smith 1981). For example, the more time a male can devote to singing, the more fit it may be (see Greig-Smith 1980, 1982; Reid and Sealy 1986).

In this study, I examined experimentally five cues that might be used by both predators and parasites to locate nests: nest concealment, nest height, vegetation supporting the nest, host activity, and host aggression.

Predation has been shown to be an important factor in nest-site selection (Murphy 1983) and that better-concealed nests suffer less predation (McLean *et al.* 1986, Sugden 1987, Brown and Fredrickson 1989). Cowbirds, therefore, should parasitize better-concealed nests because they will also benefit from this reduced level of predation (see Gates and Gysel 1978).

Predation by visual predators apparently is related to concealment (Knapton 1978, Wray and Whitmore 1979) with better-concealed nests being preyed upon less frequently, assuming that predators do not use the activity of nest owners to locate nests (Collias and Collias 1984). Olfactory predators should not be affected by the degree

of concealment of a nest (Clark and Nudds 1991, Holway 1991). I predicted that concealment is not related to nesting success of Clay-colored Sparrows because the Franklin's ground squirrel (*Spermophilus franklinii*), an olfactory predator, is the main predator.

Nest height and supporting vegetation may be used to locate nests. If nests are at a set height or in a particular species of plant, this would allow predators and parasites to form search images and "know" where to look. Briskie *et al.* (1990) showed that higher nests were parasitized more frequently. Filliater *et al.* (1994) discussed five hypotheses that explain how both nest height and vegetation could provide cues for predators when looking for nests. These hypotheses involve nest inaccessibility, nest height (high, mid-height and low nests) and vegetation (common and rare plants). They indicate that there is a wide variety of possible explanations for where nests are placed depending on the type of predators in the area. I predicted that both nest height and supporting vegetation would be related to nesting outcome.

Nest activity may be used by cowbirds to locate nests (Friedmann 1929, Hann 1941, Buech 1982, Wiley 1988). I tested this by placing out old nests (see Thompson and Gottfried 1981). To be able to use host activity to find nests, activity must be centred near or at the nest and occur when parasitism is appropriate. These activities may include nest building, mate guarding, nest visits and egg laying. Several studies have shown that when old nests were placed out, even with eggs, cowbirds did not lay eggs in them (e.g., Laskey 1950, Thompson and Gottfried 1976). Thus, Lowther (1979) and Thompson and Gottfried (1981) attempted to simulate host activity by adding one egg per day to each nest, but still recorded only a low frequency of parasitism (see also Wiley 1988). This suggests that host activity is indeed necessary. I investigated this by simulating five levels of increasing host activity; empty nests, nests with full clutches, nests in which one egg was placed per day, model hosts and song. I predicted that by simulating increasing amounts of host activity, the frequency of parasitism should increase.

Predators may also use nest activity to locate nests (review in Collias and Collias 1984). The activity of adults may direct the predator to the nest site or may cue it to an active nest nearby. Here, too, I predicted that by simulating increasing amounts of activity of nest owners at artificial nests, the frequency of predation should increase.

Host aggression has usually been thought to discourage both predators and parasites (Buitron 1983, Smith *et al.* 1984, Martin 1992). Some hosts can distinguish cowbirds from other potential nest threats (Nice 1937, Robertson and Norman 1976, Neudorf and Sealy 1992). Enemy recognition can be tested experimentally by placing models of different enemies near nests and quantifying the birds' responses to them. Some species react more aggressively to a cowbird model, thus providing a potential cue for cowbirds to locate active nests (Robertson and Norman 1977, Smith 1981). For the aggressive behaviours to act as a cue nesting birds must respond to a threat at a distance that would enable the cowbird to use the behaviour to locate the nest. If the birds do not react until the cowbird is very close (e.g., 0.5 m or less), then the nest probably has already been found and aggressive behaviours would not act as a cue (Neudorf and Sealy 1992). If the level of aggression increases as the nest is approached, then the cue may function (Duckworth 1991). I predicted that hosts will react to a nest threat at distances greater than 0.5 m.

Predators also may use aggression to locate nests. Some studies have found that more aggressive pairs were depredated more frequently (Searcy 1979, Röell and Bossema 1982), whereas other studies have found the opposite (Greig-Smith 1980, Blancher and Robertson 1982). I predicted that if predators use aggression to locate nests, nest owners should respond aggressively towards a model at different distances from their nests, perhaps becoming more aggressive as the model is placed closer to the nest and the threat increases.

In the present study, I examined the importance of host activity and aggression to Brown-headed Cowbirds and predators in locating nests. I also determined if nest concealment, supporting vegetation and nest height were used as cues to locate nests. The study species involved is the Clay-colored Sparrow, an accepter species (Hill and Sealy 1994).

Methods

Study Site

This study was conducted at the University of Manitoba Field Station, Delta Marsh (50°10'N,98°22'W), Manitoba, during the springs of 1993 and 1994, in an area known as the Oxbow Woods. Situated along the southern edge of Delta Marsh, this woodlot is surrounded by old-field succession dominated by snowberry and wild rose (*Rosa* sp.) (see Evans 1972, Gamble 1980, Hill 1992, Hill and Sealy 1994). I searched for sparrow nests daily from mid-May to the end of June. I searched the habitat thoroughly, checking every tuft of grass and snowberry bush. I flagged and numbered each nest approximately 2 m away, and inspected each nest daily for signs of predation, i.e. broken eggs, eggshells, tipped nests, missing eggs (see Major 1991, Sealy 1994) and parasitism, i.e. presence of a cowbird egg.

Nest Concealment

I quantified the degree of concealment at each nest by assigning cover values on a scale from 0-5, that corresponded to decreasing visibility of the nest (0=100% visible, 1=80% visible, etc.). Estimates were made at eight compass directions and one from above the nest. I then calculated an average concealment value. All measurements were taken one meter from the nest and at nest height and the observer's eye level (see Holway 1991). These measurements simulated the cowbird's or avian predator's vantage point (observer's eye level; see Gochfeld 1979) and a mammalian predator's vantage point (nest height). I estimated the cover value on the day the nest was tested (see below) or on the day the last Clay-colored Sparrow egg was laid. This ensured that the nest was active (Friedmann 1929, McGeen 1971). I then correlated concealment values with the nest outcome (predation, parasitism or success). I considered a nest successful if the clutch was still intact three days after the last egg was laid. The three-day cutoff was chosen because Clay-colored Sparrows are sometimes parasitized even after the clutch is complete. However, most parasitism occurs during the egg-laying period (Hill 1992). I ended the experiment before fledgling success was known because I wanted a comparable time frame for both parasitism and predation.

Nest Height and Supporting Vegetation

I recorded the height of the nest rim from the ground. For analysis, I broke the heights into increments of 100 mm, the approximate height of a single nest. The dominant plant species in which the nest was placed was recorded to determine if there was any relationship to nest outcome.

Host Activity

Old Clay-colored Sparrow nests (collected by D.P. Hill in 1991, and by me in 1993) were place randomly in Clay-colored Sparrow nesting habitat from 3 to 18 June in 1993 and 6 to 21 June in 1994. Nests were placed in sites with known (controlled) concealment values (Lowther 1979) for eight days, which simulates one day as an empty nest, four days of egg laying and three days of incubation (four-egg clutches are the modal clutch size for Clay-colored Sparrows at Delta (Hill 1992)). I placed the nests 3 m apart along a transect, 1 to 2 m alternately to the left or right of a rope stretched along the transect. I flagged each nest location along the rope so that I could relocate the nests. I chose a distance of 3 m between nests because Clay-colored Sparrow territories are small (natural nests are sometimes within 5 m of each other (Knapton 1978)). At this distance, nests were 4 to 6 m apart because they were placed on alternate sides of the rope 1 to 2 m from it. Nests received one of five treatments: (1) no eggs, (2) full clutch (four eggs), (3) one egg per day, (4) one egg per day plus model Clay-colored Sparrow, or (5) one egg per day plus model plus song (Thompson and Gottfried 1981). Each treatment, consisting of 20-35 nests, simulated laying and different amounts of host activity to determine if host activity influenced predation and parasitism frequencies (see Wiley 1988). Comparisons between treatments for the three nest outcomes to determine if host activity affected nesting outcome.

The models were placed 0.5 m from the nest for 30 minutes every morning from 0630-1000 (Central Standard Time) for 7 days (Wiley 1988). Cowbirds are active in nesting areas in the morning and then move off these areas to feeding areas during the late morning or early afternoon (Rothstein *et al.* 1984). The models were Clay-colored Sparrows, freeze-dried and mounted on poles, and placed facing the nest. Songs of Clay-colored Sparrows were recorded in 1993 and transferred to a loop tape at a rate of 9 songs/minute, a rate that fell within the natural song rate (Bent 1968). Song was played back for 30 minutes on a cassette recorder placed at the base of the pole. The model treatment and model plus song treatment were randomly assigned to nests and to a different 30-minute period every day so that each nest received the treatment over each 30-minute period during the experiment. Two runs of nest placements were conducted to increase sample size and these were combined because there was no difference between them (1993: Fisher exact test, $p = 0.917$; 1994: Fisher exact test, $p = 0.533$).

Artificial eggs were made of plaster-of-Paris and painted to resemble Clay-colored Sparrow eggs (Rothstein 1975). The eggs were slightly larger and heavier than real Clay-colored Sparrow eggs (2.2 g vs. 1.6 g; 17.5 mm x 13.4 mm vs. 17.1 mm x 12.7 mm; measurements from Walkinshaw 1944 and Bent 1968). The slightly greater mass and size should not affect the study because predators were able to remove the eggs (pers. obs.) and there is some natural variation in egg size (Bent 1968). Cowbirds should not be affected because they are known to parasitize species with eggs that are larger than those of Clay-colored Sparrows (e.g., Fleischer 1986). I placed nests in active territories as the study was conducted during the breeding season of Clay-colored Sparrows. Thus, there was an increased level of activity near the experimental nests that was in addition to the simulated levels of activity. This may have been a problem but the activity probably was similar for each artificial nest. This problem was not addressed in other studies using artificial nests in active territories (see Lowther 1979, Thompson and Gottfried 1981). For nest concealment, nest height, supporting vegetation, and host activity, Fisher exact tests (2-tailed) were used for desired comparisons of each cue and nest outcome (Conover 1980, Zar 1984).

Host Aggression

Enemy recognition

To test whether Clay-colored Sparrows recognized different nest threats, I used the data on responses by sparrows to three models (female Brown-headed Cowbirds, Franklin's ground squirrel and Common Grackle *Quiscalus quiscula*) placed 0.5 m from active nests. I added a fourth model, a Fox Sparrow (*Passerella iliaca*), to serve as a control. The sparrow is a good control because it is similar in shape and size to female cowbirds but neither parasitizes nor preys upon Clay-colored Sparrow nests. It is found on the study area only during migration and therefore should rarely interact with Clay-colored Sparrows. Thus, I expected the Fox Sparrow to elicit low levels of aggression (see Hobson and Sealy 1989, Neudorf and Sealy 1992, Bazin and Sealy 1993). These models allowed determination of responses to different enemies. In this series of tests, I included only tests where birds responded because I was interested in the aggressive responses of the birds and not whether or not they responded by avoiding the nest.

The tests were conducted during the egg-laying stage and data were tape-recorded and later transcribed. The responses of Clay-colored Sparrows were recorded following the methods of Smith *et al.* (1984), as modified by Hobson and Sealy (1989). Responses were: (a) time spent < 2 m, 2 m to 5 m or > 5 m from the model, (b) vocalizations (chip, quiet chip), (c) hidden in the vegetation, (d) attacks, (e) feeding, (f) incubating, (g) perching, (h) out of area, and (i) singing. I scored categories a, c, e, f and h as the number of 10-second intervals in which they occurred while I scored all other categories as the actual number of times they occurred in the 5-minute test. The time Clay-colored Sparrows took to react to the model was also recorded as an indication of host attentiveness. The responses of both male and female were combined as the sexes could not be distinguished in this unmarked population. Each test was run for 5 minutes with 15-minute rest periods between each model presentation to reduce carry-over aggression. Observations were made from a blind 5 to 10 m from the nest. The models used in the distance testing were taxidermically mounted in upright, non-threatening postures. Models were placed facing the nest. Nests were tested from 0600 to 1900 (CST), each nest was tested only once at all

three distances. The test was started when a bird returned to within 5 m of the model. If no bird showed up within 30 minutes, the test was ended and this was considered no response.

Distance testing

To test the nest-cue hypothesis, I placed a female cowbird model 0.5 m, 2.5 m and 4.5 m from nests to determine at what distance Clay-colored Sparrows reacted to a cowbird. The farthest distance was selected on the basis of territory size, which sometimes placed nests as close as 5 m apart (Knapton 1978). This test permitted determination of the possibility that a cowbird could use host aggression to locate nests. To determine if aggressive behaviour could be used as a cue by predators, model testing at the same three distances was done using an avian predator (Common Grackle) and a mammalian predator (Franklin's ground squirrel). The grackle was chosen as the avian predator because it breeds in the study area.

I chose the Franklin's ground squirrel as the mammalian predator because it is found on the study area in substantial numbers and is known to prey on bird nests (Sowls 1948, Knapton 1978, Sargeant *et al.* 1987). To act as a control, I tested four nests with a model Fox Sparrow placed at the three distances.

For the distance-model testing, Friedman analysis of variance was used due to the nonparametric nature of the data. For the enemy recognition testing, I used the Kruskal-Wallis test. If a significant difference was found between the distances or models, I then used nonparametric multiple comparisons to determine where the difference was (Conover 1980, Conover and Iman 1981; also see Neudorf 1991).

Results

I found 112 Clay-colored Sparrow nests, of which 13 were parasitized (11.6%), 12 were preyed upon (10.7%), and 87 were successful (77.7%). The outcomes of the nests did not differ between the two years (Fisher exact test, $p = 0.712$).

Nest Concealment

Most nests (>67%) were highly concealed (concealment values between 4 and 5). For all concealment values taken at both eye-level and nest-level, there was no significant difference for the three possible outcomes (eye-level, Fisher exact test, $p = 0.391$; nest-level, Fisher exact test, $p = 0.642$). Concealment values measured from above were also not significant for the three possible outcomes (Fisher exact test, $p = 0.149$).

Nest Height and Supporting Vegetation

Nest height did not affect nest outcome (Fisher exact test, $p = 0.203$). Forty-one percent of the nests were built at heights from 101 to 200 mm. Snowberry was the dominant plant with 77% of nests built in this species. Nest outcome was not related to supporting vegetation (Fisher exact test, $p = 0.826$).

Host Activity

Only one of the five treatments affected nest outcome. The fifth treatment (one egg/day plus model plus song) was significantly different from the other treatments (Fisher exact test, $p = 0.009$), because no nests in this treatment were depredated. None of the nests from any treatment was parasitized, approximately 33% of nests were depredated and 66.6% of nests were successful for the first four treatments. Distribution of nests according to concealment values for both eye-level and nest-level were similar to active nests. Most nests fell in the 80-100% concealment category. Concealment also did not effect the outcome for any treatment at eye-level. However, for concealment values at nest-level, 80%-100% concealment had a significant effect on the outcome

for treatment five (Fisher exact test, p = 0.001). Again this was due to the lack of predation on nests in this treatment.

Host Aggression

Enemy recognition

The 0.5-m distances from the model testing described below were used to test for enemy recognition. There were two significant responses, distance <2 m and distance >5 m (Table 1). Clay-colored Sparrows spent more time closer to the cowbird model than any of the other three models and they also spent more time farther from the Fox Sparrow model than the others. The alarm call, 'chip' (Walkinshaw 1944) frequency was not quite significant but increased in response to the cowbird and sparrow models but not for either predator model.

Table 1. Summary of responses of Clay-colored Sparrows to four models presented at 0.5 m from the nest, and results of Kruskal-Wallis test and associated multiple comparisons.

	Type of model presented				
Response[a]	BHCO[b] (17)[c]	COGR (10)	FGSQ (10)	FOSP (4)	p-value[d]
< 2 m	31.8 ± 4.8[1]	9.6 ± 4.2[2]	9.7 ± 4.0[2]	0.3 ± 0.3[2]	0.0014
> 5 m	1.4 ± 0.8[1]	3.1 ± 2.5[1]	3.3 ± 3.2[1]	11.8 ± 4.8[2]	0.0171
Chip	8.1 ± 2.7	1.0 ± 0.7	2.7 ± 2.7	5.0 ± 4.7	0.0562

Responses are given as mean ± s.e.

[a] Categories of distance, incubation, in vegetation and leaves area were measured as the number of 10-sec intervals that birds were engaged in the behaviours. All other behaviours were measured as the actual number of times they occurred within a trial.

[b] BHCO=Brown-headed Cowbird, COGR=Common Grackle, FGSQ=Franklin's ground squirrel, FOSP=Fox Sparrow.

[c] Combined sample sizes for male and female are given in parentheses.

[d] Results of the Friedman test for comparisons among the four models.[1,2] Results of multiple comparisons for determining differences between models. Means with different superscripts differed significantly (p<0.05).

Distance testing

Seventeen nests were tested with a model female cowbird placed at three distances from the nest. Of the recorded responses to the model, only four were significant: distance <2 m, distance 2-5 m, chips, and perch changes (Table 2). The rate of chip calling increased as the model was placed closer to the nest. The time females incubated was greatest when the model was placed the farthest from the nest, although this difference was not quite significant (Table 2). None of the more aggressive behaviours, such as flybys and chips, was significant because each was rare. The time adults took to respond and the number of adults that responded also were not significant for all three distances.

Table 2. Summary of responses of Clay-colored Sparrows to cowbird models presented at three distances from the nest, and results of Friedman test and associated multiple comparisons.

	Distance (m)			
Response[a]	0.5 (16)[b]	2.5 (16)	4.5 (17)	p-value[c]
< 2 m	33.5 ± 4.3[1]	22.4 ± 4.0[2]	6.8 ± 3.1[3]	0.0001
2-5 m	5.6 ± 1.8[1]	14.6 ± 2.8[2]	29.5 ± 2.6[3]	0.0001

Chip	9.8 ± 2.9[1]	7.3 ± 2.8[1,2]	1.0 ± 0.7[2]	0.0166
Close passes	0.5 ± 0.4	0.0	0.0	0.1302
Incubation	3.4 ± 2.3	2.5 ± 1.9	13.0 ± 3.6	0.0529
Perch changes	30.8 ± 5.9[1]	21.2 ± 5.0[2]	12.2 ± 3.3[2]	0.0018

Responses are given as mean ± s.e.

[a] Categories of distance, incubation, in vegetation and leaves area were measured as the number of 10-sec intervals that birds were engaged in the behaviours. All other behaviours were measured as the actual number of times they occurred within a trial.

[b] Combined sample sizes for male and female are given in parentheses.

[c] Results of the Friedman test for comparisons among the three distances.

[1,2,3] Results of multiple comparisons for determining differences between distances. Means with different superscripts differed significantly ($p<0.05$).

Clay-colored Sparrows did not react aggressively to the model Franklin's ground squirrel as only one behaviour recorded was significant, the quiet chip (Table 3). Bent (1969) described a "tsip" call that is similar to the quiet chip. Incubation and perch changes showed distinct but not significant trends. Incubation increased as the model distance from the nest increased, whereas perch changes decreased.

Table 3. Summary of responses of Clay-colored Sparrows to Franklin's ground squirrel models presented at three distances from the nest, and results of Friedman test and associated multiple comparisons.

	Distance (m)			
Response	0.5 (9)	2.5 (8)	4.5 (8)	p-value
Quiet chip	1.9 ± 0.6[1]	2.6 ± 1.0[1]	5.3 ± 1.7[2]	0.0443
Incubation	0.0	2.0 ± 2.0	6.0 ± 4.1	0.1567
Perch changes	21.0 ± 5.8	13.9 ± 5.6	7.6 ± 3.0	0.1885

Responses are given as mean ± s.e. Conventions as in Table 2.

Clay-colored Sparrows did not react aggressively to the model Common Grackle, as only two behaviours recorded were significant, distances <2 m and >5 m (Table 4). The sparrows spent more time closer to the model when it was closer to the nest and more time farther from the model when it was farthest from the nest. This indicates that the birds centred their behaviour around the nest, not around the model. Perch changes showed a strong but nonsignificant trend, decreasing in frequency as the model was placed farther from the nest. Only the quiet chip was significant for the Fox Sparrow model (Table 5). Chipping decreased as the model was placed farther away, though not significantly.

Table 4. Summary of responses of Clay-colored Sparrows to Common Grackle models presented at three distances from the nest, and results of Friedman test and associated multiple comparisons.

	Distance (m)			
Response	0.5 (7)	2.5 (8)	4.5 (10)	p-value
< 2 m	9.6 ± 4.2[1]	2.9 ± 2.0[2]	0.0[2]	0.0111
> 5 m	3.1 ± 2.5[1]	14.6 ± 5.2[2]	20.2 ± 4.1[2]	0.0361
Perch changes	29.3 ± 11.5	17.0 ± 4.4	15.2 ± 3.2	0.1027

Responses are given as mean ± s.e. Conventions as in Table 2.

Table 5. Summary of responses of Clay-colored Sparrows to Fox Sparrow models presented at three distances from the nest, and results of Friedman test and associated multiple comparisons.

	Distance (m)			
Response	0.5 (4)	2.5 (4)	4.5 (4)	p-value
Chip	5.0 ± 4.7	0.3 ± 0.3	0.0	0.1537
Quiet chip	0.5 ± 0.5[1]	2.8 ± 0.6[2]	0.5 ± 0.5[1]	0.0029
Responses are given as mean ± s.e. Conventions as in Table 2.				

Discussion

Nest Concealment

The non-significant findings suggest that there is no relationship between nest concealment and nest outcome. As the major predator in the Oxbow Woods area on Clay-colored Sparrow nests is the Franklin's ground squirrel, a mammalian predator, predation frequencies are not expected to be related to concealment. As host species do not benefit from a decreased predation frequency with increasing concealment a cowbird egg also would not benefit. Thus, cowbirds apparently lay in any nest regardless of concealment. Indeed, in this study, parasitism frequencies did not increase significantly with decreasing concealment values. However, Clay-colored Sparrows experience low levels of predation and parasitism, and build fairly well concealed nests (most fell in the range of 4-5 or 80-100% concealed). Therefore, differences in concealment among nests may not provide enough selective pressure for concealment to be used as a nest-finding cue. This cue may work better on a species with a higher frequency of parasitism, and more variable nest concealment values or whose main nest predator is avian and therefore more likely to be affected by concealment.

Nest Height and Supporting Vegetation

Nest height cannot be used as a cue by predators nor by parasites to locate nests because outcome did not vary with nest height. This finding is contrary to what Knapton (1978) found for Clay-colored Sparrows. He found that pairs that nested within 10 cm above the ground suffered less predation than those that nested higher. He had many more nests less than 10 cm from the ground than I did. Most of the nests in the present study were higher than 10 cm. This may indicate a population or habitat difference and explains why the findings from the two studies are different. Buech (1982) conducted a similar study on nest height using three sparrow species: Field Sparrow (*S. pusilla*), Chipping Sparrow (*S. passerina*) and Clay-colored Sparrow. He found no differences in nest height between parasitized and non-parasitized nests for these species, results that are similar to my study.

Several studies have shown that higher nests were parasitized more often (e.g., Dappen 1967, Fleischer 1986). Other studies have recorded opposite results (e.g., Briskie *et al.* 1990), whereas other studies have found no relationship between nest height and nest outcome (e.g., Best 1978, Smith 1981). These studies show that there is much variation with respect to the effect of nest height on predation and parasitism rates. It may be that for species with only slight differences in nest height, such as Clay-colored Sparrows, height is not used to locate nests.

Supporting vegetation also did not affect outcome. Snowberry is abundant and it may decrease the chances of a predator or parasite locating a Clay-colored Sparrow nest (see Martin and Roper 1988, Filliater *et al.* 1994). However, Clay-colored Sparrows seem to show a preference for snowberry (Walkinshaw 1939, Fox 1961, Salt 1966). In this study, 77% of nests were in this species of plant. Predators and parasites could use the plant species as a cue to know where to look, that is, look in snowberry instead of in grass tufts. Snowberry also offers a high degree of nest concealment and may be chosen for this reason (Knapton 1978, Filliater *et al.* 1994).

Host Activity

None of the experimental nests was parasitized. The prediction of increased parasitism as host activity increased was not upheld. Some experimental nests, however, were depredated independent of all levels of host activity and concealment for all but the highest level of activity (one egg per day plus model plus song), which experienced no predation. Here, too, the prediction of increased predation as host activity increased was not upheld. Other studies have produced similar results, some with low levels of parasitism (Laskey 1950, Thompson and Gottfried 1976, 1981, Lowther 1979, Yahner and DeLong 1992).

In all of the studies, including the present one, parasitism on artificial nests was at a much lower frequency than on natural nests. One possibility why little or no parasitism was observed on artificial nests was that a critical level of activity or type of activity was not simulated, and before this point is reached, cowbirds will not cue in on model hosts and/or their nests. Perhaps the presence of a living nest owner(s) and/or its movement is required. This was not simulated in the above experiments. Simulation of movement may be impossible.

Cowbirds may need to see birds going to or from their nests to pinpoint their location or to ensure that nests are active. Female cowbirds have frequently been observed perched in trees watching hosts carrying nesting material directly to their nest sites (Norman and Robertson 1975, Wiley 1988). Cowbirds have also been seen flying over nesting areas or flying directly to nests as soon as a host has left. These behaviours ensure that the nest location and stage are known (Wiley and Wiley 1980). Several studies have found that cowbirds occasionally lay in inactive nests suggesting that host activity is not necessary (Thompson and Gottfried 1981, Wiley 1988, Weatherhead 1989, Sealy in press). Cowbirds may be interpreting stealing of nesting material or previous host activity at a nest as building of an active nest and parasitize these nests inappropriately (Wiley 1988).

Few investigators have looked at predation as well as parasitism using artificial nests (but see Yahner and DeLong 1992). Predation frequencies on my artificial nests was similar to that on natural nests, which indicates that activity of nest owners is less necessary for predators to locate nests. No nests in my fifth treatment, however, were depredated, which suggests song may deter predators. However, Clay-colored Sparrows rarely sing above their nest (Knapton 1978). If predators attempt to minimize their search effort, they should not look near a singing Clay-colored Sparrow because a nest is probably not below it. This may explain why no nests in treatment 5 were depredated.

Few workers have looked at predation in relation to host activity simulated at artificial nests or active nests. Nor have many references been made to how predators find nests. Collias and Collias (1984) stated that predators probably find nests by watching birds building nests but they did not cite studies to support this claim. Hammond and Forward (1965) stated that avian predators locate duck nests by observing the female's activity. It is reasonable to expect that passerine nest predators use a similar technique to locate nests.

Host Aggression

Enemy recognition

Rothstein (1990) stated that aggression may be a general response to nest intruders and not a defense against parasites. Smith *et al.* (1984) found support for this in Song Sparrows. However, other studies have found that hosts recognize the parasite as a unique threat (Hobson and Sealy 1989, Duckworth 1991, Neudorf and Sealy 1992). It may be that some hosts recognize the cowbird as a specific threat and others do not (Neudorf and Sealy 1992). Nest owners have also been shown to recognize different predators. Patterson *et al.* (1980) found that responses varied with different predator models. Buitron (1983) found responses to natural predators varied with predator type and situation.

The different responses to the female cowbird model compared to the control suggests that Clay-colored Sparrows recognize cowbirds as a specific threat. Indeed, they responded more aggressively to the cowbird model as more time was spent near the nest and they chipped more frequently (Table 2).

Clay-colored Sparrows apparently did not distinguish between different predators (Table 1). Nor did they react aggressively to the predators. The sparrows only gave quiet chips to the predator models. Bent (1968) described the quiet chip or "tsip" call as a communication call. This suggests that the birds are not disturbed by the presence of the predator models. Another fact that suggests that they were not disturbed is that the birds centred their behaviours around the nest and not the model as would be expected if the model posed a real threat. Neudorf and Sealy (1992) were the first to test an avian predator, the Common Grackle, along with a female cowbird and a control. They showed that some species reacted differently toward the predator and brood parasite whereas others did not. My study is one of the few to test two different types of predators, avian and mammalian (see also Knight and Temple 1988). These tests allowed me to determine if responses varied for different predators and if predators are recognized as unique threats. Clay-colored Sparrows were not highly aggressive and apparently did not recognize unique predators (Tables 3 and 4).

The Fox Sparrow elicited some aggression, perhaps due to its similarity in shape and size to a cowbird. The only significant behaviour was quiet chipping, which suggests that the birds were not disturbed. However, chipping was greatest at the closest distance indicating that they were slightly disturbed as chip calls were given as alarm calls (Walkinshaw 1944, Bent 1968). Other studies have found only low levels of aggression elicited from a variety of hosts when presented with a Fox Sparrow model (Hobson and Sealy 1989, Neudorf and Sealy 1992). Clay-colored Sparrows, therefore, may recognize a shape or size and not individual species but due to the small sample size for Fox Sparrow, it is impossible to say with certainty if they recognize cowbirds per se or simply shape and size. Neudorf *et al.* (unpubl. data) found that bill shape was more important than plumage colour or pattern in recognizing cowbirds. Fox Sparrows and cowbirds have similar bills, although it is slightly shorter in the former. This similarity may account for the slight aggressive responses recorded in these studies.

Sealy *et al.* (1995) placed a female cowbird on the nest and found that the Clay-colored Sparrows responded aggressively and even knocked the model off the nest. This study demonstrates that Clay-colored Sparrows can be aggressive but may respond aggressively only to threats right at the nest (see also Neudorf and Sealy 1994, Sealy *et al.* 1995). They may not react until the threat is at or on the nest so that their behaviour does not reveal the position of their well-concealed nests.

Distance testing

Host aggression generally has been assumed to deter predators (Blancher and Robertson 1982, Buitron 1983). However, several workers have suggested that host aggression may be used by both predators and parasites to locate nests (Smith 1981, Smith *et al.* 1984, Hobson *et al.* 1988). McLean *et al.* (1986) found that alarm vocalizations attracted avian predators. Wiley (1988) found that cowbirds were attracted to areas where residents aggressively defended against intruders. These behaviours seem to be "maladaptive" unless they indeed deter parasites and predators, and the nest owners benefit by this behaviour (Smith *et al.* 1984).

Clay-colored Sparrows responded but not aggressively at all three distances, which reveals that aggression could be used as a cue to locate nests. Aggressive behaviours were, however, observed infrequently and were not elicited by all individuals, therefore, aggressive behaviours probably cannot be used as reliable cues for cowbirds. However, for those individuals that exhibit aggressive behaviour, cowbirds may be able to cue in on them, opportunistically. Cowbirds may be able to use the distance between them and the host, the number of perch changes, and the frequency of chips as cues to the presence of a nest. Clay-colored Sparrows spent more time closer to the model, changed perches and chipped more frequently when the model was closer to the nest. There was also a gradation in responses for <2 m, perch changes and chips, which increased in frequency as the distance from the nest decreased. Chip calls indicate that adults were disturbed and may indicate aggression. These three behaviours may be used by cowbirds to locate nests. For most of the responses, the two closest distances seem to be similar and the responses more frequent than the third and farthest distance. This may indicate a threshold distance, where the adults ignore the model cowbird (intruders) until a certain distance (somewhere between 2.5 and 4.5 m) and then respond as the threat increases (intruder closer to nest).

Clay-colored Sparrows did not react aggressively toward the two predator models. The responses that were significant were not aggressive behaviours and therefore host aggression cannot be used as a cue by predators to

locate nests. The quiet chip was given frequently and seems to be given most often when the birds are foraging or communicating with one another (pers. obs.). This suggests that the birds were not disturbed. The prediction of increased aggression as the predator model was placed nearer to the nest was not supported for either type of predator. Clay-colored Sparrows may not want to draw attention to the nest and, therefore, are not aggressive towards predators, thus eliminating this as a nest-finding cue or perhaps they know they cannot deter predators (Knight *et al.* 1985, Sealy 1994).

Model testing at different distances from the nest has only been done in one other study (Gill *et al.*, unpubl. data). These results show that responses vary with distance and that this is important when looking at nest success with respect to cowbird and predator models because conclusions about nest finding cues and behaviours that attract predators and parasites (McLean *et al.* 1986) may vary depending on testing distance.

None of the five cues (host activity, host aggression, nest concealment, nest height, or supporting vegetation) examined in this study was used by parasites or predators to locate Clay-colored Sparrow nests. These cues may work to varying degrees, either alone or in combination, for other species. Nest finding is probably species-specific, with nests of some species being found more readily. The question, therefore, still remains: what specific cues do parasites and predators use to find Clay-colored Sparrow nests?

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Response of aquatic invertebrates to experimental nutrient enrichment of a wetland

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Introduction

Delta Marsh, a large lacustrine wetland on the southern shore of Lake Manitoba, is bordered with fertile agricultural land and aspen parkland. Fertilizers and pesticides in runoff from these lands and in groundwater are filtered through the marsh, impacting the aquatic environment including the biota. However, the effects of nutrient enrichment of a eutrophic prairie marsh are poorly known. Nutrient additions have been shown to enhance primary productivity in oligotrophic, nutrient-poor wetlands in the Interlake area of Manitoba (Murkin *et al.* 1991; Murkin *et al.* 1994; Gabor *et al.* 1994). Effects on aquatic invertebrate community diversity and abundance are equivocal (Schoenberg 1988; Rader and Richardson 1992; Murkin *et al.* 1994; Gabor *et al.* 1994). Grazing and nutrient recycling by zooplankton and macrophyte-associated invertebrates are potential mechanisms for effecting control over primary producers in lakes and wetlands.

This study sought to examine the effects of controlled additions of nutrients to experimental wetland enclosures. Two temporal patterns of additions were employed: (1) pulse additions at two times during the season, to simulate sudden, large loadings such as following heavy rainfall or seasonal flooding, and (2) press additions trickled in at regular, frequent intervals as might occur from groundwater flow. Specifically, we studied the relationship between temporal pattern of nutrient additions and invertebrate abundance and diversity, and between invertebrate communities and their algal food resources. The manipulative experiment (May - August 1994) was designed to examine "bottom-up" influences on the primary producers and aquatic invertebrates in the marsh food web. With differential nutrient enrichment, community composition and abundance of primary producers (phytoplankton, periphyton, metaphyton, and macrophytes) is expected to change, as would associated grazer communities.

Methods

We carried out a nutrient enrichment experiment in Blind Channel in Delta Marsh, MB (50°11'N, 98°12'W), a 22,000 ha freshwater wetland on the southern shore of Lake Manitoba. Six enclosures (5 m x 5 m) were constructed using impermeable woven polyethylene curtains supported on floating platforms (see Goldsborough 1991). The bottom margins were weighted with rebar and sunk into the sediments at least 30 cm, thereby isolating the water in the enclosures from the channel. Water depth was less than 1 m throughout the summer, and the enclosed water volume in each enclosure was approximately 20 m^3. Fish that had been trapped in the enclosures during installation were removed using commercial minnow traps, set and emptied daily.

Experimental treatments were assigned to enclosures in a semi-random manner so that no replicate enclosures were adjacent or contiguous to each other (Fig. 1). Sampling was initiated 24 May (week 1) and continued weekly until 26 August (week 14). Weeks 1-4 constituted a pre-treatment period, followed by 10 weeks of treatment period. Nutrients were added according to the ratio 7N:1P, nitrogen (N) as $NaNO_3$ and phosphorus (P) as $NaH_2PO_4.2H_2O$. Additions were made in the press treatment three times per week (Monday, Wednesday, Friday) of the experiment (beginning on 20 June) in 2 replicate enclosures and in the pulse treatment at week 5 (20 June) and week 10 (25 July) of the experiment in 2 replicate enclosures. Equal total nutrients were added to all treatment enclosures by the end of the experiment. No nutrients were added to control enclosures. Each nutrient addition was prepared in the laboratory by dissolving the requisite weight of inorganic chemical in 1L of carbon-filtered water. Prior to application of the nutrient solution to each enclosure the volume was diluted to 10L and sprinkled uniformly over the water surface.

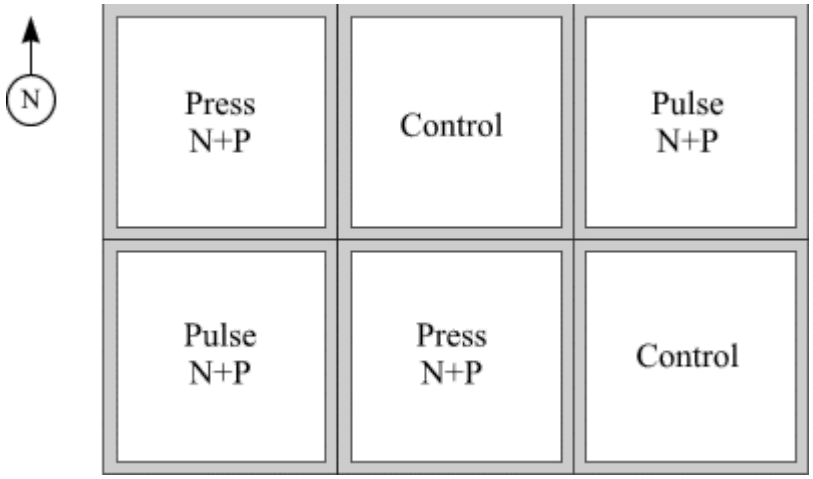

Figure 1. Arrangement of replicated treatments (control, press and pulse) in 5 m x 5 m enclosures deployed in the Blind Channel, 1994.

Algal communities parameters (biomass as chlorophyll *a* and productivity) were determined for phytoplankton, periphyton, metaphyton, and epipelon components. Irradiance profiles, turbidity, and water chemistry (including ammonia, orthophosphate, silicon, nitrate, pH, dissolved oxygen, temperature) were monitored during the experiment (see McDougal and Goldsborough 1995 for detailed methods).

Weekly sampling for invertebrates included zooplankton in the water column, zooplankton associated with periphyton, and macrophyte-associated invertebrates. The water column was sampled for zooplankton using a transparent acrylic cylinder 50 cm in length and 5.5 cm in diameter. A 4 L volume was then filtered through a conical net with a mesh size of 80 µm. Samples were preserved with formalin and the volume of each was standardized to 20 mL. Zooplankton that graze periphyton were sampled using a transparent acrylic cylinder (50 cm x 7 cm) placed around extruded acrylic rods (90 cm x 5 mm) arranged in a 10 x 10 grid in each enclosure. These rods were planted in mid-May and allowed to colonize with periphyton. A 1.6L volume was treated in the same fashion as for zooplankton in the water column. Invertebrates associated with aquatic macrophytes were sampled semi-quantitatively in two ways: (1) using activity traps of a design modified from Whiteside *et al.* (1978), and (2) using a macrophyte-invertebrate sampler of a design modified from Pip and Stewart (1976). An activity trap consisted of 3 10-cm diameter wide-bore funnels attached to a 20 x 20 cm acrylic plate. Polyethylene sample bottles (125 mL) were secured to the opposite face of the acrylic plate. To set for sampling, activity traps with sample bottles pre-filled with water were lowered through the water column with funnel openings directed downward to rest on macrophytes or sediment. To retrieve, traps were gently raised to the surface using an attached rope, inverted below the water surface, and contents of 3 sample bottles pooled into a 500 mL collection bottle for transport to the laboratory for further processing. Samples were concentrated by passing them through a 80 µm mesh net, then preserved with 4% formalin. The macrophyte sampler is described in McDougal and Goldsborough (1995).

Zooplankton (Cladocera and Copepoda) were identified to species using various standard references including Pennak (1978), Edmondson (1959), and Smith and Fernando (1978). Rotifers were counted but not identified. Species data are not reported here.

Results

The N and P concentrations in the water column in both press and pulse treatments were found consistently to exceed control levels (McDougal and Goldsborough 1995).

Cladocera predominated in all enclosures throughout the experiment, probably due to fish predator exclusion. Zooplankton in the water column (especially Cladocera) increased in abundance through the season and effectively grazed the phytoplankton crop maintaining it at very low levels.. Mean cladoceran densities for all treatments showed no differential response to experimental nutrient additions (Fig. 2). Copepods and rotifers

showed pre-treatment population density peaks, but remained at low density throughout the treatment period (Fig. 3).

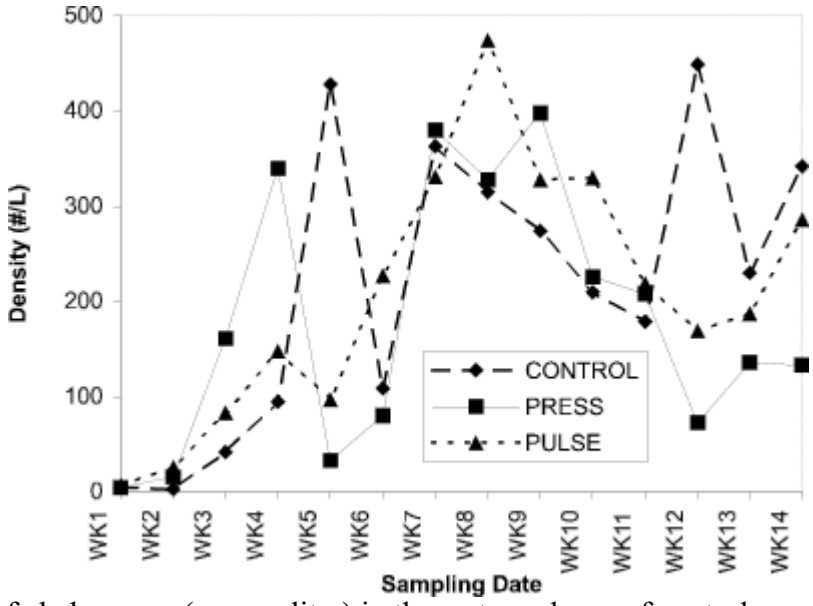

Figure 2. Abundance of cladocerans (no. per liter) in the water column of control, press and pulse enclosures over a 14-week period.

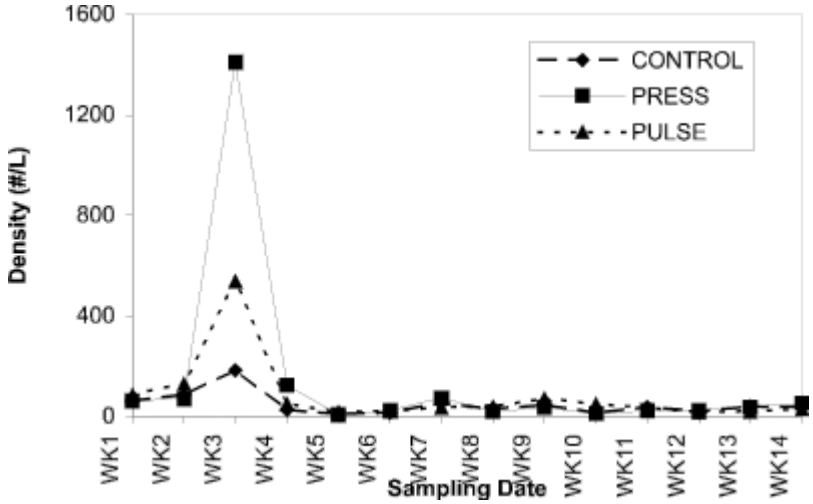

Figure 3. Abundance of cyclopoids (no. per liter) in the water column of control, press and pulse enclosures over a 14-week period.

Cladoceran grazers associated with periphyton on acrylic rods (Fig. 4) occurred at densities similar to those in the water column during the pre-treatment period. In response to nutrient additions, their densities increased substantially. Cladoceran densities increased four-fold in response to initial press nutrient additions, then declined by week 9 and remained at pre-treatment levels for the duration of the experiment. Increased cladoceran grazer densities were apparent in response to both pulse nutrient additions (Fig. 4). Copepods grazing periphyton on rods showed a similar response to those in the water column, existing at low densities throughout the treatment period (Fig. 5).

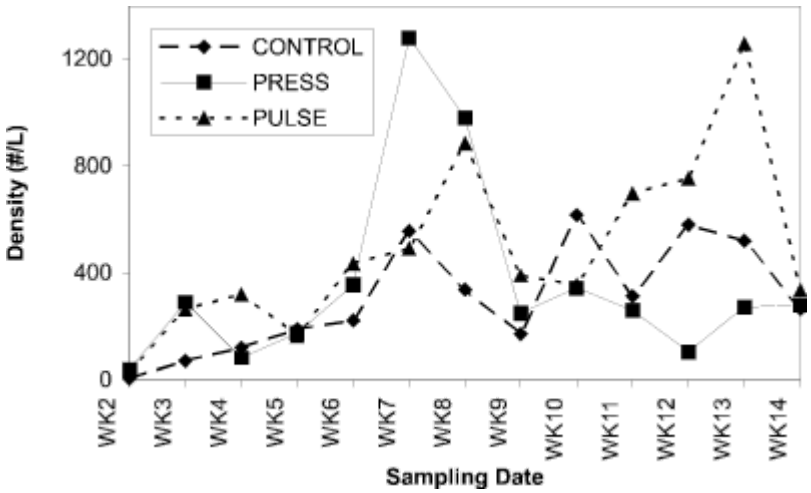

Figure 4. Abundance of cladocerans (no. per liter) associated with acrylic rods in control, press and pulse enclosures over a 14-week period.

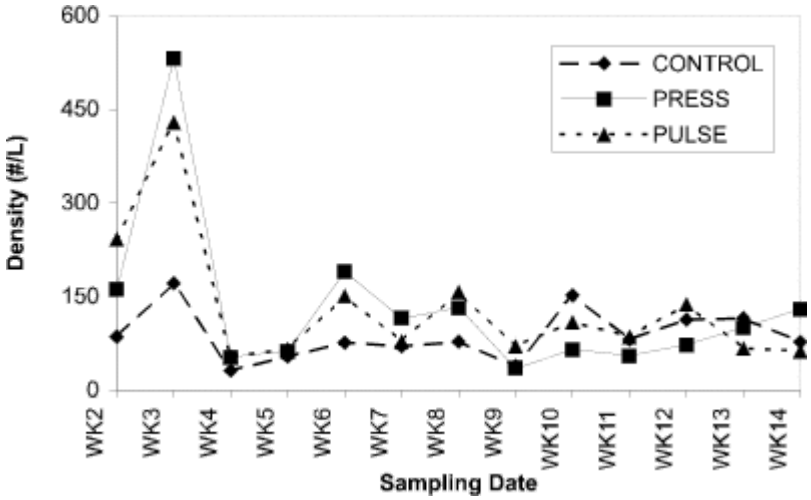

Figure 5. Abundance of cyclopoids (no. per liter) associated with acrylic rods positioned in control, press and pulse enclosures over a 14-week period.

Microcrustacean grazers associated with macrophytes increased in abundance during early phases of treatment (week 7-9), in parallel with macrophyte biomass, then declined substantially. Cladocerans responded strongly to the first pulsed nutrient addition (Fig. 6), whereas copepods showed larger increases in abundance in response to press additions (Fig. 7).

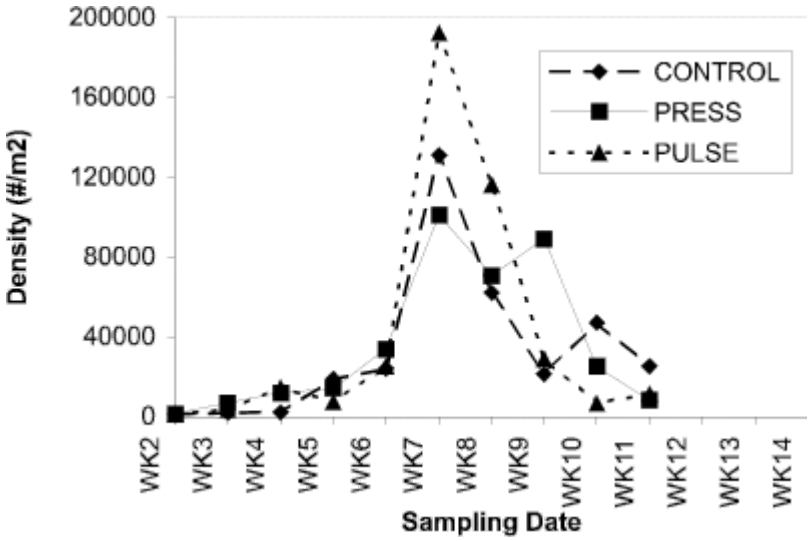

Figure 6. Abundance of cladocerans (no. per m2) associated with macrophytes in control, press and pulse enclosures over a 14-week period.

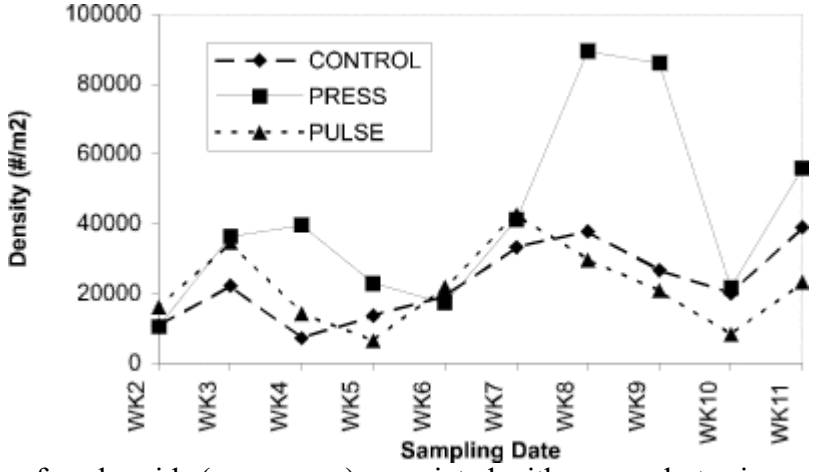

Figure 7. Abundance of cyclopoids (no. per m2) associated with macrophytes in control, press and pulse enclosures over a 14-week period.

Metaphyton showed its most pronounced development in the press nutrient treatment, with substantial, though lagged, development in the pulsed treatment (McDougal and Goldsborough 1995). Grazing pressure on metaphyton was not quantified in our study. However, an increase in abundance of the trichopteran, *Agraylea multipunctata*, which makes its case from filamentous green algae (Wiggins 1977), in samples of the phytophilous invertebrate community was noted.

Discussion

Invertebrate response to nutrient enrichment of wetlands has been equivocal. Results of preliminary experiments in Florida wetlands showed that nutrient additions generally led to an increase in density of macroinvertebrates (Rader and Richardson 1992). Similarly, water column (=nektonic) herbivores and detritivores (cladocerans, copepods) increased in abundance and biomass in response to inorganic nutrient addition in enclosures in an oligotrophic wetland (Campeau *et al.* 1994). Epiphytic herbivores and detritivores also increased in abundance and biomass in response to both inorganic and organic (litter) additions (Campeau *et al.* 1994). When a single large pulsed addition of inorganic or organic (alfalfa) nutrients was made in early spring to two oligotrophic marshes, benthic and nektonic invertebrates showed an increase in abundance in response to the high inorganic treatment. In contrast, Murkin *et al.* (1994) observed no significant differences in numbers or biomass of total invertebrates or invertebrate functional groups that could be attributed to press fertilization of the same marshes. Our study demonstrated no consistent pattern of invertebrate response to enrichment. However, definitive conclusions must await detailed comparisons between invertebrate densities and the algal/macrophyte biomass within these quite discrete components of the wetland ecosystem.

Due to variable microhabitat preferences and requirements, responses of invertebrates to resource (nutrient) manipulations will differ. Water column microcrustaceans (Cladocera, Copepoda) graze phytoplankton and bacteria (Downing 1981; Schoenberg and Maccubbin 1985), whereas epiphytic species scrape macrophyte surfaces (Downing 1981; Fryer 1968), feeding on attached algae, detritus, and fungi, collectively known as "aufwuchs" (Bowen 1979). Large cladocerans are very efficient grazers and reduced the phytoplankton biomass and primary productivity to low levels despite the nutrient treatments.

Life history characteristics influence the ability of each invertebrate group to respond to changes in food quality and quantity. Cladocerans were the predominant component of the grazing community throughout the treatment phase of the manipulation, in contrast to the pre-treatment phase which was dominated by copepods and rotifers. The exclusion of vertebrate planktivores from the enclosures and the existence of an ephippial (diapause) cladoceran egg bank in the sediments resulted in a large hatch of neonates which, when mature, reproduce parthenogenetically, allowed a rapid response in population size when food resources became available. Conversely, increase in population size of copepods which reproduce exclusively sexually (Pennak 1978) is dependent upon hatching of new cohorts or species from their egg banks over the season. Seasonal distribution and life histories of copepod species are under investigation in Delta Marsh (Zrum and Hann 1995).

Conclusions

Bottom-up experimental manipulation of a wetland food web via nutrient additions has demonstrated a differential response among primary producers and associated invertebrate grazers. Zooplankton grazers effectively depressed phytoplankton biomass in control, press, and pulse enclosures in the absence of fish predators. Zooplankton grazers increased in density in response to increased availability of periphyton on acrylic rods in both press and pulse nutrient treatments, but especially in pulse additions. Macrophyte-associated invertebrates changed in abundance in parallel with macrophyte biomass changes. Metaphyton shading (in both press and pulse treatments) led to macrophyte decline and eventual decomposition, and substantial reduction in phytophilous invertebrate density.

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Neotropical migrant banding program at the University Field Station, Delta Marsh, 1994 and comparisons with 1992 and 1993

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Introduction

There is growing concern that neotropical migrant songbirds, those species that winter in the American neotropics and breed in temperate North America, appear to be declining dramatically (Robbins et al. 1989; Askins et al. 1990; papers in Hagan and Johnston 1992; Finch and Stangel 1993). Much of this concern is based on population trends that are well documented for migrants that move through and breed in the hardwood forests of the eastern United States BUT the status of populations of songbirds in the central prairie provinces of western Canada remains poorly understood. This is due, in part, to the low density of routes of the North American Breeding Bird Survey (BBS) occurring here and the fact that many of these species of neotropical migrants breed in forests that are not well suited to survey by the BBS.

In order to address this paucity of information, the Canadian Wildlife Service, in cooperation with the Long Point Bird Observatory, has created and supported migration monitoring stations at Beaverhill Bird Observatory in Alberta and at Last Mountain Lake in Saskatchewan. Constant effort mistnetting will help us establish indices of population status and reproductive success of several species that breed over broad geographic areas. However, these efforts will not allow us to establish historical population trends to date in this region. Fortunately, a unique banding study conducted in the early 1980s has provided an excellent opportunity to monitor longer-term population trends of warblers moving through south-central Manitoba.

From 1982 to 1984, Heidi den Haan, under the supervision of Dr. Spencer G. Sealy of the Department of Zoology, University of Manitoba, conducted regular spring and fall banding of warblers moving through the narrow dune forest along the south shore of Lake Manitoba. This area is an ideal location to mistnet migrant songbirds because it is bordered on one side by the Lake and on the other by Delta Marsh. Migrants are thus likely to stop at and move along this strip of forest before continuing on their way to breeding or wintering grounds. In early 1992, I approached Dr. Sealy and Heidi den Haan and suggested that, during the years 1992 through 1994, it would be appropriate to repeat a banding program at this site in order to evaluate possible population changes of these birds during the intervening decade. It was agreed that such a study was valuable and that unpublished data would be provided from the early 1980s so that such a comparison could be made. In addition, it was my ambition to use this study as a springboard for a permanent migration monitoring station at Delta Marsh. As a result of these discussions, the Canadian Wildlife Service allowed me to use personal Green Plan research funds to conduct the 3-year banding program at Delta Marsh from 1992 through 1994. The results of 1992 and 1993 operations are summarized in Hobson (1992) and Hobson (1993), respectively. This report summarizes the results of the 1994 fall banding program at Delta Marsh and presents preliminary analyses of banding at this site for the period 1992-94. When data are made available from the early 1980s, a historical comparison will be made.

Methods

During the 3-year study, eleven mistnets were established at the same positions as used previously by den Haan and Sealy in the early 1980s. These sites are located between the University Field Station and the Assiniboine River Diversion. All mistnets were standard 3x12 meter, four-tier design. In keeping with the 1982-84 protocol,

half of the mistnets were 30 mm mesh and the other half were 36 mm mesh. Mistnets were operated typically for six hours after one half hour before sunrise and again for two hours in the late afternoon or early evening. Nets were checked every 20-30 minutes or more frequently when necessary. Nets were not operated in rain or heavy winds.

All birds were banded and mass, wing length, furculum fat level measured. In addition, where possible, age and sex was determined through plumage characteristics, skulling and evidence of breeding status (presence of a brood patch or cloacal protuberance). Presence of molt and feather wear was also recorded for each individual. During the banding season of 1993, blood and feather samples were taken from a subset of birds captured to be used in genetics and stable-isotope analysis. Starting in 1993, we also incorporated several recommendations of the Long Point Bird Observatory (LPBO). In particular, we established Daily Estimate Totals (ET) of all birds recorded in the vicinity of our banding station. As originally conceived at LPBO, the ET was designed to incorporate the advantages of several sampling procedures while minimizing the disadvantages of relying on any single method. At Delta Marsh, the ETs are based on banding totals, a daily hour-long census along a route incorporating the Ridge forest, Delta Marsh and the shoreline of Lake Manitoba, and other incidental but more or less continuous observations by banders and observers.

Results

Data are currently being analyzed for weather effects by Dr. Ken Jones of the Department of Environment in Saskatoon. If significant correlations can be found between species capture rate and environmental conditions, then data will be normalized before comparison both within and between decades. From 1 July through 30 September 1994, 5,877 captures were recorded representing 81 species (Table 1).

Table 1. Bird banding data from 5 July through 30 September 1994 at the University Field Station (Delta Marsh).

Common Name	Code	Latin name	No.
Yellow Warbler	YWAR	*Dendroica petechia*	1435
Tennessee Warbler	TEWA	*Vermivora peregrina*	1100
Myrtle Warbler (Yellow-rumped)	MYWA	*Dendroica coronata*	432
Northern Waterthrush	NOWA	*Seiurus novaboracensis*	211
Least Flycatcher	LEFL	*Empidonax minimus*	210
Common Yellowthroat	COYE	*Geothlypis trichas*	199
American Redstart	AMRE	*Setophaga ruticilla*	179
Song Sparrow	SOSP	*Melospiza melodia*	155
Tree Swallow	TRES	*Tachycineta bicolor*	125
Baltimore Oriole	BAOR	*Icterus galbula*	124
White-throated Sparrow	WTSP	*Zonotrichia albicollis*	123
Nashville Warbler	NAWA	*Vermivora ruficapilla*	109
House Wren	HOWR	*Troglodytes aedon*	104
Ruby-crowned Kinglet	RCKI	*Regulus calendula*	99
Swainson’s Thrush	SWTH	*Catharus ustulatus*	92
Warbling Vireo	WAVI	*Vireo gilvus*	86
Gray Catbird	GRCA	*Dumetella carolinensis*	79
Black-and-white Warbler	BAWW	*Mniotilta varia*	67
American Robin	AMRO	*Turdus migratorius*	62
Ovenbird	OVEN	*Seiurus aurocapillus*	55

Orange-crowned Warbler	OCWA	*Vermivora celata*	51
Blackpoll Warbler	BLPW	*Dendroica striata*	50
Slate-colored Junco	SCJU	*Junco hyemalis*	45
Magnolia Warbler	MAWA	*Dendroica magnolia*	40
Red-winged Blackbird	RWBL	*Agelaius phoeniceus*	37
Rose-breasted Grosbeak	RBGR	*Pheucticus ludovicianus*	32
Hermit Thrush	HETH	*Catharus guttatus*	31
Chipping Sparrow	CHSP	*Spizella passerina*	28
Cape May Warbler	CMWA	*Dendroica tigrina*	25
Orchard Oriole	OROR	*Icterus spurius*	24
Canada Warbler	CAWA	*Wilsonia canadensis*	23
Morning Warbler	MOWA	*Opornis philadelphia*	21
Cedar Waxwing	CEDW	*Bombycilla cedrorum*	19
Eastern Wood-Pewee	EAWP	*Contopus virens*	19
Traill's Flycatcher	TRFL	*Empidonax traillii*	19
Black-billed Cuckoo	BBCU	*Coccyzus erythropthalmus*	17
Chestnut-sided Warbler	CSWA	*Dendroica pensylvanica*	17
Eastern Kingbird	EAKI	*Tyrannus tyrannus*	17
Eastern Phoebe	EAPH	*Sayornis phoebe*	16
American Goldfinch	AMGO	*Carduelis tristis*	15
Barn Swallow	BARS	*Hirundo rustica*	15
Red-eyed Vireo	REVI	*Vireo olivceous*	15
Western Palm Warbler	WPWA	*Dendroica palmarum*	13
Brown-headed Cowbird	BHCO	*Molothrus ater*	12
Clay-colored Sparrow	CCSP	*Spizella pallida*	12
Common Grackle	COGR	*Quiscalus quisaula*	12
Fox Sparrow	FOSP	*Passerella iliaca*	12
Philadelphia Vireo	PHVI	*Vireo philadelphicus*	12
Pine Siskin	PISI	*Spizella pinus*	12
Blackburnian Warbler	BLBW	*Dendroica fusca*	11
Brown Creeper	BRCR	*Certhia familaris*	10
Gray-cheeked Thrush	GCTH	*Catharus minimus*	10
Lincoln's Sparrow	LISP	*Melospiza lincolnii*	10
Marsh Wren	MAWR	*Cistothorus palustris*	10
Wilson's Warbler	WIWA	*Wilsonia pusilla*	10
Downy Woodpecker	DOWO	*Dendrocopos pubescens*	9
Yellow-shafted Flicker	YSFL	*Colaptes auratus*	9
Bank Swallow	BANS	*Riparia riparia*	8
Solitary Vireo	SOVI	*Vireo solitarius*	8
Golden-crowned Kinglet	GCKI	*Regulus satrapa*	7

Red-breasted Nuthatch	RBNU	*Sitta canadensis*	7
Yellow-bellied Sapsucker	YBSA	*Sphyrapicus varius*	7
Bay-breasted Warbler	BBWA	*Dendroica castanea*	6
Mourning Dove	MODO	*Zenaida macroura*	6
Yellow-bellied Flycatcher	YBFL	*Empidonax flaviventris*	6
Swamp Sparrow	SWSP	*Melospiza georgiana*	5
Black-throated Green Warbler	BTNW	*Dendroica vireus*	4
Hairy Woodpecker	HAWO	*Dendrocopos villosus*	4
Sharp-shinned Hawk	SSHA	*Accipiter striatus*	4
Purple Finch	PUFI	*Carpodaccus purpureus*	3
White-breasted Nuthatch	WBNU	*Sitta carolinensis*	3
Connecticut Warbler	CONW	*Opornis agilis*	2
Rufous-sided Towhee	RSTO	*Pipilo erythrophthalmus*	2
Veery	VEER	*Catharus fuscescens*	2
Black-throated Blue Warbler	BTBW	*Dendroica caerulescens*	1
Great-crested Flycatcher	GCFL	*Myiarchus crinitus*	1
Harris' Sparrow	HASP	*Zonotrhichia querula*	1
Northern Cardinal	NOCA	*Cardinalis cardinalis*	1
Olive-sided Flycatcher	OSFL	*Contopus borealis*	1
Yellow-headed Blackbird	YHBL	*Xanthocephalus xanthocephalus*	1
Yellow-throated Vireo	YTVI	*Vireo flavifrous*	1

For 28 species representing at least 35 unique captures in any given year, the phenology of capture at the study site are presented in Appendix 1. Relative capture rates of 28 most abundant species are presented in Fig. 1. For 1992, 1993 and 1994, nets were operated between 07:00 and 12:00 h for 2,916.9, 4,027.3 and 4,674 net hours, respectively.

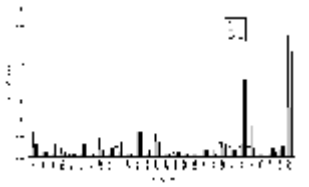

Figure 1.
Yearly capture rate for 28 species of migrants moving through the dune-ridge forest, Delta Marsh, 1992-94.

Comments

Phenology of migration was consistent between years for most species with the exception of American Redstart that showed an earlier passage in 1994 compared to previous years. Yellow Warbler, Song Sparrow and Least Flycatcher captures involved resident breeding and hatch-year birds as well as migrants.

Relative abundance of most species did not change significantly between years with the notable exception of Tennessee Warblers that peaked in 1994 compared with the previous two years. Tennessee Warblers are specialist feeders of spruce budworm and are known to undergo large population fluctuations. Variation in numbers of tree swallows reflects changes in effort for that particular species (i.e. not all captured birds were banded during busy periods). Breeding Yellow warblers departed earlier from the Ridge in 1993 compared with

other years and so their relative abundance values may also be misleading. More detailed analysis of all species awaits correction of data after consideration of weather effects.

Future Direction

Banding will continue at the University Field Station as part of the Delta Marsh Bird Observatory. This non-profit organization will maintain a constant effort mistnetting operation that will form part of a national network that is supported by the Baillie Birdathon and the Canadian Wildlife Service. In addition to regular banding, this facility will also serve as a research node for studies of migrating songbirds. For further information, please contact the author or Heidi den Haan (R.R. #1, Box 1, Portage la Prairie, Manitoba, R1N 3A1, 204-239-4287).

Acknowledgements

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Northern range extension of *Tilia americana* L. (Basswood, Linden) at Delta, Manitoba

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Species Description

Tilia americana L. (known as basswood, linden, lime or whitewood) is indigenous to North America. A large tree (in Manitoba, to 25-30 m in height and 1 m in diameter), it forms a straight trunk that is branch-free on its lower portions. The main branches are slender and somewhat arching, forming a pyramidal to rounded crown. The species commonly regenerates from the base of old stumps, and it is not uncommon for individuals to occur as a clump of trunks with a common base. The dark grey-brown bark is smooth on young trees but forms into long, narrow scaly ridges on mature specimens. The root system is wide-spreading and deep. Leaves are relatively large, alternate, and heart-shaped. The fruit is globose, indehiscent, and nut-like, and is attached by a long rachis to the back of a large bract that acts like a samara wing (Boivin 1967).

Ecology

Tilia americana normally grows in mixture with other hardwood species, and rarely forms pure stands. In Canada, it is characteristic of deep, fertile soils (Hosie 1979), although it may be found on less fertile soils in parts of the United States. According to Fowells (1965), inadequate precipitation limits the distribution of the species in the mid-western United States. Few established seedlings are found where the species forms a major component of the canopy. It is thought that seedling loss is mainly the result of herbivory by rabbits and deer (Fowells 1965). The ability of the species to regenerate from stump sprouts has ensured its survival in areas where it has been logged.

World Distribution

Tilia americana is native to the Northern Deciduous and Great Lakes - St. Lawrence forest regions of North America. However, it also extends into grassland areas along river courses in Manitoba and the mid-western United States, where it forms a component of riverine gallery forests. In Canada, it is found from western New Brunswick into southern and central Québec and Ontario, extending as far west as north-western Ontario (along the U.S. border) and southern Manitoba. In the United States, the species occurs as far south as the mountainous regions of North Carolina, Tennessee, and northern Arkansas. The western limit for the species is south-central Manitoba and North Dakota, and along the Niobrara River in north-central Nebraska.

Tilia americana reaches its northern limit in the province of Manitoba (Scoggan 1957), where it occurs sporadically in gallery forests along the Red and Assiniboine rivers and their tributaries. According to Scoggan (1957), the species occurs as far west as Brandon (WIN specimen no. 17996), though Oswald and Nokes (1988) give its western limit as Spruce Woods (about 40 km east of Brandon). Along the Red River, the species occurs naturally as far north as the city of Winnipeg. Scoggan (1957) lists the most northerly locality as Portage la Prairie (49°58'N, 98°15'W, WIN specimen no. 17994).

In Canada, basswood has been widely planted outside its range. Boivin (1967) reports that the species has naturalized in the Moose Jaw, Saskatchewan area.

Tilia americana L. at Delta, Manitoba

In May 1994, while undertaking a reconnaissance survey of Oxbow Woods (50°09'N, 98°22'W, about 2 km south of the southern shore of Lake Manitoba), I found a single specimen of basswood (two trunks with a common base, DBH » 80 cm). The tree is an 'emergent' (taller than the main canopy), and occurs near the shore of the Blind Channel, a former (3000 year old) channel of the Assiniboine River. The tree appears to be very healthy and has no large dead branches. Associated tree species are *Acer negundo* (Manitoba maple), *Fraxinus pennsylvanica* (green ash), *Quercus macrocarpa* (bur oak), *Ulmus americana* (American elm) and *Populus balsamifera* (balsam poplar). An extensive search of Oxbow Woods (an area > 70 ha) revealed no other individuals of the species. No seedling regeneration was observed, although the tree was observed to be fruiting in the fall of 1994. A fruiting specimen has been deposited in the University of Manitoba herbarium (WIN specimen no. 56298), and another in the herbarium of the University Field Station.

The species has not been previously recorded from the area. Löve and Löve (1954) do not mention the occurrence of basswood, nor is it included in the list prepared by Shay (1975). It seems likely that the specimen, despite its size, was missed by previous investigators since it is the only one in the area.

The occurrence of *Tilia americana* L. at Oxbow Woods, Delta represents a 22 km northern range extension of the species. This single tree is the most northerly naturally-established specimen of the species on the planet.

Historical Aspects

Tilia americana L. has long occurred in Manitoba, as evidenced by the presence of small amounts of basswood pollen in sediment cores taken from the southern basin of Lake Manitoba (Nambudiri and Shay 1986). The occurrence of the species along the Blind Channel is perhaps not surprising given the Holocene evolution of southern Manitoba. Teller and Last (1981) report that the Blind Channel is a former main channel of the Assiniboine River that drained into Lake Manitoba between 4500 and 3000 B.P. About 3000 years ago, the Assiniboine changed course to flow into the Red River as it does today. Rannie et al. (1989) undertook a more detailed Holocene study based on radiocarbon dating and paleochannel morphology. They concluded that at least part of the Assiniboine channel flowed into Lake Manitoba between 6000-7000 and 3000 years B.P., with the Blind Channel phase occurring between 4520 and 2980 years B.P. Given that basswood is today found sporadically along the Assiniboine River between Brandon and Winnipeg, its occurrence along the former river channels might have been anticipated. A botanical exploration should be undertaken along the Blind Channel between Lake Manitoba and Portage la Prairie to determine whether the species occurs elsewhere in the region.

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Demography of clonal Ostrich Fern (*Matteucia struthiopteris*). II. Year two of a long-term study

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Introduction

Plant demography is the study of population dynamics and its underlying causes (Silvertown and Lovett Doust 1993). Demographic information can be obtained either by following the fate of individuals over time, or by estimating age-specific mortality probabilities from the age structure of a population at a given time.

In many plant species, recruitment through the production of vegetative offshoots (clonal growth) is an important method of establishment and spread. A number of clonal plant populations have been studied from a demographic standpoint. Clonal ramets, like individual plants (genets), have individual demographic profiles (birth, death, size, reproductive capacity). Ramets differ in that they often remain attached to one another (via rhizomes or roots), and may therefore remain physiologically interconnected. Intraspecific competition in clonal species may be extremely important. It has been found that clonal growth often leads to large, dense stands of a single genotype dominating a population, even though there may initially have been many genets (Langer et al. 1964). This appears to be the case in the clonal bracken fern (*Pteridium aquilinum*), which forms large genetically uniform stands in burned areas in Finland (Oinonen 1967).

While a number of studies have demonstrated that the size and proximity of neighbours can affect growth rates of individuals in a population (Kenkel 1991), few studies have related spatial interactions and demographic processes. In this contribution, I report the second year results of a study established to examine long-term dynamics of a clonal Ostrich Fern (*Matteucia struthiopteris*) stand in Oxbow Woods, Delta, Manitoba. The biology of the species is well known, but age-specific mortality rates and longevity have not been studied (Prange and von Aderkas 1985).

The objective of the study is to relate individual ramet productivity (ramet size), reproduction (production of fertile fronds), and longevity to the size and proximity of ramet 'neighbours' in the stand. The first year results are reported in Kenkel (1994).

Matteucia struthiopteris (L.) Todaro

This fern species is a member of the Polypodiaceae. It is commonly known as the 'ostrich fern', or more generally as 'fiddle heads' after the edible frond shoots produced in the spring. A large clonal species, it occurs throughout much of northern North America and Eurasia. It often forms extensive, monodominant stands in moist deciduous forest, but it also occurs in the southern boreal forest. The species prefers rich alluvial sites, and is particularly common on river plain fluvial deposits. It is a good indicator of soil moisture conditions, preferring moist by well-drained soils (Mueller-Dombois 1964). In Manitoba, vegetative fronds have a stipe up to 40 cm in length and a blade to about 1 m in length. Individual ramets are erect rootstocks with a projecting crown of one or (usually) more fronds, and are connected by a stout, persistent runner. Some ramets, usually the largest, produce separate and distinctive fertile fronds that have a nutrient depletion effect on the vegetative fronds (Prange and von Aderkas 1985). In Manitoba, vegetative fronds complete their elongation in 2 to 3 weeks in late May and begin dying back in early to mid-August. Low moisture and high light reduce frond height and dry mass, and the species is considered to be 'shade-adapted' (Prange and von Aderkas 1985). Fertile fronds are persistent but not common. In New Brunswick, Prange and von Aderkas (1985) found that under shaded

conditions only 1% of ramets produced fertile fronds, but that "in conditions of direct sunlight, a much higher percentage of plants (sic) develop fertile fronds".

Study Area

The population studied occurs in a gallery forest (known locally as Oxbow Woods) on the property of the University of Manitoba Field Station (Delta Marsh), at 50°11'N, 98°23'W, approximately 3 km south of Lake Manitoba along a former oxbow of the Assiniboine River. The study plot was located within an extensive monodominant stand of ostrich fern located near Inkster Farm, Oxbow Woods (Kenkel 1992). The forest in this area is dominated by mature bur oak (*Quercus macrocarpa*) and green ash (*Fraxinus pennsylvanica*). Younger individuals of Manitoba maple (*Acer negundo*) occur at low abundance. The understory is locally variable and patchy. Few other species were found within the study plot, but in adjacent areas (where ostrich fern is not present) conspicuous understory species include *Aralia nudicaulis*, *Carex assiniboinensis*, *Rhus radicans*, *Osmorhiza longistylis*, *Actaea rubra* and *Rudbeckia laciniata*. Löve (1959) characterizes most of these species as having an 'eastern' floristic affinity.

The climate of the area is humid sub-continental, with short warm summers and long cold winters. Mean annual temperature is 1.5°C. July is the warmest month (mean of 19.1°C), and January the coldest (-19.8°C). Mean annual precipitation is 49.9 cm, approximately 75% of which falls as rain.

Soils in the Oxbow Woods are rich clay-loams, with approximately 20% organic matter content and a near-neutral pH.

Results

Vegetative Fronds - 1993 vs. 1994

There was little change in the number of rootstocks between 1993 and 1994, and rootstock turnover was very low. Of the 235 rootstocks in 1993, only 13 had died by 1994. In 1994, 12 new rootstocks were mapped (for a total of 234). The number of vegetative fronds was somewhat reduced in 1994, however. In 1993, 1002 vegetative fronds were counted (mean of 4.264 per rootstock), versus 902 in 1994 (mean of 3.855 per rootstock). These mean values are somewhat lower than the value of 6.75 reported by Prange and von Aderkas (1985) in New Brunswick populations. Most of the rootstocks that died between 1993 and 1994 were classed as 'tiny' (much smaller than the majority) in the 1993 survey, and most had a single vegetative frond (mean of 1.692 per rootstock). There was a statistically significant correlation between the number of fronds produced by rootstocks between 1993 and 1994 (sterile rootstocks only, $n = 192$, $r = 0.612$, $p < 0.001$); see Fig. 1.

Fertile Fronds - 1993 vs. 1994

There were 26 fertile rootstocks (11.11% fertility) in 1994, up from 21 (8.94% fertility) in 1993. These values are considerably higher than the 1% value reported for shaded populations in New Brunswick (Prange and von Aderkas 1985). The total number of fertile fronds was also higher in 1994, increasing from 31 (mean of 1.476 per fertile rootstock) in 1993 to 42 (mean of 1.615 per fertile rootstock). Of these, 17 were also fertile in 1993, and 9 were fertile in 1994 but not in 1993. Of these 9, two had persistent 'old' fertile fronds, indicating that they had been fertile at some time prior to 1993. An additional 4 ramets were fertile in 1993 but not in 1994. Of the 17 rootstocks that produced fertile fronds in both years, 8 produced the same number of fertile fronds in both years, while 5 produced more and 4 less than in 1993.

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Population biology and the control of Common Burdock (*Arctium minus* (Hill) Bernh.) at the University Field Station, Delta Marsh

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Introduction

Common Burdock is an Eurasian weed that has become widely distributed in waste places and on disturbed ground throughout much of North America (Gross et al. 1980). In recent years, common burdock has apparently increased in abundance in the understory of gallery forests adjacent to the south shore of Lake Manitoba, particularly in the region of the University of Manitoba Field Station (Delta Marsh). The success of the species is largely attributable to its production of bur-like fruit that are readily dispersed through attachment to animal fur and human clothing. Common burdock is so abundant in some areas that it is now the dominant understory species. Floristic diversity on the forested ridge has been appreciably reduced as a result.

This report summarizes a study of the population biology and control of common burdock at the University Field Station. The project was funded by Canada Trust and the Friends of the Field Station. The objectives of the study were:

- to develop a minimal-impact program for controlling common burdock at the University of Manitoba Field Station, Delta Marsh.
- to examine the population dynamics of common burdock by examining size distributions and biomass allocations.
- to establish permanent plots for long-term monitoring of individual plants.
- to quantify seed production and germination requirements of the species.

Arctium minus (Hill) Bernh. (Common Burdock)

Common Burdock (also known as bur, or cockle buttons) belongs to the Asteracae family. The name *Arctium* is derived from the Greek word arktos, meaning bear. The plant is native to Eurasia but has become widely established in North America, where it has become a pernicious weed. A closely related species, *A. lappa* or Great Burdock, was also introduced to North America from Europe. It is also considered a weed, but is not as common nor as widely distributed as *A. minus*.

Biology and Ecology

Common Burdock is sometimes referred to as a 'biennial'. Strict biennials are species that in the first year germinate, grow, and produce a large overwintering storage taproot. In the second year, the photosynthate energy stored in the taproot is used to produce a large number of flowering heads, a phenomenon known as 'bolting'. The plant dies in the fall, having produced and dispersed its seed. Like many so-called biennials, common burdock is more correctly termed a 'facultative' biennial (i.e. short-lived perennial). Such species can take a number of years before flowering; like biennials, they die once they have flowered (Silvertown & Lovett Doust 1993). In these so-called semelparous (once-flowering) perennials, flowering is related to plant size rather than age. Examples include common burdock, teasel, wild parsnip, wild carrot and evening primrose (Kelly 1985). Semelparous perennial species are generally poor competitors, depending on site disturbance for survival of the

population. Most have large seed pools and employ seeds as a means of colonizing gaps as the opportunity arises. Observations made at the University Field Station suggest that common burdock may remain in the vegetative (non-flowering) phase for up to 4 - 5 years, and possibly longer.

Common burdock produces a basal rosette of large ovate to cordate leaves, and a taproot up to 1 m in length. Flowering plants produce a 1 - 2 m angled stem of alternate leaves topped by globose flowerheads (purple tubular disk-florets with hook-tipped involucral bracts). The spiny burs of the fruit readily attach to animals fur and human clothing, thus assuring long-distance dispersal. Common burdock is said to grow in full sun, and to prefer heavy, moist soils rich in nitrogen. However, at the University Field Station it grows on relatively well-drained, nutrient-poor sand in semi-shaded habitats.

Distribution

Both Common and Great Burdock are native to Europe, where they are commonly found growing in fields and pastures, waste places, and other disturbed sites. Common burdock is naturalized in North America, and now occurs in every province in Canada. It is recognized as a weed of waste places, usually on moist fertile soils (Frankton & Mulligan 1970).

Economic Uses

Common Burdock is a traditional herbal medicine in Europe and parts of North America. The boiled root of year-old plants is used, and recent research has indicated that the plant has diuretic, antiseptic, diaphoretic, hypoglycaemic and choleretic properties. An external poultice of leaves said to be effective against skin irritations, and external antiseptic properties have been demonstrated scientifically (Dwyer & Rattray 1986).

Alternative Methods for Controlling Common Burdock

It was necessary to develop a method for the careful removal of common burdock plants, while minimizing substrate disturbance as well as damage to the native vegetation. The options considered were:

- Selective or 'spot' herbicide application. This method has the advantage of not disturbing the substrate. However, there is the potential for accidentally spraying native vegetation. Furthermore, the use of herbicides is expensive and not environmentally friendly. Finally, there was some concern that herbicides might not kill common burdock, since it has a large, deep taproot.
- Pulling up and/or digging. The main advantages of this approach is that it is environmentally friendly, and it is effective unless the taproot is not completely (or largely) removed. A potential disadvantage is that digging necessarily results in localized substrate disturbance. However, preliminary digging trials indicated that substrate disturbance was minimal, in large part because of the sandy substrate along the forested ridge. This option was therefore implemented.

Population Biology of Common Burdock

Controlling Common Burdock will undoubtedly be a continuing project, at least for a few years. The species likely has a persistent soil seed bank, so that removal of existing plants is no guarantee of immediate species extirpation. Furthermore, it is likely that small seedlings will be missed even by the most careful worker. It is therefore important to obtain more information on the population biology of the species at Delta Marsh, so that an appropriate long-term control program can be implemented. We have collected the following information:

- Determination of the age-size structure of populations. Two major 'age' classes of burdock can be readily distinguished: flowering and non-flowering. In addition, non-flowering individuals can be classified by size (based on leaf size and/or the total number of leaves produced). We have calculated population size

distributions to determine the proportion of seedlings that survive to flowering. Permanent plots with marked plants have also been established to follow the fate of individuals over time.
- Seed viability and germination. Seed was collected from one-year old burs to determine seed viability and germination requirements.
- Biomass allocation studies. Allocation to taproot, stem/leaf and reproductive parts (in flowering plants only) was determined. Biomass allocation patterns between non-flowering and flowering plants were compared, and determination of flowering likelihood based on taproot biomass was examined.

Materials and Methods

1. Species Removal

Smaller plants were dug up using a standard garden 'dandelion fork', and larger ones using a long-handled bulb planter. Non-flowering plants were carefully dug up (obtaining as much of the taproot as possible) and scattered on the ground to decay. In this way, nutrients were recycled back into the ecosystem. However, flowering-fruiting individuals (bolting) were removed from the site and burned to prevent further seed spread. At least 5000 individuals were removed during the summer of 1994.

2. Population Size Structure

Plots for determining population size structure were established at various locations. Within each plot, individual plants were randomly selected for measurement. The number of leaves was recorded, and each leaf was measured from the point of blade-petiole attachment to the leaf tip. Each individual was placed into one of three age-size classes: class 1 = all leaves < 20 cm; class 2 = at least one leaf > 20 cm, but not bolting; class 3 = bolting plants, regardless of leaf size. The height of all bolting plants was recorded, and the number of burs counted. Whenever possible, the taproot of each plant was measured from the base of the leaf crown to the tip.

3. Phenology

Throughout the summer months (June - August, 1994), observations on timing of leaf production, bolting and flower and fruit production were made.

4. Species Associations

At each plot location, all plant species within the plot were recorded (nomenclature follows Scoggan 1957), and the surrounding trees and shrubs identified to species. Canopy cover was recorded using three classes: full shade, >70% canopy cover; semi-shade, 30-70% canopy cover, and high light, < 30% canopy cover.

5. Biomass and Reproductive Allocation

Plants were randomly selected for biomass allocation determination in mid-August 1994. Only plants of size classes 2 and 3 (see section 2 above) were selected. Non-flowering plants were divided into above-ground (basal leaves) and below-ground (taproot) parts. For flowering plants, the following divisions were made: taproot, basal leaves, vegetative bolt, and fruit. All material was collected, sorted, and dried to constant mass in a standard drying oven at 85°C.

6. Establishment of Permanent Plots

Six square permanent plots for long-term monitoring were located in various regions of the forested ridge. Sites were chosen to be representative of various site conditions, including proportion of vegetation cover (herbaceous

and canopy layer) and proximity to animal pathways. Plot size varied depending on the number and size of common burdock individuals within them. Most plots contained between 15 and 20 individuals.

In June 1994, all burdock individuals >10 cm in height were carefully marked with a stake (placed on the north side of the plant) and given a number. Plants < 10 cm tall were recorded on a map of the plot and labelled as 'seedlings'. Plant measurements were made (as outlined in section 2 above) in June and August of 1994.

7. Germination Experiments

Common Burdock burs from the previous year (1993) were collected from six dead plants on July 8, 1994. Seeds were removed from the involucre and placed in an open petri dish to dry. In August 1994 the following germination trial were undertaken:

(a) Immediate germination in petri dishes:
Petri Dish
1 - 20 seeds placed between 2 paper towels.
2 - 40 seeds placed between 2 paper towels.
3 - 20 seeds placed on top of soil.
4 - 20 seeds placed in soil.

(b) As above, but seed was first refrigerated at 4°C for 24 hours, lowered to -6.5°C for 2 hours, and then returned to 4°C for 15 days prior to the germination trials.

Soil used in the germination experiments was collected from the field station 'garden' and dried for 2 days at 90°C before use. Petri dishes with lids were placed in a growth chamber (light for 15 hours at 22°C, dark for 9 hours at 8°C) and watered as required. Light was from fluorescent tubes measured at 106 µmol/s/m.

Results

1. Species Removal

Common Burdock plants have been removed from the forested ridge in an area extending from the western boundary of the University Field Station to just east of the three cottages (linear distance along the beach about 350m). Plants have not been removed from the area south and west of the Lawrence lab, however. Plants have also been removed from the area of the forested ridge west of the Assiniboine River Diversion road for a distance of approximately 300 m. Due to time constraints, plants along a 300 m section of the forested ridge immediately east of the cottages have yet to be removed.

2. Population Size Structure

Of the 349 individuals collected for measurement, 263 (75.4%) were in the small size class, 64 (18.3%) in the large size class, and 22 (6.3%) were bolting. This suggests that seedling recruitment into the existing population is high, and that a large proportion of plants die before they have a chance to flower.

Summary size information for each of the three classes in presented in Table 1. Plants in the smallest size class produced on average less than two leaves, and had a comparatively small taproot. Larger, non-flowering plants averaged more than 3 leaves per plant, and had a much larger taproot. The mean number of leaves, mean leaf size, and taproot length was greatest for the flowering individuals. These plants averaged almost a meter in height (94.9 ± 44 cm), and produced on average 77.4 ± 56.6 burs per plant.

Table 1. Summary of the size structure of burdock (*Arctium minus*) populations at the University Field Station, Delta Marsh (mean ± 1 S.D.).

	Size Class		
	1 (small)	**2 (large)**	**3 (flowering)**
Taproot Length	9.63 (6.08)	22.3 (11.1)	29.14 (10.23)
Taproot Diameter	0.32 (0.25)	1.18 (0.53)	1.88 (0.74)
Number of Leaves	1.83 (0.25)	3.42 (1.32)	17.59 (7.05)
Length of Leaves	7.14 (5.73)	22.45 (5.97)	29.02 (7.82)
Plant Height (Bolting)			94.87 (44.04)
Number of Burs			77.36 (56.57)

3. Phenology

Initial growth of the species begins in middle to late May. In non-flowering individuals, a full set of leaves is normally produced by late June, though smaller leaves may continue to be produced well into the summer.

Flowering individual showed the first clear signs of bolting by the second week of June, 1994. The developing inflorescence is fully exposed by the end of June. Flowers first appear in mid-July, though flowering continues well into September. Each bur holds an average of about 40 seeds, and over 100 burs can be produced per plant.

Bolting appears to be physiologically-based. One individual had its bolting stem cut off at the base on June 22, 1994 (leaving only the basal rosette of leaves). By late July a new, smaller bolting inflorescence had been produced from one of the basal leaf axils.

4. Species Associations

Common Burdock was most frequently found along the forested ridge, and was most abundant along roadsides and in disturbed areas. The overstory was generally dominated by Green Ash (*Fraxinus pennsylvanica*), Manitoba Maple (*Acer negundo*), Eastern Cottonwood (*Populus deltoides*) and/or Peachleaf Willow (*Salix amygdaloides*). Major tall shrubs include *Salix interior* (forest margins), *Sambucus canadensis*, *Cornus stolonifera* and *Prunus virginiana*. Small shrubs and herbaceous species are generally not abundant in areas where common burdock dominates. Species encountered include *Urtica dioica*, *Humulus lupulus*, *Ribes americana*, *Rubus idaeus*, *Parthenocissus quinquefolia*, *Smilacina racemosa*, *Rhus radicans*, *Galium triflorum*, *Osmorhiza longistylis*, *Solidago canadensis*, *Poa pratensis*, *Bromus inermis*, *Cirsium arvense*, *Taraxacum officinale*, *Convolvulus sepium*, *Artemesia absinthium* and *Lappula deflexa*.

5. Biomass and Reproductive Allocation

A random sample of 14 non-flowering individuals suggested approximately equal allocation to above and below-ground biomass (56.2% above-ground, 43.8% below-ground). Mean values for flowering individuals (sample size = 4) were as follows: basal leaves, 8.53%; vegetative bolting tissue, 60.43%; fruit, 21.37%, and taproot, 9.67%. These results confirm that the plant allocates considerable photosynthetic storage to the taproot, and that this stored energy is utilized at the time of flowering.

6. Establishment of Permanent Plots

A summary of the six permanent plots is presented in Table 2. All plants except the seedlings have been marked and will be revisited in the summer of 1995 to determine mortality, plant size and the proportion of plants bolting.

Table 2. Summary of the six permanent plots established to monitor long-term population dynamics in burdock (*Arctium minus*).

Plot	Location	Size	Habitat	Burdock plant sizes	Associates
1	West side of Wardle residence, UFS (DM)	2 x 2 m	sunny, forest edge	small = 21, large = 10, bolting =3, seedlings (estimated) = 91	*Cirsium arvense*, *Urtica dioica*, *Humulus lupulus*, *Convolvulus sepium*
2	East of Cottages, UFS (DM)	3 x 3 m	semi-shaded, high canopy forest, no shrubs	small = 50, large = 18, bolting = 2, seedlings (estimated) = 21	*Ribes americana*, *Urtica dioica*, *Rubus idaeus*, *Parthenocissus quinquefolia*, *Acer negundo* (seedlings), *Sambucus canadensis*
3	Along mist net trail, east of cottages, UFS (DM)	2 x 2 m	moderately shaded, low tree canopy, some shrubs present	small = 7, large = 4, bolting = 2, no seedlings	*Rubus idaeus*, *Galium triflorum*, *Parthenocissus quinquefolia*
4	Between plots 2 and 3, east forested ridge, UFS (DM)	3 x 3 m	somewhat shaded, close to beach. Isolated population	small = 10, large = 10, bolting = 4, no seedlings	*Artemesia absinthium*, *Rubus idaeus*, *Humulus lupulus*, *Galium triflorum*, *Poa pratensis*, *Parthenocissus quinquefolia*, *Osmorhiza longistylis*, *Ribes triste*
5	west of beach path on Portage Country Club property	2 x 2 m	moderate to full shade, evidence of old (dead) burdock plants	small = 15, large = 6, bolting = 2, seedlings (estimated) = 172	*Ribes triste*, *Urtica dioica*, *Taraxacum officinale*, *Fraxinus pennsylvanica* (seedlings), *Solidago canadensis*, *Humulus lupulus*
6	West of Plot 5	1 x 1 m	highly shaded	small = 48, no others observed	*Uritica dioica*, *Galium triflorum, Lappula deflexa*

7. Germination Experiments

Germination rates varied between the different treatments, but not in any systematic way. Percent germination ranged from 30% (40 seeds on paper, without cold treatment) to 75% (20 seeds on soil, with cold treatment), averaging approximately 50%. It should be kept in mind that these germination experiments were performed using one-year old seed still attached to dead plants, indicating that the seeds remain viable for at least one year. Additional experiments should be undertaken to determine whether new seed (produced in the late fall) will germinate, or whether a winter 'cold treatment' is required.

Discussion

Removal of Common Burdock from the forested ridge must be a continuing project, at least into the foreseeable future. Since the removal of all plants is very labour-intensive, an alternative approach may have to be sought. One approach requiring minimal effort would involve removing only bolting individuals, before they flower and produce seed. To be effective, this strategy would have to be done every year for the next four or five years. Removal of fruiting plants will effectively deplete the seed pool in the area, and should eventually result in population depletion. The bringing in of seed from external sources must also be prevented. Anyone walking in areas of high burdock infestation (particularly the Portage Country Club property west of the Field Station)

should be encouraged to remove and dispose of all burdock burs from their person before reentering Field Station property.

A few other studies need to be undertaken. In particular, soil cores should be taken to determine the size of the burdock seed bank. The permanent plots will be monitored by Dr. Norm Kenkel for the next few years. With some volunteer help, further removal of Burdock from the Field Station property will hopefully take place over the next few years. With minimal effort and the cooperation of Field Station users, common burdock control can be achieved.

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Responses of wetland algae and macrophytes to press and pulse additions of inorganic nitrogen and phosphorus

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Introduction

Wetlands are endangered havens of biodiversity. They are complex and changeable by nature, relying on fluctuating water levels for rejuvenation. Many of the natural cycles, such as fire, flooding and drought, that maintain the health of wetlands are regarded by humans as disastrous events to be controlled. Human activities, including agricultural and road development, urbanization, industrial development and deliberate efforts at preservation and enhancement, often have negative impacts on prairie wetlands (Millar 1989). The degradation and loss of wetlands through human intervention is viewed as one of the major land use issues facing both federal and provincial jurisdictions (Rubec and Rump 1985). Recent estimates place the loss of prairie wetlands in North America at 40% (Canada-United States Steering Committee 1985, cited in Millar 1989). While wetland losses in Canada are not as rapid as in the United States, the pattern of degradation and loss is similar.

Wetlands are defined as shallow-water or littoral-dominated systems (generally < 2 m depth) with ephemeral standing water or continuously waterlogged soil (Goldsborough and Robinson 1996). Globally, wetlands comprise as much as 6% of the total land area (Mitsch and Gosselink 1993). About 14% of Canada's land area is classified as wetlands, including the extensive northern peatlands (Zoltai 1988). These northern peatlands are particularly important because of their possible role in moderating climate change by providing a major sink for carbon dioxide gas (Kusler *et al.* 1994). Wetlands provide shoreline buffer zones which limit the damaging effects of waves and floodwaters. Wetlands may also reduce pollution by trapping phosphorus and other chemicals in sediments and providing large populations of aerobic and anaerobic decomposers to break down excess organic matter (Kusler *et al.* 1994). The Prairie Pothole Region, two-thirds of which occurs in the southern part of the prairie provinces of Canada, is one of the major duck production habitats in North America (Millar 1989). It produces 50% of the duck population in an average year, although it comprises only about 10% of the North American waterfowl breeding area. Wetlands also provide habitat for small mammals, nesting grounds for a wide variety of migratory birds, and spawning grounds for fish, reptiles and invertebrates. Natural shifts in water levels can give rise to the biological diversity of wetland ecosystems. Moisture gradients provide a continuum of growing conditions that can support terrestrial, partially aquatic and fully aquatic vegetation (Kusler *et al.*, 1994). In wetlands where water fluctuation is limited or artificially regulated, other factors such as nutrient loading, grazing pressure and water column stability may interact to affect the structuring of the wetland ecosystem (Goldsborough and Robinson 1996).

Wetzel (1964) suggests that the greatest significance of littoral-dominated ecosystems such as wetlands may be their contribution to primary production for utilization by higher trophic levels. Primary productivity in wetlands is high, ranging from 30 to 80 metric tons per hectare per year (mT/ha/yr) for emergent macrophytes; 5 to 60 mT/ha/yr for epiphytic algae; 2 to 20 mT/ha/yr for submersed macrophytes and 2 to 10 mT/ha/yr for planktonic algae (Wetzel 1983). In particular, the level of the algal standing crop plays an important role in wetland food webs. Because of their small size, algae are more readily consumed than macrophytes by fish and invertebrates (Goldsborough and Robinson 1996). Algae also provide a relatively stable food supply that is available throughout the growing season. The algal standing crop affects the density of invertebrates, which in turn dictates the food supply for waterfowl and other marsh birds (Murkin *et al.* 1991).

Algal communities in wetlands differ in their ecological requirements and their physical location within the water column. Algal communities considered in this study include phytoplankton, epiphyton, metaphyton and epipelon. Phytoplankton includes algae free-floating in the water column, which may or may not be motile. Epiphyton includes algae growing attached to the surfaces of submersed or emergent vascular and nonvascular

plants, termed macrophytes. The term periphyton is used in this study to denote the attached algae growing on the submersed surfaces of experimentally placed acrylic rods, thus differentiating it from the epiphyton for measurement purposes, although its ecological requirements would be similar to those of epiphyton. Metaphyton forms large mats, often composed of filamentous green algae. These mats originate as epiphyton, but detach due to water turbulence and float at or near the water surface due to oxygen trapped within the mats. Epipelon includes algae within the soft sediments which exhibit vertical migration in response to environmental cues such as light.

Goldsborough and Robinson (1996) proposed a model of algal abundance in wetlands that is made up of four alternative stable states dominated alternately by epipelon, epiphyton, metaphyton, or phytoplankton. This model explains the development of a wetland based on the interacting effects of nutrient loading, grazing pressure and fluctuating water levels. According to this model, the four possible stable states that a wetland may attain are (1) the dry marsh state; (2) the open marsh state; (3) the sheltered marsh state; or (4) the lake marsh state. (1) The dry marsh state is characterized by very low water levels that occur following a drought or deliberate drawdown. Because irradiance at the sediment surface is high, epipelon tend to be the predominant algal assemblage. (2) The open marsh state is maintained by periodic natural disturbances in the wetland, leading to epiphyton predominance on the surfaces of submersed and emergent macrophytes. Natural disturbance by benthivorous fish, wind action and high grazing pressure keeps the epiphyton biomass at a level that does not shade the macrophyte substrata to the point of decline. The combined shading effect of the macrophytes and the epiphyton reduces irradiance to the epipelon, keeping epipelon abundance low. Metaphyton is usually knocked back by wind action, and phytoplankton is outcompeted by epiphyton and macrophytes for nutrients in the water column. (3) The sheltered marsh state develops if there is protection from wind action, or there are enough macrophytes in the water column to reduce water movement that causes disaggregation of metaphyton mats. The metaphyton mats that develop shade the macrophytes and the other competing algal communities, thus becoming the dominant assemblage in the sheltered marsh. (4) The lake marsh is characterized by high water levels, abundant nutrients in the water column and low grazing pressure, leading to phytoplankton predominance. Epiphyton, metaphyton and epipelon are not as successful due to low irradiance and low macrophyte abundance. Goldsborough and Robinson (1996) predict that a wetland will proceed in either direction to one of these four stable states, depending on the outcome of the interacting variables of nutrient levels, grazing pressure and water levels. In this study, we looked at one of these interacting variables, the effect of nutrient loading on the structuring of the algal communities.

There has been a great deal of research on the role of increased nutrient supply in the eutrophication of lake ecosystems (Schindler *et al.* 1971). Increased phosphorus inputs, in particular, have been linked to increased algal growth in lakes (Schindler 1974). Lakes with phosphorus concentrations of 30 to 100 µg/L are defined as eutrophic and above 100 µg/L as hypereutrophic (Wetzel 1983). Under extremely eutrophic conditions, nitrogen utilization may exceed inputs, causing nitrogen to become the growth-limiting nutrient in the system (Wetzel 1983). Most of the current eutrophication research has focused on lakes, which have a significant deep-water or pelagic zone as well as some proportion of littoral zone. The extent to which lake eutrophication research can be generalized to completely littoral-dominated systems such as wetlands is questionable. Nutrient dynamics in wetlands may differ significantly as compared to deeper aquatic ecosystems. Nutrient-rich sediments may be resuspended more frequently as a result of wind action, benthivorous carp, or burrowing invertebrates (Goldsborough 1993). Epipelic algae may produce on oxygen-rich microzone at the sediment-water interface which prevents the efflux of nutrients from the sediments (Goldsborough and Robinson 1985). Waterfowl feces may contribute significantly to the nutrient budget of wetlands, as they do in lakes (Manny *et al.* 1994). It has been shown that the outcome of resource competition may change along a nutrient gradient and affect the structuring of competing algal communities (Tilman 1977). The extent to which external nutrient loading changes the nutrient gradient and thus affects the structuring of algal communities in wetlands is unknown.

In this study, we perturbed a microcosm of a wetland ecosystem with two patterns of nitrogen (N) and phosphorus (P) additions and measured the growth responses of several algal communities. We hypothesized that the nitrogen and phosphorus additions would cause the wetland ecosystem to progress to one of the alternative stable states described by Goldsborough and Robinson (1996). The periodicity and magnitude of the nutrient additions would alter the composition and relative abundance of epipelon, epiphyton, metaphyton, and

phytoplankton. Small regular (press) additions of N and P would encourage either phytoplankton (a “lake marsh” state) or metaphyton (a “sheltered marsh” state) to develop. Phytoplankton may predominate because of its physical position near the top of the water column as first consumer of the regularly added quantities of N and P. Metaphyton may predominate in the sheltered microcosm environment if macrophytes provide sufficient substrata from which to develop. Large spike (pulse) additions of N and P would encourage macrophytes and epiphyton to predominate (an “open marsh” state). The occasional spikes of nutrient would likely not remain in the water column long enough to allow phytoplankton to become dominant. The increased nutrient deposited in the sediments would favor macrophyte growth, thus providing ample substrata for epiphyton abundance.

Study area and methods

Study area

This study was conducted from 1 May to 31 August 1994. The study site was a stretch of open water in the center of the Blind Channel where the channel was approximately 45 m across. Stands of hybrid cattails, *Typha* x *glauca* lined the channel edges and submersed vegetation grew within the channel, including pondweeds (*Potamogeton pectinatus*, *Potamogeton zosteriformis*), water-milfoil (*Myriophyllum spicatum*), hornwort (*Ceratophyllum demersum*) and stonewort (*Chara* sp.). The channel was well populated with small fish species, including sticklebacks (*Pungitius pungitius*), spottail shiners (*Notropis hudsonius*) and fathead minnows (*Pimephales promelas*), as well as the larger benthivorous carp (*Cyprinus carpio*). The channel edges provided habitat for waterfowl and songbirds, as well as beaver and muskrat. The flocculent bottom sediment was a fine-grained black mud that was rich in decomposing organic matter. At the study site, the channel had a relatively flat bottom resulting in uniform water depths of 80 to 100 cm at the beginning of May 1994.

Experimental enclosures

Six large enclosures were installed at the site during the first week of May. Four of the enclosures had been constructed and used for previous research at Delta Marsh (Goldsborough 1991, 1993a). We repaired these four and constructed two new enclosures on the same design. Each enclosure consisted of a 5 m by 5 m wooden frame floating on high-density foam block supports which held the frame just above water level. The plywood top of the frame also provided a 40 cm wide walkway around the enclosure to allow sampling access. A translucent plastic curtain was secured to the inside of each frame and extended through the water column and into the bottom sediments. Metal rebar was enclosed in a pocket at the bottom of the curtain and embedded into the sediments to prevent direct water movement between the enclosure and the surrounding marsh. The total enclosed water volume in each enclosure was about 20,000 L. The six enclosures were bolted together and anchored in the center of the Blind Channel.

We attempted to limit primary consumers, and thereby reduce the number of variables in the experiment, by removing all fish from the enclosures. Minnow traps were immediately placed in each enclosure and emptied on a daily basis. Early in the season, muskrats chewed small holes in each of the curtains, allowing fish to enter the enclosures. The holes were patched immediately and the fish trapped out but not before numerous eggs were laid on the inner side of the curtain. Therefore, the minnow traps were maintained for the duration of the experiment to trap out the fry as they hatched. Several live traps were deployed outside the enclosures to discourage further damage by muskrats.

Periphyton colonization substrata

To provide uniform colonization substrata for periphyton, vertically positioned cylindrical acrylic rods (0.64 cm diameter, 90 cm length) (Goldsborough *et al.* 1986) were placed in each enclosure on 18 May 1994. The rods were pushed 30 cm into the sediments leaving the uppermost 60 cm of each rod available for algal colonization. One hundred rods were placed in a 10 x 10 grid pattern with equal spacing between each rod and the ones adjacent to it in each enclosure. The rods were positioned far enough from the curtain to avoid abrasion through any contact with it. Prior to placement, we had notched the rods at specific intervals using a bandsaw to provide subsample segments of a predetermined surface area.

Nutrient addition treatments

Sampling began on 24 May, designated as week 1, and continued on a regular schedule until 26 August (week 14). During weeks 1 to 4, the enclosure site was allowed to recover from the disturbance effect of rod installation. This period also allowed time for initial periphyton colonization of the rods. During this period, sampling was conducted inside and outside the enclosures, as described below, to determine background levels of nutrients and initial measurements of the productivity of algal communities. Nutrient addition began on 20 June, designated as week 5 of the experiment. The manipulated variable was the timing of the nutrient additions. The same total loads of nitrogen and phosphorus were added in two temporal regimes, one designated as the pulse addition and the other designated as the press addition. Two enclosures (labeled C and D) were arbitrarily chosen to receive the pulse nutrient additions, while two more (labeled A and E) were chosen to receive the press nutrient additions. The remaining two enclosures (labeled B and F) were designated as unmanipulated controls. The location of each replicate enclosure was chosen so that no two replicate enclosures were side by side nor on the same side of the Blind Channel. The spacing of the replicates attempted to account for the spatial heterogeneity arising from minor position effects due to prevailing wind direction, water currents and incident angle of light.

The pulse nutrient addition was added at two times over the course of the 15 week experiment, the first one on 20 June 1994 and the second one on 25 July 1994 (Table 1). The press nutrient addition was added every Monday, Wednesday and Friday, beginning 20 June 1994, with a total of 29 additions made over the course of the 15 week experiment. The press addition on the last day of the experiment was not made as no further sampling was carried out after that. At each addition, the measured nutrient chemical for each enclosure was dissolved in 1 L of carbon-filtered water to make an aqueous nutrient solution. At the study site, the aqueous nutrient solution was mixed with 10 L of water from the designated enclosure and sprinkled uniformly from the nozzle of a watering can over the entire surface of the enclosure.

Table 1. The amount of phosphorus (as $NaH_2PO_4.2H_2O$) and nitrogen (as $NaNO_3$) added to each of the pulse and press treatment enclosures. The total load reflects the proportion of the inorganic chemical that was elemental N or P. The ratio of total N to total P was 7:1.

Designated enclosure	Experimental treatment	Weight of chemical per addition (g) per enclosure	Loading per addition (g) per enclosure	Number of additions per enclosure	Total load (g) per enclosure in 15 weeks
C and **D**	**Pulse** N	910.17	145.63 g N	2	291.26 g N
	P	100.72	20.14 g P	2	40.28 g P
A and **E**	**Press** N	60.678	9.71 g N	29	281.59 g N
	P	6.715	1.34 g P	29	38.95 g P
B and **F**	**Control**	unmanipulated			

Water chemistry sampling and analysis

Every Tuesday and Friday, seven 1 L water samples (~ 30 cm depth) were collected, one from each enclosure and one from the Blind Channel. These were analyzed for orthophosphate according to the methods of Stainton *et al.* (1977). Nitrate was measured by the ultraviolet screening method and alkalinity was measured by the titration method (APHA 1992). Seven additional samples were collected at the same time and submitted to Norwest Labs (Winnipeg) for analysis of nitrate+nitrite using the automated cadmium reduction method (APHA 1992).

Phytoplankton sampling and analysis

Every Tuesday, three 1 L samples of water were collected from random positions in each enclosure and from the Blind Channel for analysis of phytoplankton carbon fixation rate, chlorophyll and particulate phosphorus

content. The samples were collected using a water column sampler, which consisted of a transparent acrylic tube, 6.4 cm in diameter and 50 cm in length, which could be sealed at each end with a rubber stopper. The open-ended tube was lowered vertically into the water. Once submersed, first the top and then the bottom stopper was pushed into place to obtain an integrated water column sample including both phytoplankton and zooplankton. The samples were then filtered through a 100 µm pore size mesh plankton bucket to remove the zooplankton (Hann 1991). One liter of the remaining filtered water was collected from each of the three sample sites in each enclosure and transported back to the field lab for analysis. Phytoplankton productivity was measured according to the methods of Goldsborough (1993b). One mL of radiolabeled (14C) bicarbonate solution (1 µCi/mL) was added to clear glass tubes containing 25 mL of each collected water sample. The tubes were placed in a waterbath at a constant temperature of 25ºC, provided with a light source (500 µE/m2/s), and allowed to photosynthesize over a period of four hours. Blackened glass tubes containing another 25 mL of each water sample, also with 1 mL of radiolabeled bicarbonate solution added, were placed in the same water bath over the same period as controls. After the four hour incubation period, the algal cells from each sample were collected on 0.45 µm pore size glass microfiber filters (Whatman GF/C) under vacuum. The filters containing the samples were fumed over concentrated HCl to release any residual inorganic radiolabeled bicarbonate as carbon dioxide. The filters were then placed in 5 mL glass vials of liquid scintillation cocktail (Beckman ReadySafe™). Radioactivity of the samples was determined by liquid scintillation counting in a Beckman LS 3801 scintillation counter. Using these values for radioactivity, plus measurements of the pH and alkalinity of the incubation medium, the carbon fixation rate (µgC/L/h) during the incubation period was calculated for each sample.

For chlorophyll analysis, a known volume (~ 400 mL) of each remaining water sample was filtered through GF/C filters. About 1 mL of MgCO3 solution was added to the water sample during filtration to preserve the algal cells on the filters. The filters containing the phytoplankton cells were frozen for at least 24 hours to disrupt the algal membranes. The filters were then thawed, placed in 90% methanol and stored in the dark for 24 hours to allow complete extraction of chlorophyll pigments from the algal cells. Measurements of the light absorbance of the pigment extract were made at 665 nm and 750 nm (1 cm path length) for chlorophyll *a* and its derivatives, using a Milton-Roy Spectronic 601 spectrophotometer. One hour after acidification with 10-3 N HCl to facilitate conversion to pheophytin, the pigment extract's absorbance was again measured at 665 nm and 750 nm. Calculation of chlorophyll concentration (µg/L) followed Marker *et al.* (1980).

Periphyton sampling and analysis

Six colonized acrylic rods were chosen randomly from each enclosure every Thursday. The rods from each enclosure were sampled without replacement. At the time of rod removal, the water column surrounding three of the rods in each enclosure was collected for zooplankton sampling. A modified water column sampler, with notches in the center of the both the top and bottom stopper to accommodate the diameter of the rod, was carefully lowered around the rod. The stoppers were fitted into place around the rod and into each end of the sampler tube. The sampler tube and the rod were then drawn up simultaneously as one unit. The water column sample was slowly drained from the tube to minimize disturbance of the periphyton colonizing the rod and the water was collected for zooplankton sampling (Hann 1995). In the field, each rod was separated at the pre-scored notches into its predetermined subsample segments, using two pairs of needle-nosed pliers placed close to the notches to minimize hand contact with the rods. The two segments for productivity were placed in capped tubes (one clear and one blackened) in 25 mL of water from that enclosure that had previously been filtered GF/C filters. The two segments for chlorophyll analysis were placed in empty capped tubes for transport back to the field lab.

Periphyton productivity was analyzed as for phytoplankton, except that the colonized rod segment was retained on the filter and placed into scintillation cocktail with the filter. Periphyton chlorophyll analysis followed the phytoplankton procedure as above, except that the colonized rod segments were placed in the solvent.

Metaphyton sampling and analysis

Once the metaphyton community had developed (beginning 29 June, week 6), it was sampled every Thursday at the same time as periphyton was sampled, using the same six random locations within each enclosure as for periphyton. If metaphyton was present at a location, a fine mesh sieve (area 175 cm^2) was carefully slid into place under the metaphyton and lifted straight up through the mat (Goldsborough 1993b). Any metaphyton overhanging the edges of the sieve was carefully sheared off, so that the surface area of sample obtained corresponded to the known area of the sieve. The samples were dried to constant weight at 104ºC and their dry weights (g/cm^2) were recorded.

Macrophyte sampling and analysis

Macrophytes were sampled every second Monday using a macrophyte sampler modified from Pip and Stewart (1976). Three random locations within each enclosure were sampled. The macrophyte sampler was lowered carefully into an enclosure, enclosing the macrophytes in a 30 x 30 cm area of the bottom. The sampler consisted of a heavy-gauge aluminum frame with inside dimensions of 30 x 30 x 100 cm, which was wrapped in two layers of fine mesh screen, the outer nylon mesh screen and the inner Nitex™ screen (pore size 100 µm), around the four vertical sides to contain the zooplankton. A sharp moveable blade attached to screen was set in guide slits at the bottom of the frame with a stationary blade facing it along one side of the bottom. When a messenger released the trigger mechanism, taut heavy-duty rubber bands attached to the ends of the blades pulled the moveable blade and attached screen rapidly across the bottom to meet with the stationary blade. This effectively sheared the macrophytes just above the sediment surface, containing them and their associated epiphytes and zooplankton within the mesh-enclosed sampler. The sampler was then lifted out of the water column and placed in a rubber tray, where carbon-filtered water was used to wash the sample off the mesh screen into the tray. This water was then filtered through 100 µm pore size mesh to remove the zooplankton. The filtered water and the macrophytes were then placed in a large closed container and shaken vigorously to dislodge the epiphyton from the macrophytes.

In the field lab, macrophyte samples were placed in plastic bags and refrigerated at 4ºC prior to measurement. They were later dried to constant weight at 104ºC and weighed.

Epipelon sampling and analysis

Epipelon sampling was carried out biweekly on alternate Mondays to macrophyte sampling. Samples of surface sediments (~ 1 to 2 cm deep) were obtained from three random locations in each enclosure. Lengths of open-ended PVC pipe (10.2 cm diameter) were lowered through the water column and pushed firmly into the bottom sediments to delineate the sample sites. Using a hand operated vacuum pump attached to a long piece of tubing supported by a length of acrylic rod, the surface sediments inside the diameter of the PVC pipe were aspirated into a vacuum bottle. The sediment slurry was transferred to black-walled beakers and stored in a dark drawer for 24 hours to allow the sediment to settle. The overlying water was carefully drawn off without disturbing the underlying sediment. The beakers were then transported to an outdoor site where they would receive natural irradiance for at least 18 hours. At the site, each wet sediment surface was covered by a circle of lens paper. The blackened sides of the beakers prevented light penetrance through the sides. After 18 hours, the lens paper circles were carefully removed from the beakers and placed in 100 mL of water (filtered through GF/C filters) from the same enclosure as the sediment sample. These samples were vigorously shaken for two minutes to dislodge the epipelic algae which had migrated up from the sediments into the lens paper. Subsamples of the water containing the epipelon were dispensed into clear and blackened tubes (25 mL each) for productivity analysis as described above. The remaining 50 mL subsample was filtered for chlorophyll analysis as above.

Results

The levels of N and P in the water column of the control enclosures were low and remained relatively constant over the 15 week experimental period (Fig. 1). In the pulse enclosures, N and P levels were elevated dramatically at the time of each of the two pulse additions, although the rise was not quite so marked at the second pulse addition. Levels of N in the water column dropped off quickly and returned to pre-addition levels

three weeks after the first pulse (Fig. 1A). From 10 July to 24 July, N levels in the pulse enclosures were similar to those in the control enclosures. After the second pulse addition on 25 July, N levels in the pulse enclosures dropped, within two weeks of the second pulse, to similar levels as in the press enclosures. Press N levels rose slightly at the time of the first addition on 20 June (Fig. 1B), after which they were relatively consistent throughout the remainder of the experiment. Levels of P in the water column followed a similar pattern, except that P levels did not drop back as dramatically. The second P pulse on 25 July produced a noticeably smaller peak than the first pulse. P levels in the pulse enclosures never dropped back to pre-addition conditions. Although the major peaks dropped off quickly, the P levels in the pulse enclosures showed an increasing trend through to the end of the experimental period. The press P levels increased from the first addition on 20 June through to the end of the experiment.

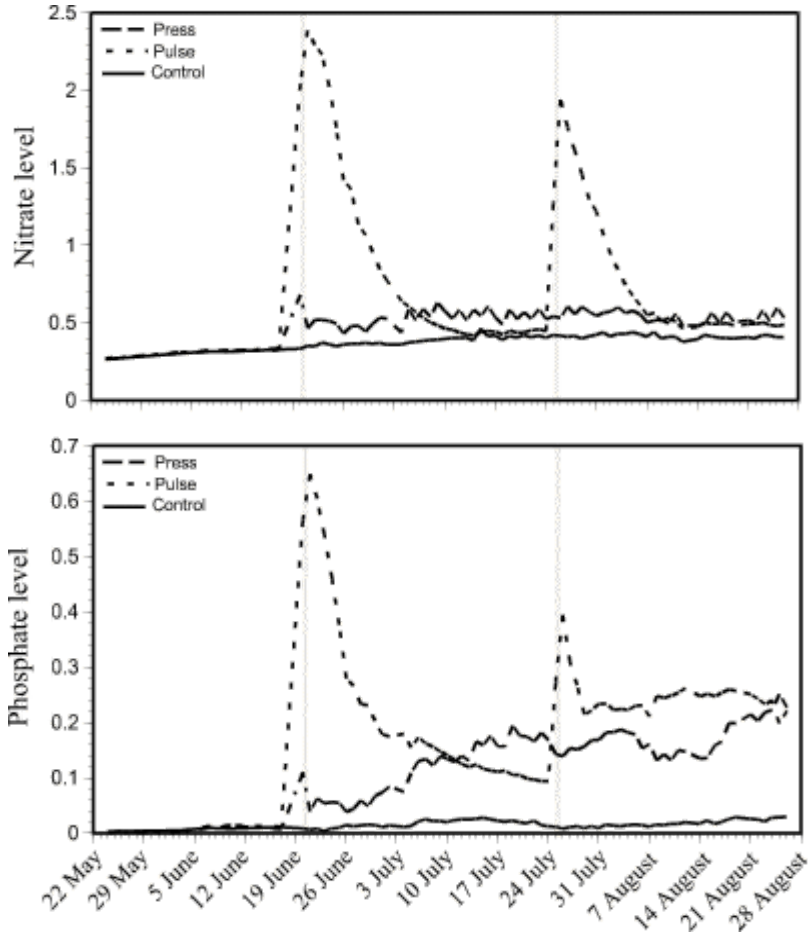

Figure 1. Nitrate (as $NaNO_3$) levels (A - top) and phosphoate (as NaH_2PO_4-$2H_2O$) levels (B - bottom) in the water column over a 15-week period in press, pulse, and control treatments. Vertical bars indicate N and P pulse additions on 20 June and 25 July 1994. Press additions of N and P were made thrice weekly from 20 June to 24 August 1994.

Phytoplankton chlorophyll concentration was similar in all three experimental treatments (Fig. 2). Levels were highest early in the season in all enclosures, prior to nutrient addition (Fig. 2A). A peak of 20 to 30 µg/L occurred around the end of May in all enclosures. Chlorophyll concentrations then declined slowly and remained around 2 to 8 µg/L for the remainder of the summer in all enclosures. Phytoplankton productivity profiles (Fig. 2B) exhibited the same seasonal trend.

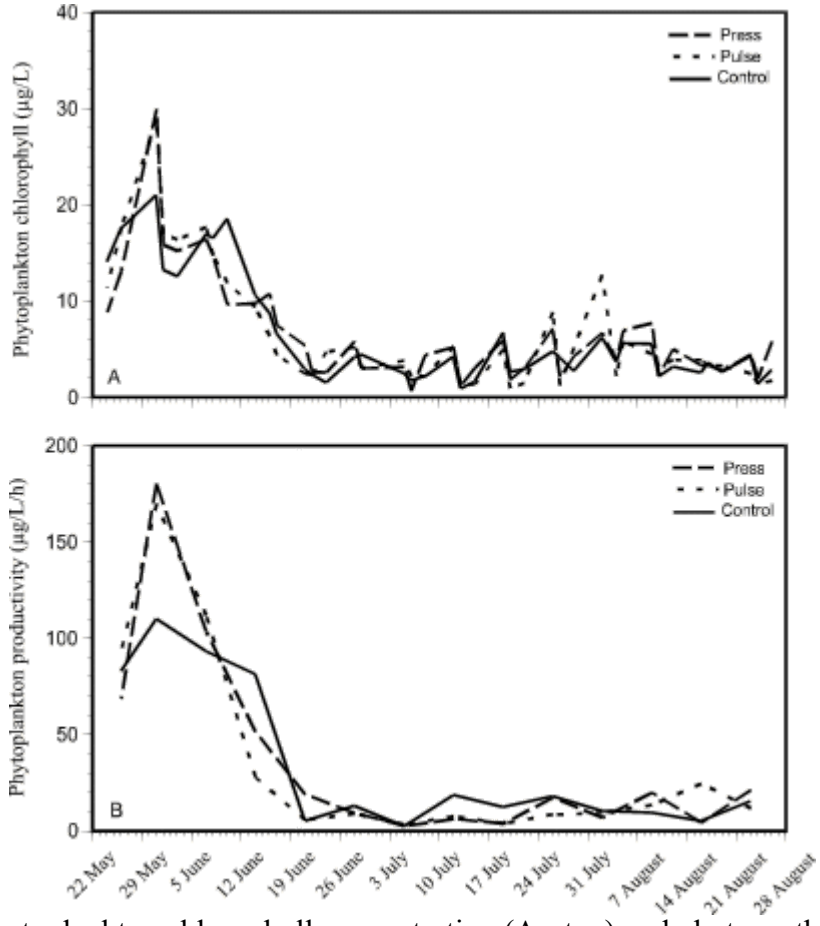

Figure 2. Changes in phytoplankton chlorophyll concentration (A - top) and photosynthesis (B - bottom) over a 15-week period in press, pulse, and control enclosures.

Periphyton production increased in all enclosures through the 15 week experimental period (Fig. 3). Periphyton productivity increased to 6 µgC/cm2/h in the pulse enclosures at the time of the first addition on 20 June (Fig. 3B). By 3 July, periphyton productivity in the pulse enclosures decreased to the productivity rate in the control enclosures (around 3.5 µgC/ cm2 /h), after which they both leveled off and remain nearly constant for the rest of the experimental period. There was no noticeable increase in periphyton productivity in the pulse enclosures at the time of the second pulse addition. Press treatment periphyton productivity peaked at 5.5 µgC/cm2/h somewhat later than in the pulse treatment, around 14 July. For the remainder of the season, periphyton productivity in the press enclosures remained around 4 µgC./cm2/h, slightly higher than in the pulse and control treatment enclosures. Periphyton chlorophyll concentrations (Fig. 3A) exhibited much the same trend as for productivity. Chlorophyll concentrations in pulse and control treatments were similar, while in the press treatment, chlorophyll concentrations continued increasing to the end of the experiment.

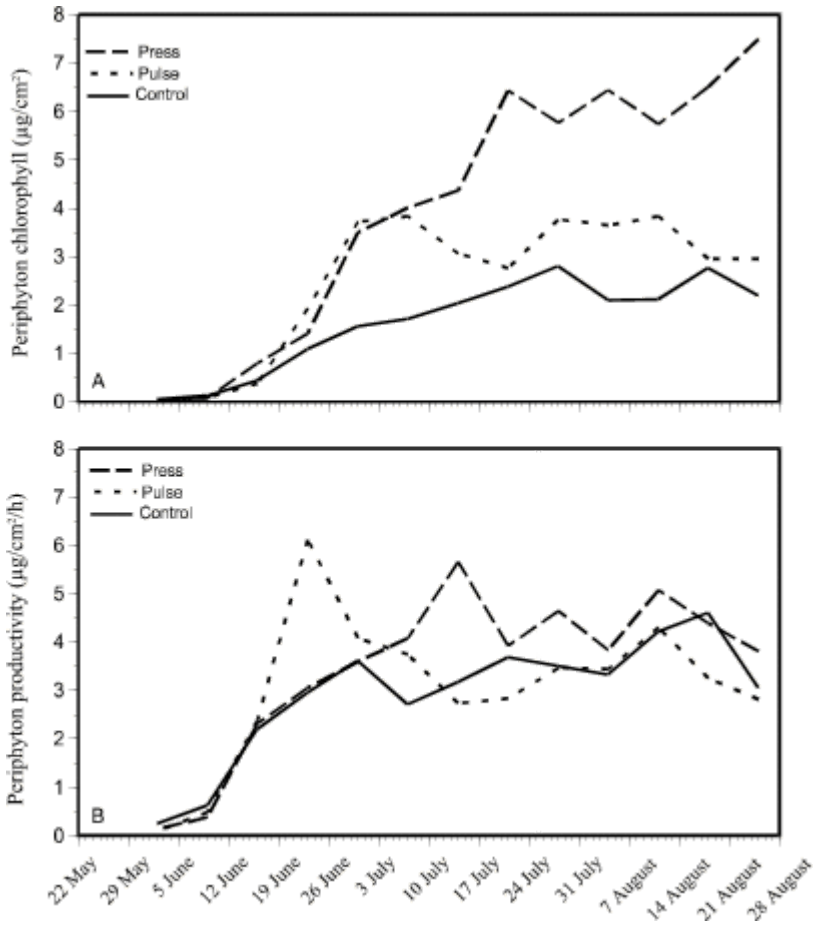

Figure 3. Changes in periphyton chlorophyll concentration (A - top) and photosynthesis (B - bottom) over a 15-week period in press, pulse, and control enclosures.

Epipelon chlorophyll concentrations were highest in all enclosures at the beginning of the experiment (Fig. 4). However, it should be noted that even these highest concentrations were not high as compared to periphyton concentrations (0.2 to 0.3 µg/cm2 for epipelon compared to 2 to 7.5 µg/cm2 for periphyton). By 20 June, when nutrient addition began, epipelon chlorophyll levels in all enclosures were < 0.1 µg/cm2 and remained so for the rest of the experiment (Fig. 4A). Epipelon productivity was highest (85 to 110 µgC/cm2/h) in all enclosures around 20 June (Fig. 4B) then decreased to < 20 µgC/cm2/h from 3 July to the end of the experiment.

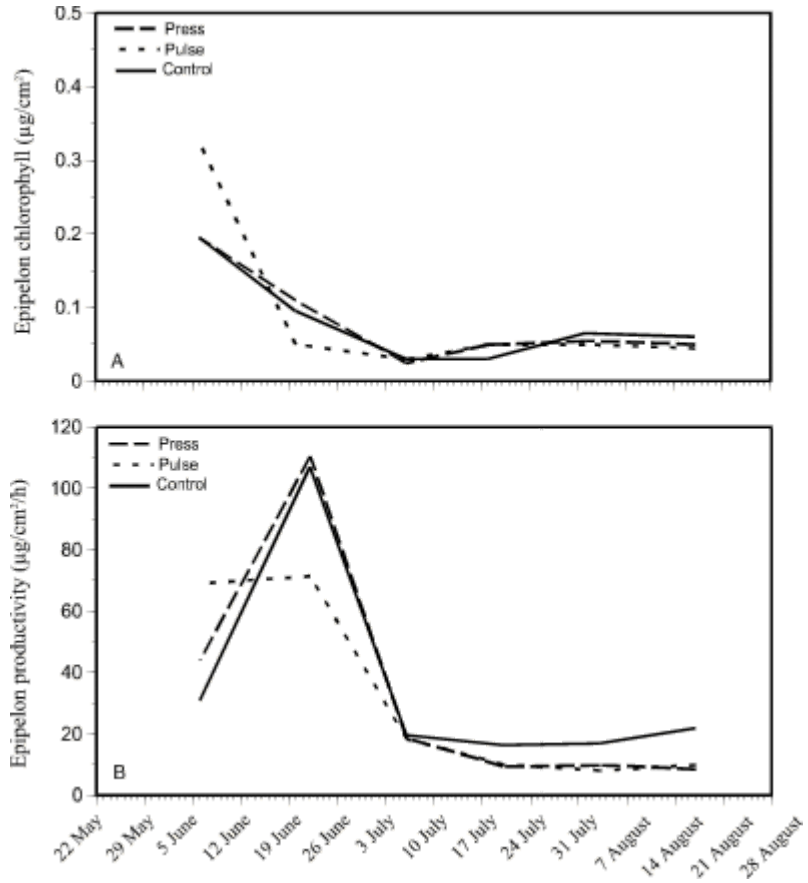

Figure 4. Changes in epipelon chlorophyll concentration (A - top) and photosynthesis (B - bottom) over a 15-week period in press, pulse, and control enclosures.

Metaphyton was absent from all enclosures until about a week after the first nutrient additions on 20 June (Fig. 5A). Metaphyton developed in both the press and the pulse enclosures around 3 July, after which the metaphyton biomass in both treatments increased rapidly. Both pulse and press treatments showed an increasing trend in metaphyton biomass production which continued to the end of the experimental period. Press treatment biomass was slightly higher (200 to 350 g/m2) than pulse treatment biomass (150 to 300 g/m2) from 24 July to the end of the experiment. Metaphyton was virtually absent from the control enclosures, although there is a small amount (100 g/m2) produced around mid-August.

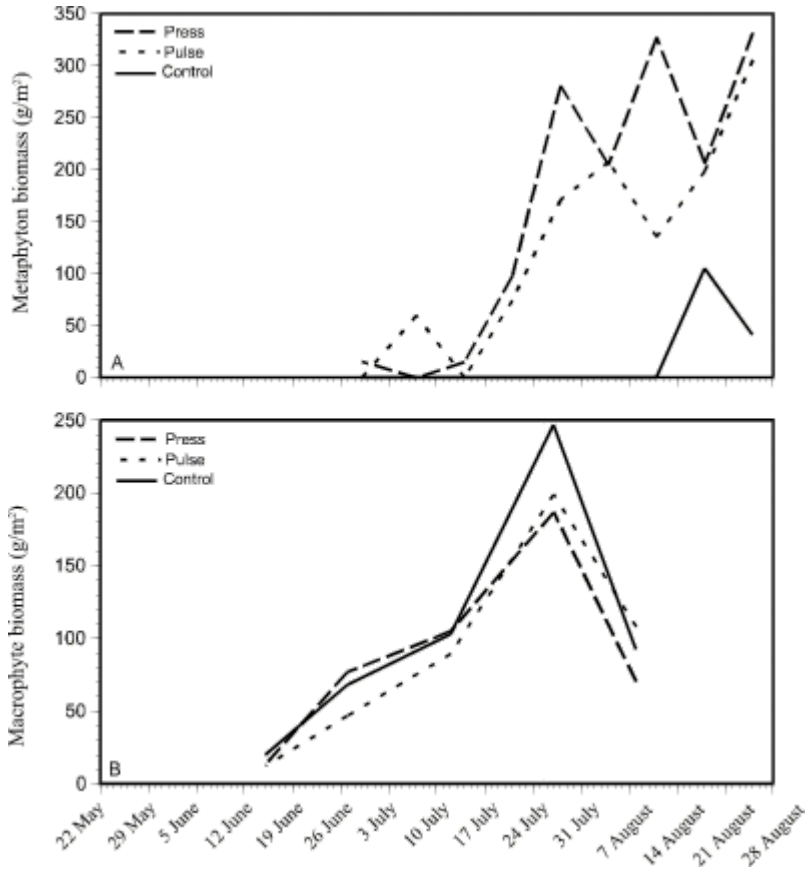

Figure 5. Changes in the dry weight of metaphyton (A - top) and macrophytes (B - bottom) over a 15-week period in press, pulse, and control treatments.

Macrophyte biomass showed very similar trends in all enclosures over the 15 week experimental period (Fig. 5B). Macrophyte biomass increased steadily from around 20 g/m2 in early June to 200 to 250 g/m2 at its peak around 26 July, after which biomass decreased.

Discussion

The profiles of the N and P levels in the water column closely reflected the patterns of pulse and press nutrient additions. Nutrient levels in the water column of treated enclosures remained consistently higher than in the controls, except for a short period in the pulse enclosures from 10 July to 24 July, when N levels were similar to levels in the controls. This suggests that the added nutrients were remaining in the water column for a significant period of time (in terms of algal life cycles, which are measured in periods of weeks), rather than sedimenting immediately to the bottom. The peaks in N and P at the time of the second pulse additions were smaller, probably due to the presence of increased algae and macrophytes which could use nutrients from the water column quickly. The smaller peak in P at the time of the second pulse addition suggests that phosphorus was being luxury-consumed, particularly by metaphyton, periphyton and macrophytes. The increasing P levels in both the press and the pulse treatments as the season progressed suggest that more P was being added than the plants could consume. Both the N and P levels in the pulse treatments fell below the levels in the press treatments prior to the second nutrient pulse, although only for a period of about two weeks. This was reflected in both the periphyton chlorophyll and productivity profiles. Periphyton productivity in the pulse enclosures dropped as the nutrient levels dropped, while at the same time, periphyton productivity in the press enclosures was increasing steadily.

Phytoplankton appeared to have been unaffected by either pattern of nutrient addition. The early peak in phytoplankton productivity was likely the result of a normally-occurring spring phytoplankton bloom. With the onset of nutrient additions, phytoplankton appeared to have been outcompeted for the available nutrients by other algal communities. Epipelon also appeared to have been relatively unaffected by either the timing or the magnitude of nutrient addition. The increase in productivity at the time of the first nutrient addition was

probably coincidental. The control showed the same increase in productivity, ruling out the nutrition addition as a causative factor. Epipelon productivity could be expected to be higher early in the season, when irradiance at the sediments was higher, before there was much macrophyte or algal biomass above to shade the sediments. The water column within all the enclosures became clear as a result of the sheltering effect of the curtain walls against strong water movements. The rise in epipelon productivity probably coincided with reduced turbidity of the water column.

It is difficult to assess whether there was a difference in response by periphyton to the timing and magnitude of nutrient additions. The trends over the season were similar in all three treatments, suggesting that the driving factor was a seasonal response to the light regime, rather than a response to manipulated nutrient levels. Periphyton productivity in the press treatment was higher, with correspondingly higher biomass, suggesting that the periphyton community gained some competitive advantage from the consistently elevated supply of N and P in the water column. While a measurement of macrophyte epiphyton is not presented here, we conjecture that its productivity profile would be similar to that of the periphyton on the acrylic rods, at least until the point when macrophytes began to decline. The high periphyton, and probably epiphyton, biomass at the time of the second nutrient pulse on 25 July would have provided ample “starter” conditions for the proliferation of metaphyton which began at that time. The timing and magnitude of the nutrient additions did not seem to have a noticeable impact on metaphyton development, as it developed equally in both press and pulse treatments. The major difference between these two treatments and the controls, which did not develop metaphyton at this time, was the higher level of phosphorus in the water column of the press and pulse enclosures. Nitrogen was also higher, but it had been at a consistently higher level in the press treatment than in the controls throughout most of the period. It was as the phosphorus levels increased in both the press and pulse treatments that metaphyton flourished. There was probably a requirement for high irradiance, as well as high nutrient availability, which would also factor into the similar timing of metaphyton development in both press and pulse treatments. There was a noticeable decline in macrophyte biomass around the time that the metaphyton started to proliferate. This may have been the result of increased shading by the metaphyton mats, or increased competition for nutrients from the metaphyton, or a combination of the two. Periphyton productivity had leveled off by the time metaphyton was developing in the treatment enclosures, but there was no evidence of a real decline in productivity.

Macrophyte biomass was a significant factor in at least two ways. Macrophytes provided abundant surface area for colonization by epiphyton, as well as initial support for large metaphyton mats. Macrophytes also competed for nutrients, both in the water column and from the sediments. Macrophytes are often thought to have a competitive advantage over algae in terms of nutrient uptake, given that they have access to nutrients in the sediments via their roots, as well as being able to absorb nutrients from the water column through their leaves. In this study, much of the added nutrient remained in the water column for extended periods, suggesting that there may not have been much competitive advantage imparted to the macrophytes in terms of increased sediment nutrients. The macrophyte biomass profiles suggest that macrophyte growth was not significantly influenced by either pattern of nutrient addition. The pulse and press profiles were similar to the control profile, suggesting that seasonal factors such as irradiance and temperature were more important in influencing their growth pattern than nutrient additions. However, the presence of high macrophyte biomass at the same time as phosphorus levels were increasing in both press and pulse enclosures (*circa* 25 July) was probably a factor in the development of metaphyton mats, as suggested earlier.

Conclusion

The control enclosures were dominated by periphyton (and probably epiphyton with high macrophyte biomass to provide abundant substrata for colonization), remaining in the open marsh state that is maintained in Delta Marsh by periodic natural disturbances. Both the press and the pulse treatment enclosures were initially dominated by periphyton, but later shifted to metaphyton dominance. This transition suggests the development of a sheltered marsh state, as predicted by the model of Goldsborough and Robinson (1996).

The transition to a sheltered marsh state in treatment enclosures supports our hypothesis that nutrient additions will alter the structuring of the algal assemblages in a wetland. However, there does not appear to be much

difference in growth response to the two patterns of treatment, pulse or press. Both patterns of addition produced a similar growth response among algal communities and macrophytes. The significant difference was between the nutrient addition treatments and the control treatment. The transition to a metaphyton-dominated system under high nutrient conditions has been observed in other studies. Fong *et al.* (1993) found that macroalgal and cyanobacterial mats were better competitors than phytoplankton for high levels of nutrients in experimental microcosms. Murkin *et al.* (1994) found that metaphyton responded to periodic (press) nutrient addition later in the growing season (mid-July, early August) and suggested that it took several additions of N and P to reach levels suitable for metaphyton growth. They noted a shading effect on epiphyton and phytoplankton from the metaphyton.

Metaphyton mats, indicative of a sheltered marsh, are relatively rare in Delta Marsh, except in areas undergoing drawdown and reflooding (Goldsborough and Robinson 1996). Increased decomposition of organic matter during drawdown and the subsequent flushing of nutrients from the sediments during reflooding would provide a natural nutrient enrichment event such as we have simulated in this experiment. We conclude that the transition to a metaphyton-dominated sheltered marsh observed in this experiment is due to the nutrient enrichment of the water column.

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Delayed hatching of artificially incubated Brown-headed Cowbird eggs

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Introduction

The incubation period of avian eggs may be influenced by the behaviour of the incubating parent (Ricklefs and Smeraski 1983; Briskie and Sealy 1990), thermal properties of the nest (Schaeffer 1980; Ricklefs and Smeraski 1983), and physical properties of the egg itself such as mass and shell thickness (O'Connor 1984). Interspecific variation in incubation periods also occurs independently of variables such as egg mass, likely reflecting species-specific differences in rates of embryonic growth and development (Ricklefs 1993). Longer incubation periods may reduce the amount of time a young bird has to fledge, molt, or accumulate fat reserves for migration, as well as extending its period of vulnerability to nest predators (Perrins 1977; Webb 1987). Therefore, short incubation periods are thought to be desirable for most bird species.

The Brown-headed Cowbird (*Molothrus ater*, hereafter cowbird) parasitizes passerine hosts with a wide range of body sizes. Nestlings of avian brood parasites must compete with host nestlings for parental care (Redondo 1993). Some parasites eliminate competition by ejecting host eggs and young, or by killing them, e.g. parasitic cuckoos and honeyguides, respectively (Payne 1977). Cowbirds have not evolved such drastic strategies, rather, their nestlings compete with host nestlings for food provisioned by the foster parents, often so successfully that some or all host nestlings starve (Briskie and Sealy 1987; Weatherhead 1989). Cowbird eggs often hatch before host eggs (Nice 1937; Hann 1937; Hofslund 1957; Nolan 1978; McMaster, unpubl. data), and the young gain competitive 'head starts' over host nestlings (Mayfield 1992). Recent research has shown that parasitic cowbirds have short incubation periods relative to nonparasitic icterines (Briskie and Sealy 1990), and instances of 10-day incubation periods have been confirmed for 3 species of parasitic cowbirds (Wiley and Wiley 1980; Carter 1986; Briskie and Sealy 1990). The mechanism that enables cowbird eggs to hatch earlier than their hosts is not known.

Four hypotheses have explained the short incubation periods of parasitic cowbirds: (1) cowbird embryos develop more rapidly (Friedmann 1927), (2) female cowbirds retain their eggs in the oviduct for up to 24 hours, thereby allowing the embryo to develop in the female prior to being laid (Hoffman 1929), (3) because incubation periods increase as a function of egg volume (Vleck and Vleck 1987), female cowbirds lay small eggs relative to their body mass to minimize their incubation periods (Briskie and Sealy 1990), (4) female cowbirds invest less energy per egg than expected by mass, forcing the embryo to hatch earlier when it runs out of yolk reserves (G. Kattan, unpubl. data).

Hypotheses #1 and #3 have not received support in the Shiny Cowbird (*Molothrus bonariensis*) (G. Kattan, unpubl. data), and the Brown-headed Cowbird (Briskie and Sealy 1990), respectively. Using the Shiny Cowbird, Kattan (unpubl. data) found support for Hypothesis #4. However, for species with short incubation periods energy investment per unit egg mass is expected to be relatively low, because the maintenance functions of the embryo are fueled for shorter periods than in species with long incubation periods (Ricklefs 1993). Also, Ankney and Johnson (1985) determined the energy investment in Brown-headed Cowbird eggs did not differ significantly from that predicted by egg mass. Although Hypothesis #2 may apply to parasitic cuckoos that lay eggs every 48 hours (Liversidge 1961), the only evidence supporting the hypothesis in cowbirds appears to have been a single case of an egg-bound female (Nice 1954).

In 1994, I tested whether Brown-headed Cowbird embryos develop more rapidly than host embryos (Hypothesis #1) by artificially incubating eggs of cowbirds and two host species. Artificial incubation in an incubator permits determination of incubation periods under constant conditions of temperature, and humidity. In the incubator it is

possible to control any effect differences in egg size, female attentiveness, nest insulation, and ambient temperature may have on egg temperature. Hypothesis #1 predicts that cowbird eggs will have shorter incubation periods in the incubator than host eggs. I also predicted that due to the constant temperature of the incubator, cowbird incubation periods would approximate the shortest incubation period observed under natural conditions (10 days, Briskie and Sealy 1990).

Methods

Freshly laid cowbird eggs were obtained from host nests at Delta Marsh in May and June, 1994. Red-winged Blackbird (*Agelaius phoeniceus*) and Yellow Warbler (*Dendroica petechia*) eggs were also obtained fresh on the day they were laid, and in all cases were either the first or second egg laid in the clutch. Eggs were relocated to the University Field Station where they were labelled, and the egg length and width measured using dial calipers (egg mass was not recorded). Before being placed in the incubator, most eggs were candled to verify no detectable embryonic development had occurred prior to collection. Eggs were placed in random positions inside the incubator, with 2 - 3 cm separating each egg. The incubator was home-made, consisting of a 0.75 x 0.75 m plywood frame, insulated with 8 cm of styrofoam. A YSI temperature controller maintained the air temperature inside the incubator at 37.5 ± 0.1°C. Relative humidity was maintained at 50 - 60% by filling a large pan in the bottom of the incubator with water. Three electric fans located at different levels of the incubator provided continuous air circulation, without blowing directly on the eggs. Eggs were turned four times daily to prevent membranes from adhering to the shells. Eggs were candled every 3 - 4 days throughout incubation to monitor embryonic development. Once an egg neared hatching, a cardboard ring was placed around it to ensure once the embryo hatched it could be identified by the presence of its labelled eggshell. The incubator was checked for hatchlings at least 4 times a day. Newly hatched birds were weighed, and the time of their discovery recorded. The hatching event was observed directly in many instances, allowing perfect accuracy of hatching time. However, if the hatching event was not observed, the hatching time was estimated to be the midpoint between the time the nestling was discovered and the time of the last visit to the incubator.

Egg volumes were calculated using the formula $V = kLB^2$ (where k = 0.515 for cowbirds, k = 0.49 for warblers, L = length of the egg, B = breadth of the egg) (Hoyt 1979; Mills 1987). The data were tested for normality using a Shapiro-Wilk test. Normally distributed variables were analyzed using standard parametric techniques.

Results

Hatching success was similar for both cowbird and warbler eggs, however, Red-winged Blackbird eggs experienced poor hatching success (Table 1). Of the three species, only cowbird eggs showed no embryonic development (10.6% of eggs incubated). Death of embryos while hatching occurred infrequently.

Table 1. Percent hatching success, embryonic death, sterility and hatching death experienced by artificially incubated eggs of cowbirds and two host species.

Species	No. Eggs	% Match Success (n)	% Embryonic Death (n)	% Sterile (n)	% Hatching Death (n)
Cowbird	61	60.7 (37)	24.5 (15)	11.4 (7)	3.2 (2)
Yellow Warbler	19	52.6 (10)	47.4 (9)	---	---
Red-winged Blackbird	10	10.0 (1)	80.0 (8)	---	10.0 (1)

Cowbird and Yellow Warbler incubation period (W = 0.96, $p = 0.28$; W = 0.97, $p = 0.85$, respectively), and egg volume (W = 0.95, $p = 0.20$; W = 0.84, $p = 0.0473$, respectively) were normally distributed. Mean egg volumes and incubation periods for each species are shown in Table 2. The sample size for Red-winged Blackbird incubation period was too small to allow further analysis. A 2 sample t-test for groups with unequal variance indicated that the mean incubation period for Yellow Warblers was significantly shorter than that for cowbirds (t

= 3.82, df = 29, p = 0.0007). Cowbird incubation periods increased with egg volume (Fig. 1; y = 15041.8 + 0.94(egg vol.), r2 = 0.098), a trend that approached significance (F = 3.58, p = 0.0674).

Table 2. Mean egg volume and incubation period for artificially incubated cowbird and host eggs that hatched successfully.

Species	Mean Egg Volume (cm^3) ± SE (n)	Mean Incubation Period (D:H:M ± H:M) (n)
Cowbird	2.99 ± 0.04 (35)	12:10:25 ± 2:14 (37)
Yellow Warbler	1.32 ± 0.04 (10)	11:22:25 ± 2:13 (10)
Red-winged Blackbird	3.73 ± 0.13 (2)	12:12:0 ± 1:0 (2)

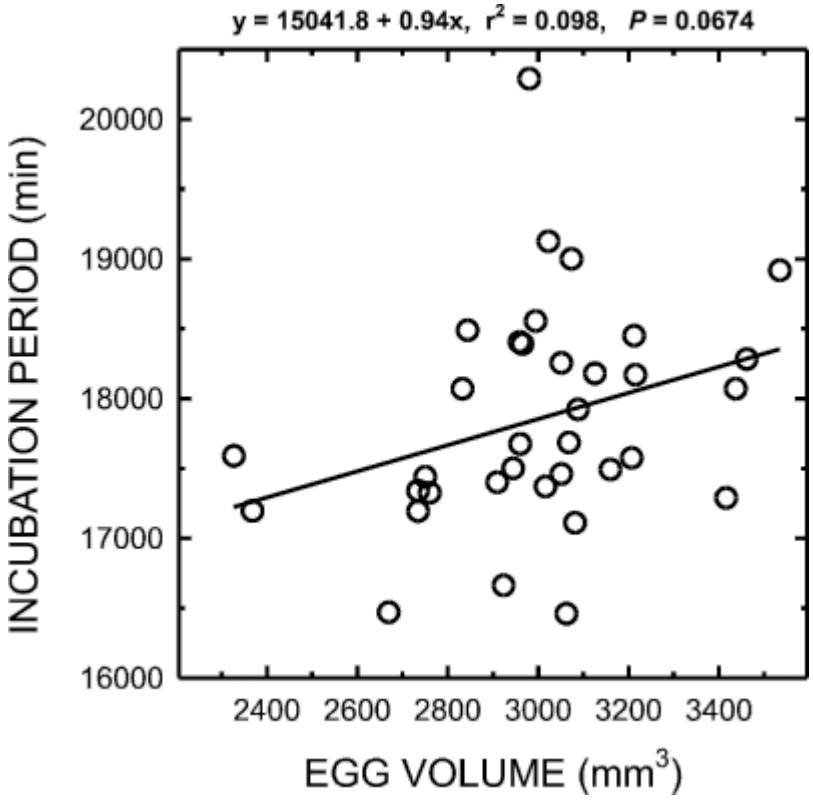

Figure 1. Cowbird incubation period (minutes) as a function of cowbird egg volume (mm^3). 16,500 min = approximately 11.5 days; 18,000 min = 12.5 days.

Discussion

Hatching success of artificially incubated eggs was lower than that observed under natural conditions at Delta Marsh (Yellow Warblers: 94.9% hatching success; Cowbirds: 75.0% hatching success; McMaster unpubl. data). Red-winged Blackbird hatching success was poor. Passerine eggs, including cowbird eggs, have been artificially incubated successfully by several researchers (e.g., Baldwin and Kendeigh 1932; Graber 1955, 3 of 5 cowbird eggs hatched successfully; Wetherbee and Wetherbee 1961; Kattan manuscript; Dufty pers. comm., 14 of 19 cowbird eggs hatched successfully). Baldwin and Kendeigh (1932) suggested the hatching success of passerine eggs could be maximized by mimicking the gradual onset of full incubation behaviour by female passerines; they increased the incubator temperature gradually from 35.0°C to 37.8°C over the first three days of incubation, with a 0.5 hour period of cooling on each of the first 4 days. Despite these procedures, the maximum hatching success obtained by Baldwin and Kendeigh (1932) was only 50%. Other researchers have found certain species of birds (Red-winged Blackbirds, Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) and Northern Cardinals (*Richmondena cardinalis*) in particular) are difficult to incubate successfully in the lab (Daniel 1957; Wetherbee and Wetherbee 1961; Dufty pers. comm.). Red-winged Blackbird eggs develop normally in the incubator up to the 7th day, or if incubated naturally up to the 7th day and then moved to the incubator, but it is

extremely difficult to incubate them through the entire incubation period (Daniel 1957). It may be that fresh passerine eggs are more difficult to incubate successfully than those that have received some natural incubation, however all 5 fresh cowbird eggs incubated by Dufty (pers. comm.) hatched. The temperature and humidity levels in my incubator were virtually identical to those employed by all other researchers for passerine eggs. Therefore, the reason for the poor hatching success in this study is not known.

Cowbird incubation periods in the artificial incubator were much longer than had been predicted. Under natural conditions cowbird eggs hatch either before (45%) or the same day (41%) as Yellow Warbler eggs (McMaster, unpubl. data). Instead of being the first eggs to hatch, cowbirds hatched at approximately the same time as Red-winged Blackbirds, and took significantly more time to hatch than Yellow Warblers. Cowbird incubation periods in the incubator were on average 2.5 days longer than the 10 day incubation period reported by Briskie and Sealy (1990), and were 12.4 hours longer than the mean cowbird incubation period under natural conditions (Briskie and Sealy 1990). However, the long cowbird incubation periods in this study were similar to those obtained by A. Dufty (pers. comm.). Dufty recorded a mean incubation period of 12.6 days for 5 fresh cowbird eggs in an artificial incubator. Other researchers have also incubated cowbird eggs artificially (Graber 1955; Wetherbee and Wetherbee 1961), but their eggs were not freshly laid, so accurate incubation periods were not determined. In contrast to the long incubation periods observed for Brown-headed Cowbirds in the incubator, the mean incubation period obtained by Kattan for Shiny Cowbird eggs in the incubator (11.7 ± 0.5, $n = 11$) was shorter than that observed in House Wren (*Troglodytes aedon*) nests (12.0 ± 0.8, $n = 7$). However, Shiny Cowbird incubation periods obtained by Kattan in the incubator were still significantly longer than the 10.0 day incubation periods observed for this species by Wiley and Wiley (1980). Due to the difference in cowbird incubation periods observed between natural and artificial conditions, one must question whether artificial incubators simulate natural conditions well enough to be used in studies of incubation periods. Evidence to the contrary is found in the fact that host eggs in this study had incubation periods similar to eggs incubated naturally (McMaster unpubl. data), as well as artificially by other researchers. Red-winged Blackbird eggs hatched successfully in artificial incubators have taken 12 - 12.5 days (Daniel 1957; Dufty pers. comm.). Wetherbee and Wetherbee (1961) note the longest incubation period observed for Yellow Warblers was 11.125 days, which they say appeared to be too short to be representative when compared to non-parulides, but they believed the eggs were fresh when collected. Nolan (1978) recorded an incubation period of 11.9 days for a freshly laid Prairie Warbler (*Dendroica discolor*) egg in an incubator.

Potential sources of error which could have influenced the rate of embryonic development in the incubator include; (1) temperature and humidity were optimal for the Red-winged Blackbird and Yellow Warbler eggs, but suboptimal for the cowbird eggs, (2) host eggs received more incubation prior to being placed in the incubator, and (3) cowbird eggs were in areas of the incubator where temperature gradients resulted in less rapid cowbird development. Neither temperature or humidity were likely suboptimal for cowbirds, given they had similar hatching success to Yellow Warblers, and much greater hatching success than Red-winged Blackbirds. Indeed, given that cowbirds are generalist brood parasites whose eggs are laid in many species of birds nests (over 200 species, Payne 1977), one might expect cowbird eggs to be more tolerant to variable incubation temperature and humidity than other bird species. Groebbels and Mobert (1930) suggest embryos of the brood parasitic Cuckoo (*Cuculus canorus*) are more resistant to chilling than host embryos. Host eggs are unlikely to have received more incubation prior to collection than cowbird eggs, as only eggs known to be freshly laid were used in this study. Yellow Warbler females spend little time on the nest on the first and second days of egg-laying (McMaster, unpubl. data), so eggs likely received little incubation before being collected. Fans were installed in the incubator with the express purpose of minimizing thermal gradients. Even if a small thermal gradient did exist in the incubator, because the eggs of all three species were randomly distributed within it, cowbird incubation periods were unlikely to have been influenced to a greater extent than eggs of the other species.

While the increase in cowbird incubation period with increasing egg volume approached significance, it is clear that much variation in incubation period exists between eggs of different volumes. Egg mass may be a better predictor of incubation period than egg volume. Kattan used egg mass rather than volume to predict Shiny Cowbird incubation periods, and although he found incubation period was significantly correlated with egg mass, egg mass only explained 44% of the variation in incubation period. It is possible that cowbird incubation periods vary between females, however the maternity of cowbird eggs was not determined in this study.

Cowbird eggs incubated artificially in 1994 had longer incubation periods than under natural conditions, whereas the incubation periods of two host species did not differ from those under natural conditions. Why cowbird egg response to artificial incubaiton differed from that of host eggs is not known. Perhaps cowbird eggs require contact with other eggs for normal incubation. This possibility will be tested in 1995 by comparing the incubation periods of cowbird eggs incubated artificially in contact with clutches of host eggs, with those of cowbird eggs incubated individually.

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The impact of invertebrate and vertebrate predation on littoral zooplankton in a wetland ecosystem

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Introduction

The importance of predation by planktivorous fish has been demonstrated to be influential in the top-down control of zooplankton communities in both the pelagic and littoral zones of freshwater ponds and lakes (Doolittle 1982; Pont *et al.* 1991; Diehl 1992). Within the littoral zone, submersed vegetation affords zooplankton protection from fish predation by providing a refugium (Straskraba 1965; Crowder and Cooper 1982). Although fish predation may become more limited within the littoral zone, the littoral zooplankton will be impacted also by invertebrate predation pressure (Goulden 1971; Daggett and Davis 1974). Thus, when investigating top-down control of a zooplankton community in a marsh system which consists largely of littoral zone, different sources of predation pressure must be considered.

The littoral zooplankton in freshwater wetlands, such as Delta Marsh, are exposed to predation by invertebrate and vertebrate predators. Among invertebrate predators are the aquatic representatives of different invertebrate groups, primarily larval insects, for example, dragonfly naiads, damselfly naiads, dytiscid larvae, notonectid nymphs, corixid nymphs, ephemeropteran larvae, as well as *Mesostoma* sp., *Chaetogaster* sp., *Hydra* sp., and water mites. Vertebrate predators include salamanders, e.g., *Ambystoma tigrinum*, planktivorous fish, e.g., fathead minnow, spottail shiner, and five- and ninespine stickleback, piscivorous fish, e.g., northern pike and yellow perch, and detritivorous/omnivorous fish, e.g., carp and black bullhead (Schneider 1983).

Planktivorous fish are primarily visual predators which tend to feed in a *size-selective* fashion, i.e. they selectively remove large individual zooplankton when foraging, allowing the small zooplankton which escape predation to become the dominants (Brooks and Dodson 1965; Hall *et al.* 1976). Invertebrate predators include both tactile and visual predators, with very different feeding strategies in comparison to fish. Predation by invertebrates has been shown to be sufficient to eliminate smaller zooplankton species because they are easier to capture and ingest, thus being *size-limited* or size-selective in a direction opposite to that achieved by fish predation (Dodson 1974; Williamson 1987).

The purpose of this study was to investigate the effects of differential predation by planktivorous fish species and invertebrates on the species richness, composition, diversity, and size structure of the littoral zooplankton community (Cladocera, Copepoda, Rotifera) over the open-water season in two contrasting areas of the Delta Marsh. In Crescent Pond (CP), a fishless location, the zooplankton community is exposed to invertebrate predation, whereas in Blind Channel (BC), with numerous fish species, both vertebrate and invertebrate predators are abundant. We considered the hypothesis that top-down control via size-selective predation is of primary importance for determining the food-web constituents in these two distinct study areas.

Methods

Study Sites

Crescent Pond is a small, self-contained pond with no direct connection to Lake Manitoba. Blind Channel, however, is a long, meandering channel with indirect exchange of water with the lake via Cram Creek. The position of Crescent Pond in Delta Marsh offers it some protection from the effects of wind. The more exposed position of Blind Channel results in a greater amount of wind-induced turbidity. An additional source of turbidity in Blind Channel is the activity of the detrivorous/omnivorous fish which feed using their snouts to

disturb the top layer of sediment, resuspending it in the process. The lack of turbidity in Crescent Pond provides the submersed vegetation with an increased amount of irradiance, permitting the earlier establishment of aquatic vegetation in Crescent Pond in comparison to Blind Channel. Thus, the water clarity of Crescent Pond is much greater than that for Blind Channel throughout the summer months, resulting in two distinct aquatic habitats.

Three transects were established along the north margin of Crescent Pond and in Blind Channel near the entrance to Canoe Ditch. Each transect consisted of a nearshore site, located at the edge of the *Typha* sp. in <<1 m of water, and an offshore site, located in approximately 1 m of water. Sites along each transect were 5 m apart and transects were 20 m apart. The water depth fluctuated (± 5 cm) throughout the summer in response to varying weather conditions.

Invertebrate Sampling

Sampling of BC and CP was carried out on a weekly basis for 14 consecutive weeks from 24 May to 24 August 1994. The water column was sampled for zooplankton using a transparent acrylic cylinder 50 cm in length and 5.5 cm in diameter. A 4 L volume was then filtered through a conical net with a mesh size of 80 µm. Samples were preserved with formalin and the volume of each was standardized to 20 mL. The water column samples for week 14 for BC were collected through dense macrophyte growth resulting in anomalously high densities of organisms. As this did not accurately represent the true densities in the water column, these samples were not included in the analyses.

Zooplankton were identified to species using various standard references including Pennak (1978), Edmondson (1959), and Smith and Fernando (1978). The Shannon diversity index (H') was used to determine the species diversity for cladocerans found in CP and BC water column samples over the 14-week sampling period.

Most aquatic predators are size-selective so body size reflects prey availability and food consumption potential in predator-prey relationships. Thus, analysis of the size structure of the zooplankton community was carried out. After each water column sample was counted, the total number of organisms in each was determined, and the proportion of each species contributing to 100% was calculated. On the basis of these proportions, length measurements for 100 individuals were obtained using the digitizing program ZOOBENTH. Length of cladocerans was determined from the top of the head to the base of the shell spine (if present) or postero-dorsal angle of the carapace. Length of copepods was determined from the top of the cephalothorax to the base of the caudal rami. Measurements for identified cladoceran and copepod species were taken from weeks 1, 4, 8, 11 and 14 for BC and CP water column samples. The 100 measurements per site per week were pooled to produce a total of 600 lengths from which the length-frequency histograms for the two locations were assembled. By standardizing the size intervals used to construct the histograms we may observe the size-frequency distribution for micro-invertebrates for either location at a particular point in time, observe changes in the size-frequency distribution for either location over time, and observe differences between the two locations at a particular point in time and over time.

Results

Community composition

A total of 20 species of cladocerans was found in CP, but only 18 species were found in BC during the course of the study. In addition, four species of cyclopoid copepod and one species of calanoid copepod were found in both locations throughout the sampling period. One harpacticoid copepod was reported from BC. Rotifers were counted but not identified. The temporal distribution of species and species richness per week is provided for CP and BC in Tables 1 and 2, respectively.

Table 1. The temporal distribution of species and species richness per week for Crescent Pond water column, 1994; results for sites 1 through 6 pooled per week.

	Week													

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
CLADOCERA														
Alona sp.				P		P			P		P	P		
Alonella sp.								P	P	P	P		P	
Bosmina longirostris	P	P	P	P	P	P	P	P		P	P	P	P	P
Camptocercus sp.				P	P	P	P	P	P	P		P	P	P
Ceriodaphnia sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Chydorus sp.1 (sm.)	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Chydorus sp. 2 (lg.)		P	P	P	P	P	P	P	P	P	P	P	P	P
Daphnia magna						P								
Daphnia pulex	P	P	P											
Daphnia rosea				P	P	P	P	P	P	P	P	P	P	P
Diaphanosoma sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Eurycercus sp.				P	P				P					
Graptolebris sp.			P	P						P			P	
Kurzia latissima										P				
Leydigia leydigi									P					
Pleuroxus denticulatus			P	P	P	P	P	P	P	P	P	P	P	P
Pleuroxus procurvus					P	P	P	P	P	P	P	P	P	P
Polyphemus pediculus			P	P	P	P	P	P	P	P	P	P	P	P
Scapholebris sp.						P		P		P	P		P	
Simocephalus vetulus		P	P	P	P	P	P	P	P	P	P	P	P	P
COPEPODA														
Cyclopoida														
Cyclops bicuspidatus thomasi	P	P	P	P	P	P	P	P	P	P	P	P	P	P
M/F	M	M/F	M			M/F	F	M	F	M	M/F	M/F	F	F
Cyclops varicans rubellus							P	P	P	P	P	P	P	P
M/F							M/F	M/F	M	M	M/F	F	M	M/F
Eucyclops agilis				P	P	P	P	P	P	P	P	P	P	P
M/F				M/F	M/F	M/F	M/F	F	M/F	M/F	M/F	M/F	M/F	M/F
Macrocyclops albidus						P	P	P	P	P	P	P	P	P
M/F						F	F	F	M		M/F	M	M/F	M/F
Calanoida														
Diaptomus nudus	P	P	P	P	P	P	P	P	P	P	P	P	P	P
M/F	F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F
ROTIFERA														
Asplanchna sp.	P	P	P	P					P	P	P			
TOTAL SPECIES	8	10	13	17	15	18	16	18	20	21	19	17	19	16

Table 2. The temporal distribution of species and species richness per week for Blind Channel water column, 1994; results for sites 1 through 6 pooled per week.

	Week													
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
CLADOCERA														
Alona sp.			P		P	P	P	P	P	P				P
Bosmina longirostris	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Camptocercus sp.					P		P							
Ceriodaphnia sp.		P	P	P	P	P	P	P	P	P	P	P	P	P
Chydorus sp.1 (sm.)	P	P	P	P	P	P	P	P	P		P	P	P	P
Chydorus sp. 2 (lg.)		P	P		P	P								
Daphnia pulex	P	P												
Daphnia rosea			P	P	P	P	P	P						
Diaphanosoma sp.	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Eurycercus sp.			P	P	P	P	P	P	P					P
Latona sp.														P
Leptodora kindti	P													
Pleuroxus denticulatus	P				P	P	P	P	P	P	P		P	P
Pleuroxus procurvus					P				P	P	P			
Polyphemus pediculus							P		P		P			
Scapholebris sp.								P	P			P		
Simocephalus serrulatus						P		P	P	P	P	P	P	P
Simocephalus vetulus				P		P	P	P	P	P	P		P	P
COPEPODA														
Cyclopoida														
Cyclops bicuspidatus thomasi	P	P	P	P	P	P	P	P	P	P	P	P	P	P
M/F				M	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F	M/F
Cyclops varicans rubellus													P	P
M/F													M/F	M/F
Eucyclops agilis					P									
M/F														
Macrocyclops albidus													P	P
M/F													M	
Calanoida														
Diaptomus nudus	P	P	P	P	P	P	P	P	P	P	P	P	P	P
M/F		M/F		M/F	F	F		M/F	F	M		M/F	M/F	M/F
Harpacticoida			P	P	P	P	P	P	P		P			P
M/F														
ROTIFERA														
Asplanchna sp.	P		P	P	P	P		P	P	P	P	P	P	P
TOTAL SPECIES	9	8	12	11	16	15	14	15	16	11	13	9	12	16

Cladoceran species diversity was similar in both sites (Fig. 1) showing low values early in May, then fluctuating around H' = 1.1 for the remainder of the summer months.

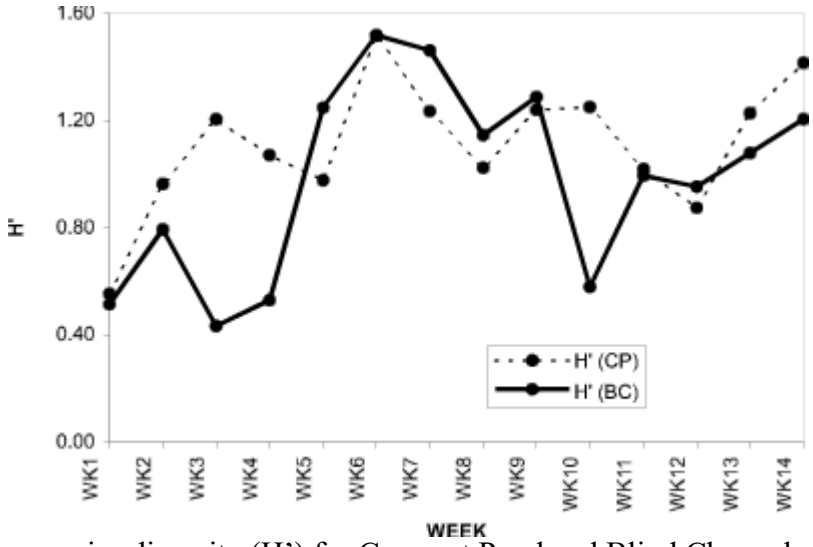

Figure 1. Cladoceran species diversity (H') for Crescent Pond and Blind Channel water column, 1994.

Crescent Pond

Densities for cladocerans, cyclopoid copepods, calanoid copepods and rotifers (*Asplanchna*) (Fig. 2) are shown for the 1994 season. At week 1 of sampling, the cladocerans were at the lowest density compared to the cyclopoids and the calanoids due to the different strategies employed by these groups for overwintering. At week 5, a large cladoceran peak was observed, with a density an order of magnitude higher than at any other time in the season. The cladoceran density declined rapidly after the bloom and remained consistently less than 100 individuals per liter for the remainder of the sampling period.

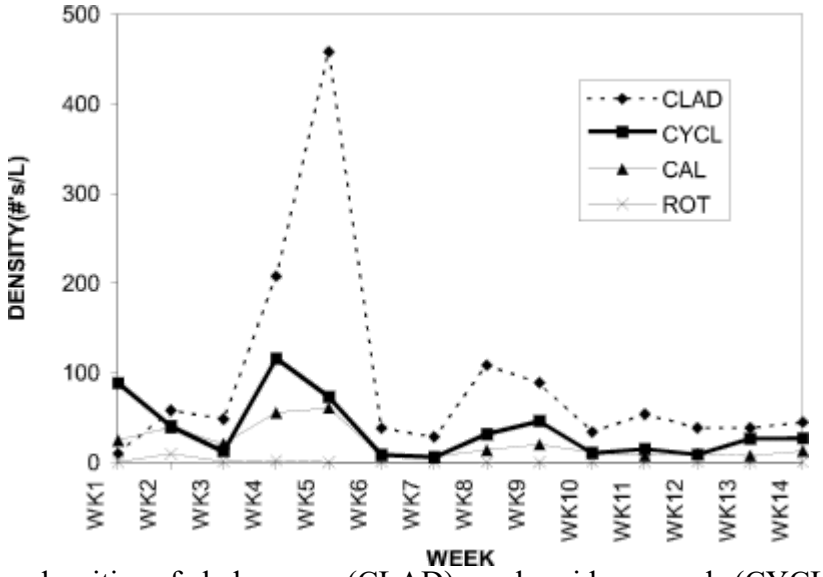

Figure 2. Water column densities of cladocerans (CLAD), cyclopoid copepods (CYCL), calanoid copepods (CAL), and rotifers (ROT) for Crescent Pond, 1994.

Both the cyclopoid and calanoid copepods were at a higher initial density in the spring than the cladocerans, but by week 2 cyclopoids had declined to a density comparable to that of the calanoids, both lower in magnitude than the cladocerans. The cyclopoid and calanoid densities remained consistently low (less than 50 individuals per liter) for the remainder of the sampling period.The stability of the copepod numbers is due in part to their exclusively sexual mode of reproduction which limits the rate of their numerical response to fluctuations in food availability.

The densities for individual cladoceran (Fig. 3) and copepod (Fig. 4) species are shown for the 1994 season. Contributing to the very large cladoceran peak at week 5 were *Ceriodaphnia dubia*, *Daphnia rosea* and *Chydorus* spp. Most cladoceran species attained their highest seasonal densities at week 5. A slight recovery was seen at week 8 with *C. dubia* dominating, but a peak similar to week 5 did not recur. The dominant cyclopoid species was *Diacyclops thomasi*; *Eucyclops agilis* took over as the dominant at week 5 only and was equivalent in numbers to *D. thomasi* at week 6.

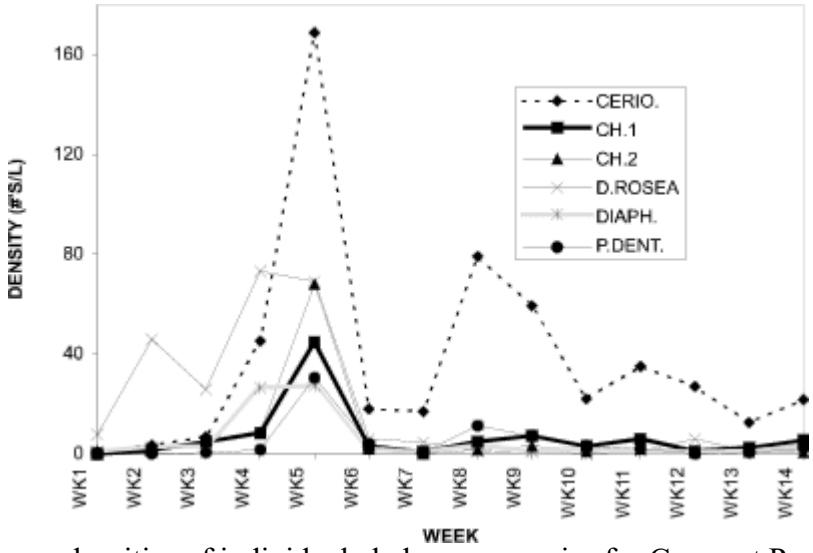

Figure 3. Water column densities of individual cladoceran species for Crescent Pond, 1994; CERIO. = *Ceriodaphnia dubia*, CH.1 = *Chydorus* sp.1, CH.2 = *Chydorus* sp.2, D.ROSEA = *Daphnia rosea*, DIAPH. = *Diaphanosoma birgei*, P.DENT. = *Pleuroxus denticulatus*.

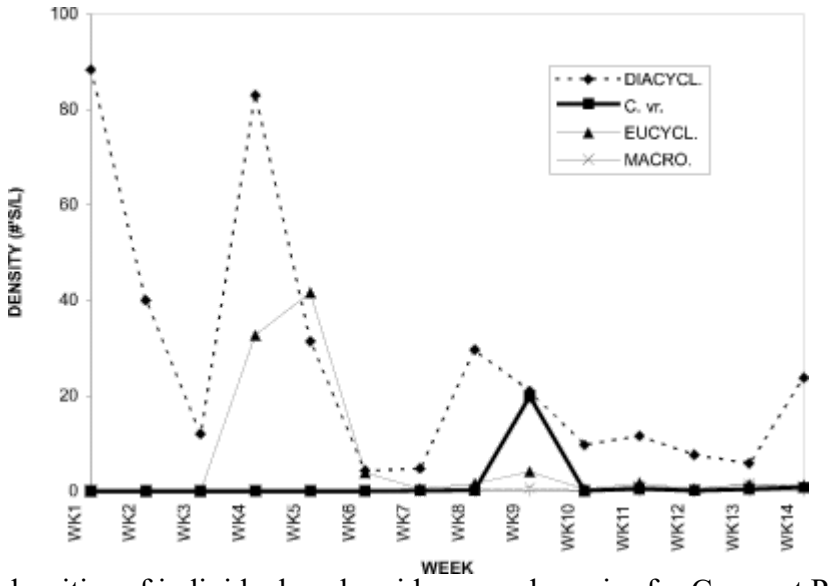

Figure 4. Water column densities of individual cyclopoid copepod species for Crescent Pond, 1994; DIACYCL. = *Diacyclops thomasi*, C. vr. = *Cyclops varicans rubellus*, EUCYCL. = *Eucyclops agilis*, MACRO. = *Macrocyclops albidus*.

Proportions

When the relative proportions of the groups were considered, the cladocerans were consistently dominant (Fig. 5). The proportion of cladocerans was initially lower than copepods (calanoids and cyclopoids) at week 1, but increased rapidly to an averaged plateau of approximately 60-70 % for the season. Therefore, although the density of cladocerans (Fig. 2) declined after the peak at week 5, their relative percentage contribution (Fig. 5) remained high until week 13, dropping to 55 %. Copepods did not contribute more than approximately 30 % of the total until week 13 when they constituted approximately 45 % of the total.

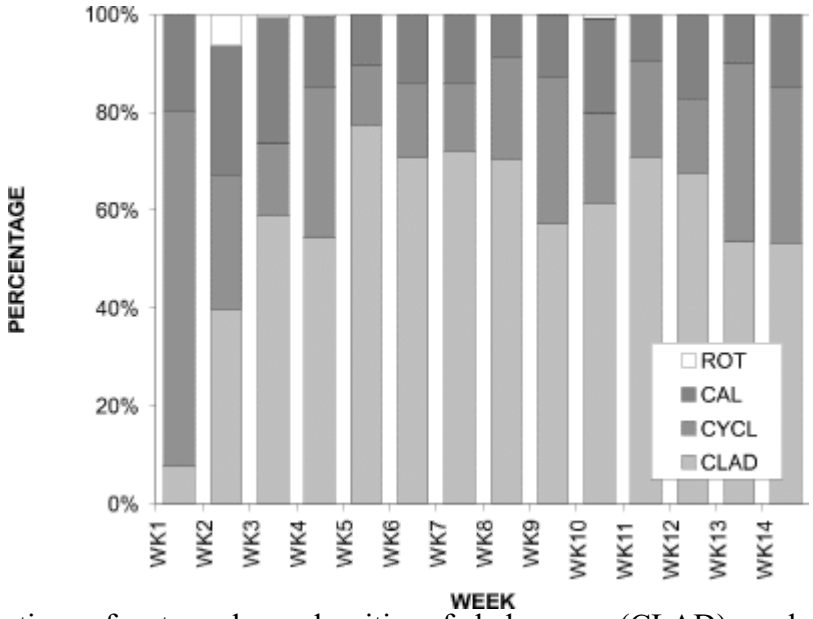

Figure 5. Relative proportions of water column densities of cladocerans (CLAD), cyclopoid copepods (CYCL), calanoid copepods (CAL), and rotifers (ROT) for Crescent Pond, 1994.

Individual Species

When the proportions of six individual cladoceran species contributing to the total for the cladoceran community were considered, two dominant patterns emerged (Fig. 6). At week 1 the dominant cladoceran was *Daphnia rosea* with a proportion of approximately 85 %. As the sampling period progressed, the proportion of *Daphnia rosea* declined. As this was occurring, *Ceriodaphnia dubia* was becoming increasingly dominant. By week 7 the proportion of *Daphnia rosea* had dropped to close to 10 %, while the proportion of *Ceriodaphnia dubia* had increased to approximately 75%. The contribution by the other four species combined never exceeded 40 %.

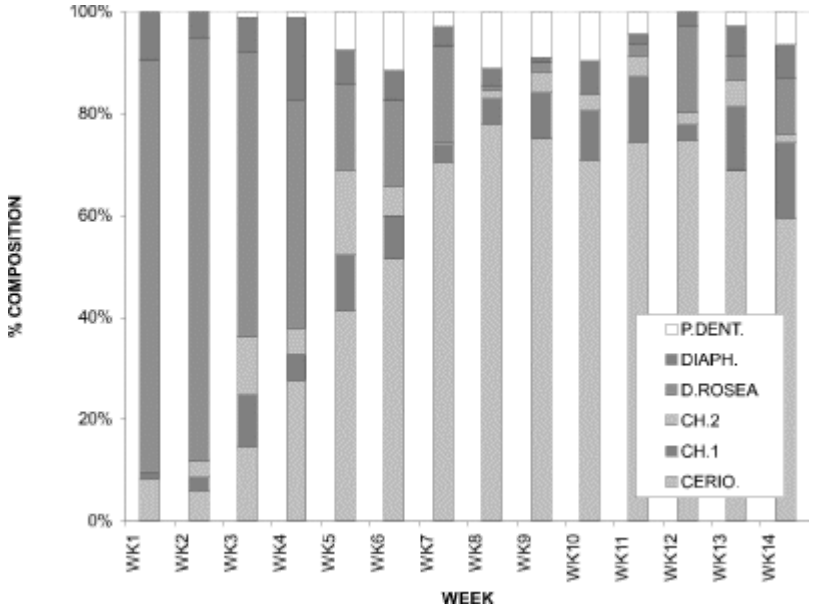

Figure 6. Relative proportions of water column densities of individual cladoceran species for Crescent Pond, 1994; CERIO. = *Ceriodaphnia dubia*, CH.1 = *Chydorus* sp.1, CH.2 = *Chydorus* sp.2, D.ROSEA = *Daphnia rosea*, DIAPH. = *Diaphanosoma birgei*, P.DENT. = *Pleuroxus denticulatus*.

The cyclopoid copepod assemblage in CP was comprised of four species (Fig. 7). When the relative proportions of each were considered for the sampling period, one species in particular stood out as being dominant, *Diacyclops thomasi*. For the first three weeks its proportion was 100 %. The only times it contributed less than 63% was at weeks 5, 6, and 9. At week 5 *Eucyclops agilis* had a proportion of 58 % and was the dominant species. *D. thomasi* and *E. agilis* contributed 53 % and 46 %, respectively, with 1 % being attributable to

Macrocyclops albidus, at week 6. The species dominating at week 9 included *Cyclops varicans rubellus* (42 %), along with *D. thomasi* (48 %); contributing the remaining 10 % are *E. agilis* (8 %) and *M. albidus* (2 %). During the intervening weeks of 7 and 8, and 10 through 14, *D. thomasi* was dominant.

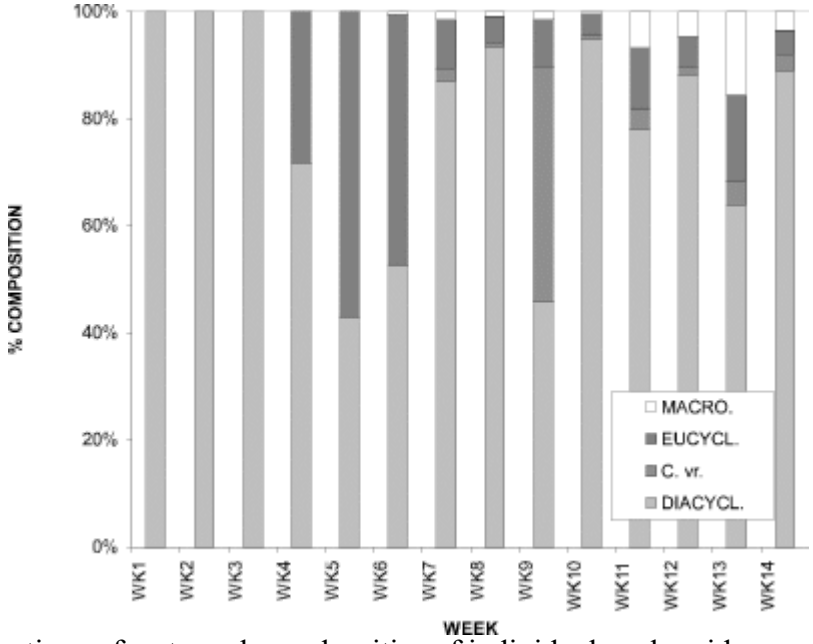

Figure 7. Relative proportions of water column densities of individual cyclopoid copepod species for Crescent Pond, 1994; DIACYCL. = *Diacyclops thomasi*, C. vr. = *Cyclops varicans rubellus*, EUCYCL. = *Eucyclops agilis*, MACRO. = *Macrocyclops albidus*.

Size-frequency Histograms

At week 1 (24 May) (Fig. 8), the histogram peak of 450 µm corresponded to cyclopoid copepods with cladoceran species making a minor contribution. Measurements of calanoid copepods skewed the distribution toward larger-sized organisms. In week 4 (Fig. 9), however, the predominant contributers were now cladoceran species throughout the size range. Cyclopoids again comprised a peak at 450 µm and calanoids at 1200 µm. In addition to calanoids, larger cladocerans (e.g., *Simocephalus vetulus*) were responsible for the histogram being skewed in the direction of larger-sized organisms. The peak at week 8 (13 July) (Fig. 10) still corresponded to cladoceran species, but their modal size had been reduced to 300 µm. Cyclopoids again formed the modal size at 450 µm and calanoids peaked at 1100 µm. By week 11 (3 August) (Fig. 11), the histogram had become more bimodal with peaks of predominantly smaller cladocerans at 450 µm and calanoid copepods and larger cladoceran species occurring at 1000 µm. A more distinct bimodal distribution was observed at week 14 (24 August) (Fig. 12) with a broad higher frequency peak at 450 µm of cladocerans and cyclopoids and a second lower frequency peak at 1100 µm of calanoids/larger-sized cladocerans. The size-distribution for CP was consistently bimodal, with cyclopoids, *Ceriodaphnia dubia,* and other cladocerans at a peak of 400-500 µm, and calanoids, and larger cladoceran species (e.g., *Daphnia rosea* and *Simocephalus vetulus*) at a peak of 1100 µm.

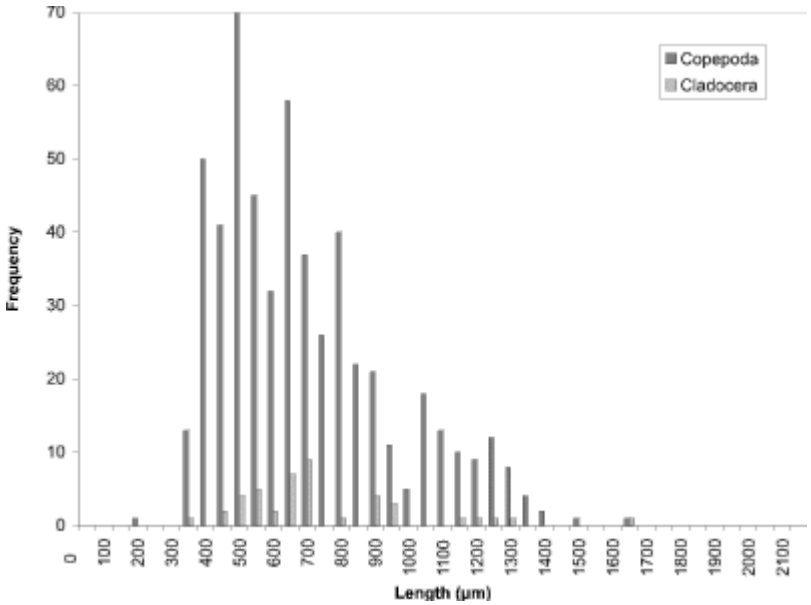

Figure 8. Size-frequency histogram of length measurements of Copepoda and Cladocera for Cresent Pond water column, May 24 1994 (Week 1).

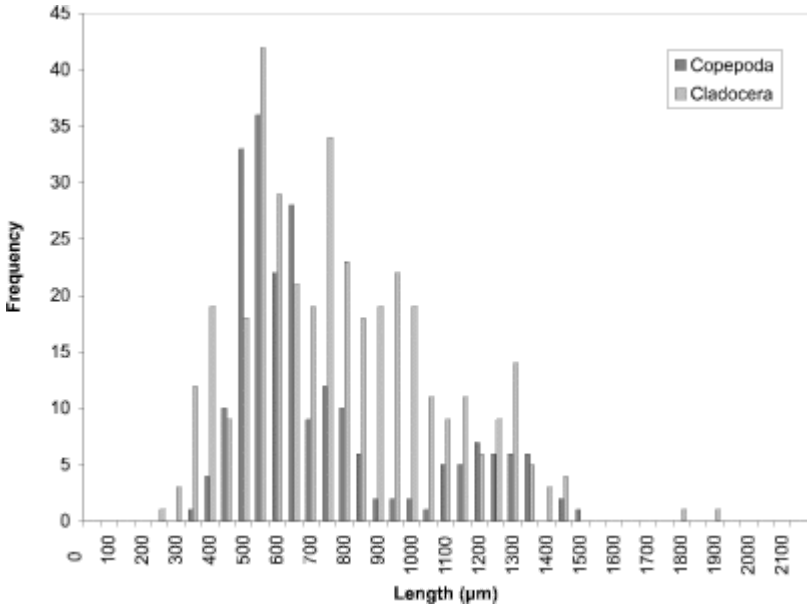

Figure 9. Size-frequency histogram of length measurements of Copepoda and Cladocera for Crescent Pond water column, June 16 1994 (Week 4).

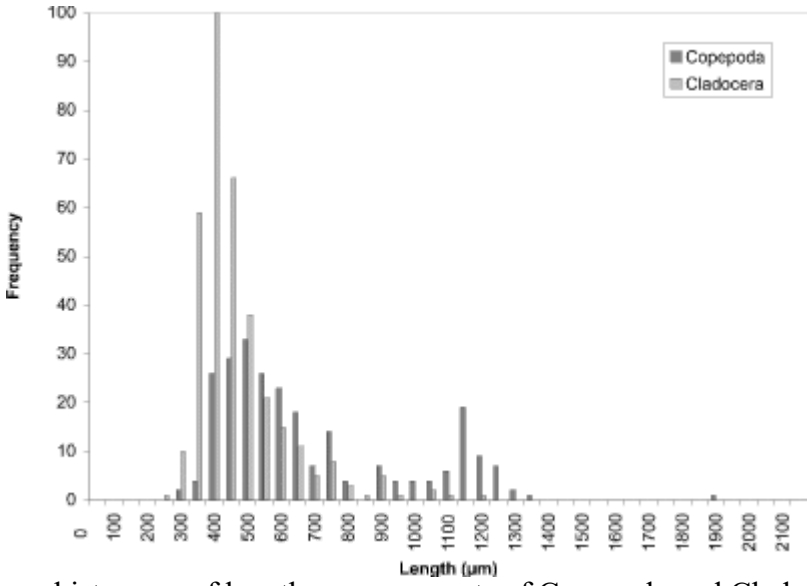

Figure 10. Size-frequency histogram of length measurements of Copepoda and Cladocera for Crescent Pond water column, July 13 1994 (Week 8).

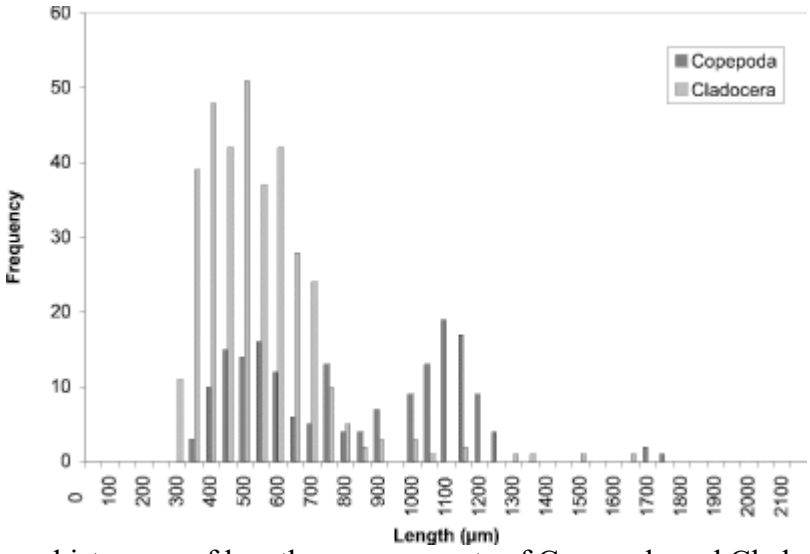

Figure 11. Size-frequency histogram of length measurements of Copepoda and Cladocera for Crescent Pond water column, August 3 1994 (Week 11).

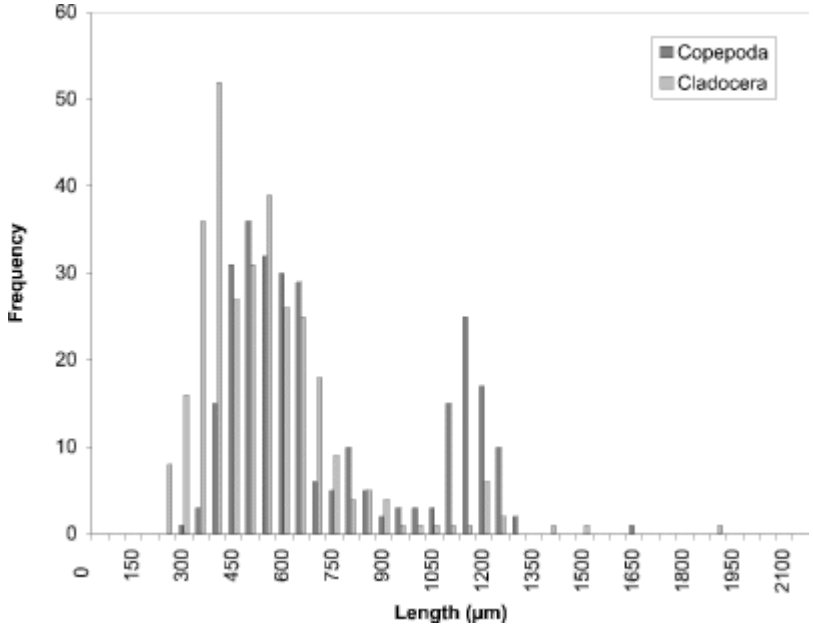

Figure 12. Size-frequency histogram of length measurements of Copepoda and Cladocera for Crescent Pond water column, August 24 1994 (Week 14).

Blind Channel

Figure 13 presents the changes in density (#/L) for the cladoceran, cyclopoid, calanoid and rotifer groups considered in BC. In contrast to CP (Fig. 2), the planktonic rotifer species *Asplanchna* contributed substantially to the total density of micro-invertebrates counted.

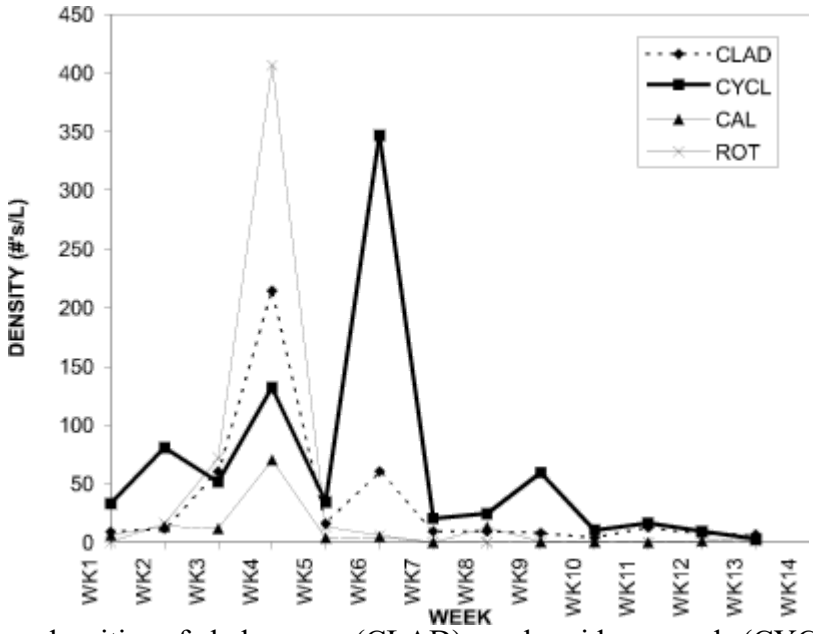

Figure 13. Water column densities of cladocerans (CLAD), cyclopoid copepods (CYCL), calanoid copepods (CAL), and rotifers (ROT) for Blind Channel, 1994.

At week 1 the cladocerans were at a very low density, but their numbers increased steadily towards a peak at week 4. A second smaller peak at week 6 was observed before the cladoceran numbers fell and remained at a low density (less than 20 individuals per liter) for the remainder of the sampling period. Aside from the peak at week 4, cladoceran numbers remained below those for the cyclopoid copepods for the entire sampling period. This is the opposite of the situation observed in the cladoceran-dominated CP.

A similar trend to the cladocerans was seen for the rotifers. From a very low density at week 1, the rotifer *Asplanchna* sp. increased to a very large peak at week 4. Both groups reproduce parthenogenetically/asexually

and have short generation times, which may contribute to the similar pattern observed. Since *Asplanchna* sp. is a predatory rotifer feeding on other rotifers, planktonic crustaceans and colonial algae, it is affected by the availability of different food sources than the cladocerans. However, the reproductive rates of both *Asplanchna* sp. and the cladocerans are related to the quality and abundance of food, in addition to water temperature.

At week 1 the cyclopoid copepods were the most dense group, with the calanoid copepods being amongst the lowest. The cyclopoid group showed three successively higher peaks at 2-week intervals from week 2 to week 6, then declined to stable densities less than 50 individuals per liter for the rest of the summer. The numbers of calanoid copepods remained low and steady (less than 10 individuals per liter) other than a slight peak at week 4.

The cladoceran peak observed at week 4, with density two orders of magnitude higher than at any other time in the season, consisted overwhelmingly of *Bosmina longirostris* (Fig. 14). *Ceriodaphnia*, *Daphnia*, and *Chydorus*, species involved in the cladoceran peak at week 5 in CP (Fig. 3), are relatively large when compared to the smaller *Bosmina longirostris* forming the BC peak at week 4. A second minor peak of *Diaphanosoma birgei* and *Ceriodaphnia dubia* was observed at week 6 in BC.

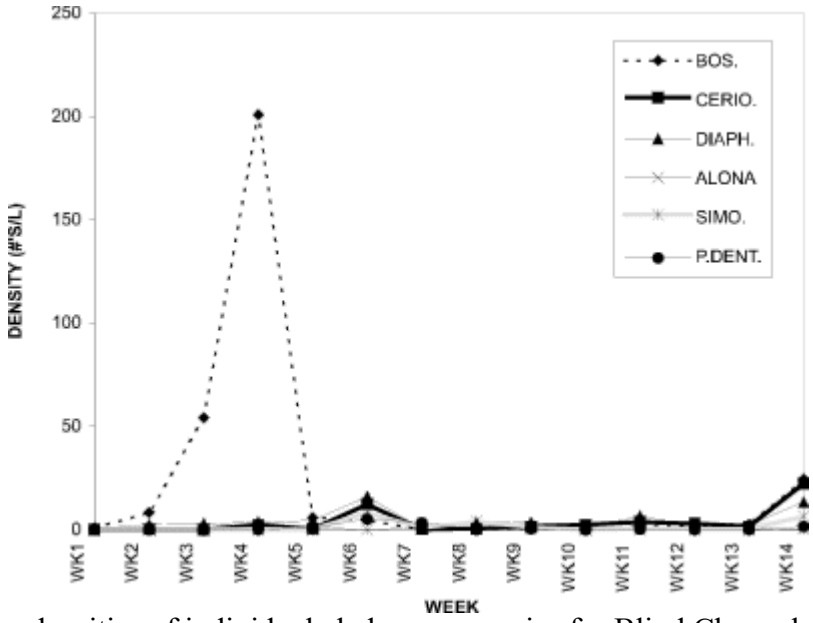

Figure 14. Water column densities of individual cladoceran species for Blind Channel, 1994; BOS. = *Bosmina longirostris*, CERIO. = *Ceriodaphnia dubia*, DIAPH. = *Diaphanosoma birgei*, ALONA = *Alona* spp., SIMO. = *Simocephalus* spp., P.DENT. = *Pleuroxus denticulatus*.

The dominant cyclopoid in BC was *D. thomasi*, a carnivorous species (Fig. 15) which preys on other micro-crustaceans, dipteran larvae and oligochaetes (Wetzel 1983). Other cyclopoid copepods and calanoids were present at very low densities. Except for the *Asplanchna* sp. and *Bosmina longirostris* peaks at week 4 (Figs. 13, 14), *D. thomasi* was the dominant microcrustacean in BC for the entire sampling period.

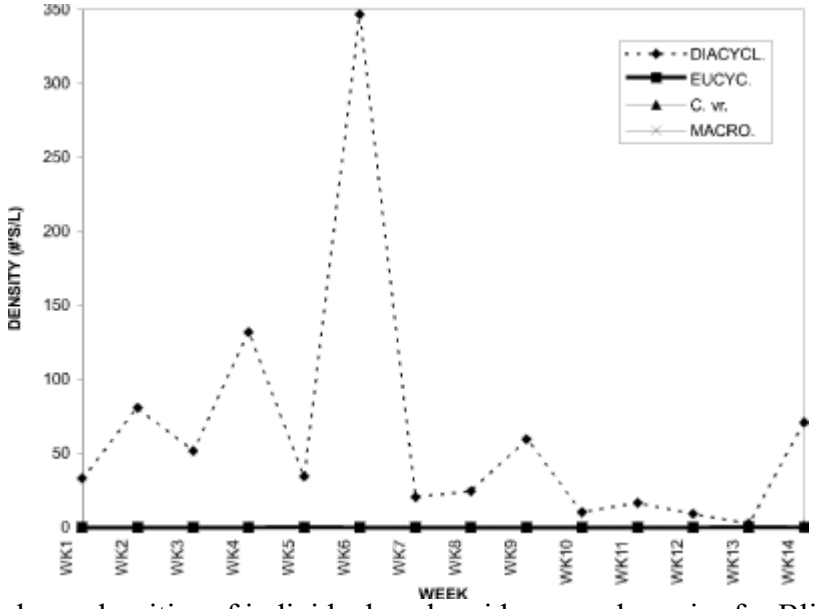

Figure 15. Water column densities of individual cyclopoid copepod species for Blind Channel, 1994; DIACYCL. = *Diacyclops thomasi*, EUCYCL. = *Eucyclops agilis*, C. vr. = *Cyclops varicans rubellus*, MACRO. = *Macrocyclops albidus*.

Proportions

In contrast to CP where the cladocerans constituted a major proportion of organisms, in BC they made up no more than approximately 35 % of the community until week 11, when their percent contribution rose to nearly 45 % (Fig. 16). A peak of close to 50 % was seen at week 13, however this higher percent contribution may be misleading as the cladoceran density and densities of all microinvertebrates at week 13 (Fig. 13) were very low. Similarly, the peaks in cladoceran density (Fig.13) at weeks 4 and 6 were not reflected in their percent contribution (Fig.16), as the cladocerans contributed only approximately 35 % at week 4 and 15 % at week 6. This may be due in part to the very large coincident peaks in rotifer (at week 4) and cyclopoid (at week 6) densities (Fig. 13).

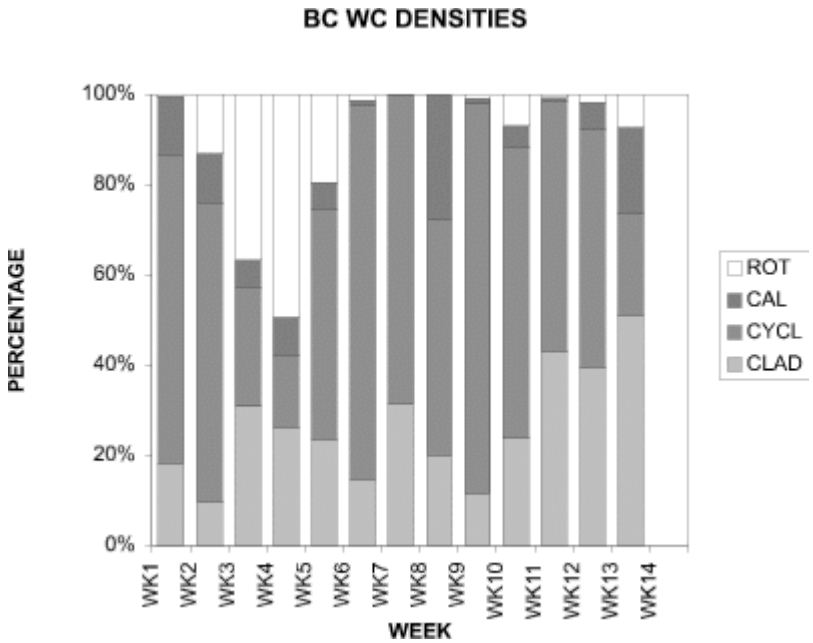

Figure 16. Relative proportions of water column densities of cladocerans (CLAD), cyclopoid copepods (CYCL), calanoid copepods (CAL), and rotifers (ROT) for Blind Channel, 1994.

The percent contribution of *Asplanchna* sp. (Fig.16) followed the same pattern as its density (Fig.13). The large peak in rotifer density in at week 4 corresponded to the large percent contribution by the rotifers on the same

date. However, after this peak, the percentage of rotifers declined to a relatively negligible amount for the remainder of the sampling period.

Of the groups considered, the percent contribution of the cyclopoid copepods to the total was the greatest. The percent contribution by cyclopoids at week 1 was comparable in both CP and BC (Figs. 5 and 16); however, this similarity ceased at week 2 when the percentage of cyclopoids in CP declined significantly. Except for weeks 3, 4 and 13, their percentage in BC was close to 60 % or greater of the total. Their peak in density at week 4 (Fig.13) corresponded to their lowest percent contribution of approximately 15 % (Fig.16). This artifact was due in part to the exceptionally high density of the rotifer *Asplanchna* sp. (Fig.13). The calanoid copepods made a significant contribution to the percentage of organisms in weeks 8 and 13 only, otherwise their percent composition ranged from approximately 2-7 %. When compared to CP, the calanoids of BC fluctuated in percentage to a greater degree; for example, at week 7 (Fig. 16) the calanoids were negligible while the next week their contribution increased to approximately 25%.

Individual Species

Bosmina longirostris increased in proportion from 62 % at week 1 to its peak at week 4 when it comprised 97 % of the six dominant cladoceran species considered in BC (Fig. 17). After week 4 its contribution declined to a low of 3 % at week 7, then gradually increased again to more than 39 % (week 13). *Diaphanosoma birgei* was consistently present, being dominant at week 6 (35 %), 9 (52 %), and 11 (52 %). Other species dominating at particular weeks were *Pleuroxus denticulatus* at week 7 (59 %), *Simocephalus* spp. at week 8 (45 %), and *Ceriodaphnia dubia* at week 10 (75 %). Therefore, following the early bloom of *Bosmina longirostris*, the cladoceran community in Blind Channel consisted of a more balanced mix of species, with densities and dominance of individual species fluctuating throughout the season. This was in contrast with the pattern in Crescent Pond (Fig. 6) where the early season cladoceran community was clearly dominated by *Daphnia rosea*, and the remainder of the season by *Ceriodaphnia dubia*.

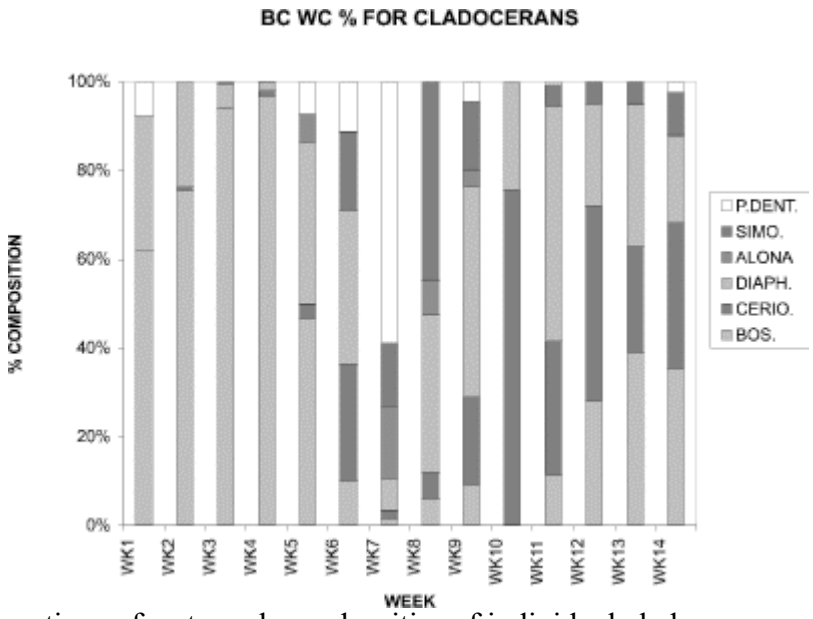

Figure 17. Relative proportions of water column densities of individual cladoceran species for Blind Channel, 1994; P.DENT. = *Pleuroxus denticulatus*, SIMO. = *Simocephalus* spp., ALONA = *Alona* spp., DIAPH. = *Diaphanosoma birgei*, CERIO. = *Ceriodaphnia dubia*, BOS. = *Bosmina longirostris*.

D. thomasi comprised 100% of the copepods from week 1 to week 12 (Fig. 18). At week 13, its proportion was 94 %, with the other 6 % being comprised of *Eucyclops agilis* (4 %) and *Macrocyclops albidus* (2 %). *Cyclops varicans rubellus* contributed only 1 % at week 14, with the remainder being *D. thomasi*.

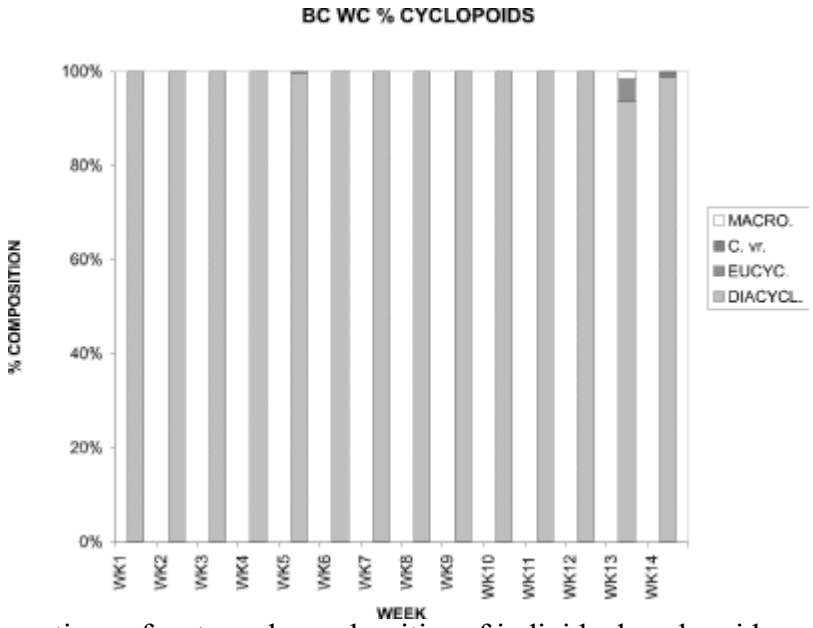

Figure 18. Relative proportions of water column densities of individual cyclopoid copepod species for Blind Channel, 1994; MACRO. = *Macrocyclops albidus*, C. vr. = *Cyclops varicans rubellus*, EUCYCL. = *Eucyclops agilis*, DIACYCL. = *Diacyclops thomasi*.

Size-frequency Histograms

At week 1 (24 May) (Fig. 19), a peak at 450 µm of cyclopoid copepods was observed. Measurements of calanoid copepods skewed the figure toward larger sized organisms. By week 4 (16 June) (Fig. 20) there had been a noticeable shift towards smaller organisms to peak at 250 µm. This peak corresponded to two groups, one comprised of cyclopoids, the second comprised of small cladocerans (e.g., *Bosmina longirostris*) and the rotifer *Asplanchna* sp. Calanoids still contributed to the few larger size measurements. A distinctly bimodal histogram was seen at week 8 (13 July) (Fig. 21) with a predominantly cyclopoid peak at 400 µm and a calanoid peak at 1150 µm. The bimodal size-distribution had disappeared by week 11 (3 August) (Fig. 22), being replaced by a single broad peak at 400 µm corresponding to both cladocerans and cyclopoids. The cladoceran portion of the peak was shifted towards smaller sizes, while the cyclopoid portion was shifted towards slightly larger sizes. Calanoids were still the predominant contributers to the larger sized measurements. The distribution observed at week 14 (24 August) (Fig. 23) was the result of slightly offset cladoceran (250 µm) and cyclopoid (450 µm) peaks. Except for week 8, the size distribution in BC was generally unimodal, with substantially fewer large zooplankters represented than observed in CP.

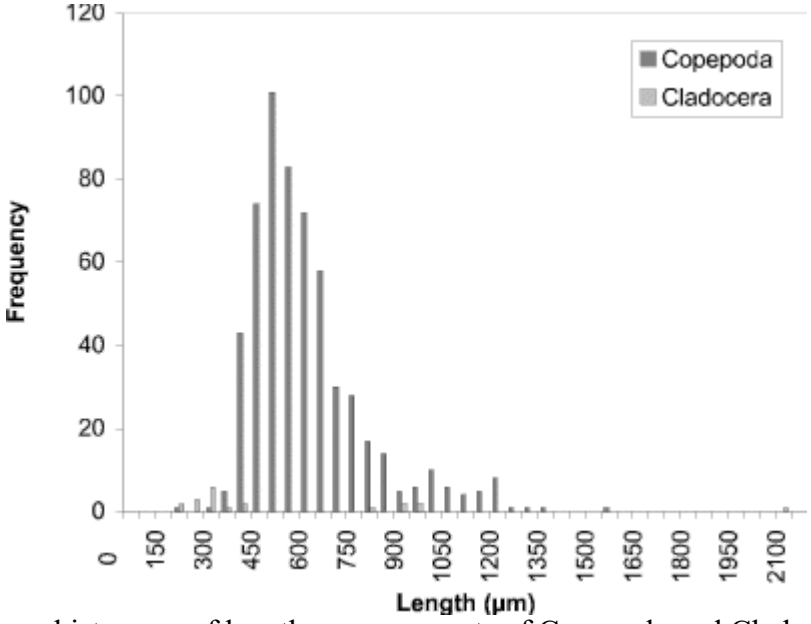

Figure 19. Size-frequency histogram of length measurements of Copepoda and Cladocera for Blind Channel water column, May 24 1994 (Week 1).

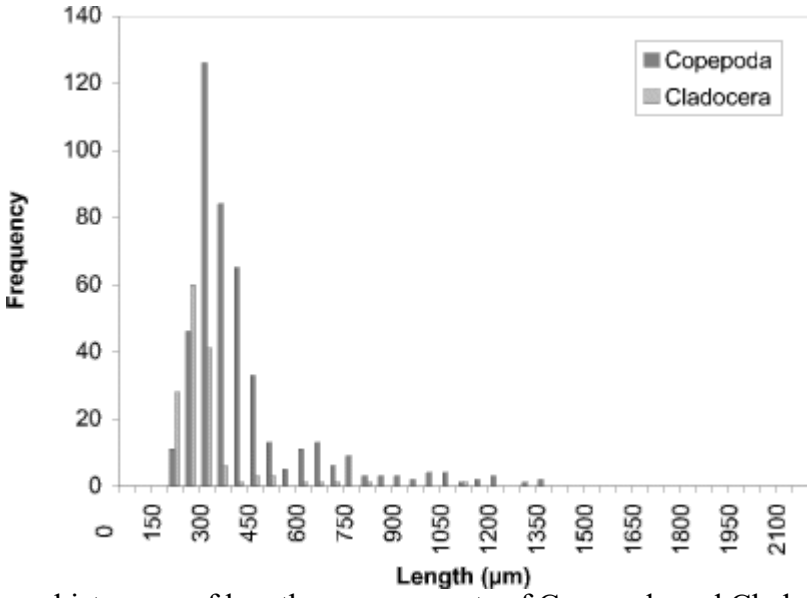

Figure 20. Size-frequency histogram of length measurements of Copepoda and Cladocera for Blind Channel water column, June 16 1994 (Week 4).

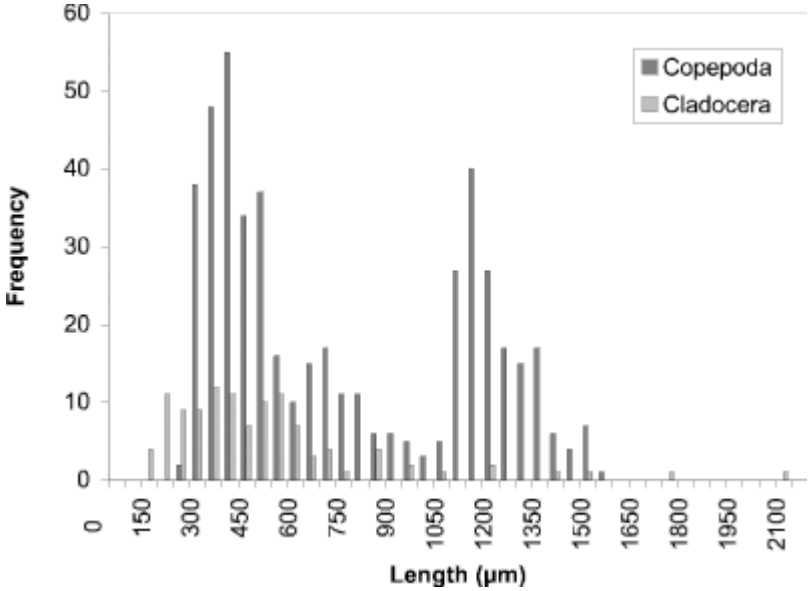

Figure 21. Size-frequency histogram of length measurements of Copepoda and Cladocera for Blind Channel water column, July 13 1994 (Week 8).

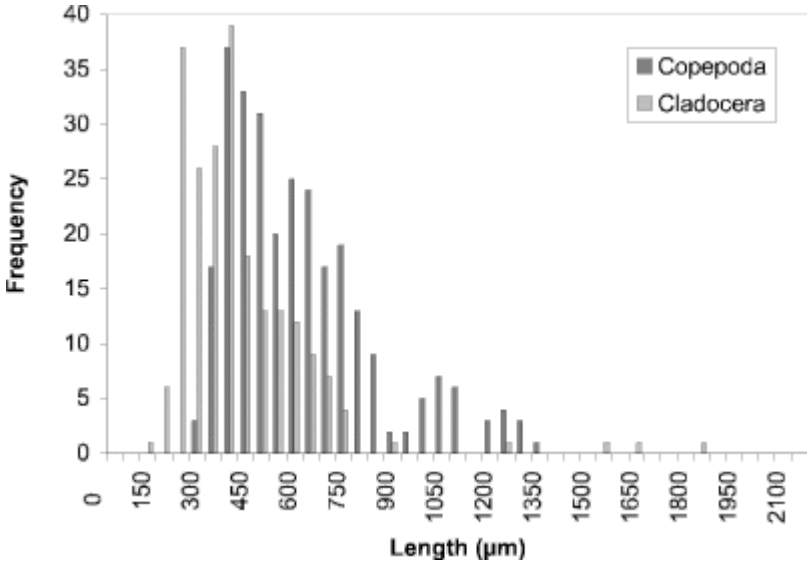

Figure 22. Size-frequency histogram of length measurements of Copepoda and Cladocera for Blind Channel water column, August 3 1994 (Week 11).

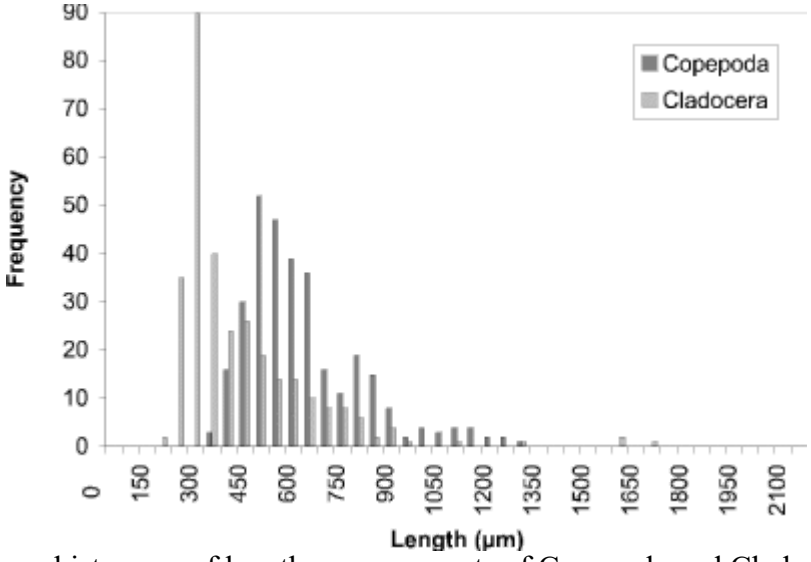

Figure 23. Size-frequency histogram of length measurements of Copepoda and Cladocera for Blind Channel

water column, August 24 1994 (Week 14).

Discussion

The visual differences between Blind Channel (turbid, sparse macrophytes, and abundant and diverse fish community) and Crescent Pond (transparent, abundant and diverse macrophytes, and no fish) are striking, and consequently one would expect to see very different invertebrate communities in the two study areas. Key differences in zooplankton abundance between the two areas were observed throughout the sampling period. In addition, size structure of the zooplankton community exhibited two distinct patterns as a result of exposure to different types of predation pressure. However, zooplankton community composition in these two distinct habitats of the Delta Marsh became more similar as the summer progressed. The total microcrustacean species pool represented in the two sites in Delta Marsh overlaps considerably with the previously known regional species pool (Smith 1968).

According to size-selective predation theory, larger zooplankton (e.g., *Daphnia* spp.) should benefit in a waterbody lacking planktivorous fish because these zooplankters are the preferred food of the fish and would be fed on selectively over smaller zooplankton. By removing this particular predation pressure, the abundance of herbivorous zooplankton species present, especially larger species which feed more efficiently than smaller herbivores, would be expected to be higher than in a system with fish present (Hall *et al.* 1976). In our study, the cladoceran component of the zooplankton community responded most strongly to the differential predation pressure. The abundance of cladocerans (including large *Simocephalus* and *Daphnia*) was considerably higher in fishless CP than in BC throughout the season, whereas copepod abundances for the latter half of the season especially were similar at both sites. Cladocerans are typically the preferred prey of planktivorous fish, showing less predator avoidance behaviour than copepods (Drenner *et al.* 1978).

Despite the markedly higher cladoceran abundances in fishless CP, cladoceran species richness and diversity were similar in the two sites throughout the summer. Cladoceran species composition differed between the two areas, with the occurrence of geographically and numerically rare species being limited to Crescent Pond. The occurrence of these rare cladoceran species in Crescent Pond affected the species diversity index. As species diversity is a combined measure of both species richness and evenness in the distribution of the number of individuals per species, the presence of several sparsely represented species caused the value calculated for H’ to be lower than expected when species richness alone is considered.

Competitive interactions in a speciose zooplankton community may also be involved in the interpretation of the temporal pattern of diversity values in Crescent Pond and Blind Channel if the environmental parameters (physical, chemical, and biotic) that undergo constant temporal variations are considered. Continuously changing environmental parameters (e.g., temperature, turbidity, and food availability) may produce a habitat in which no one invertebrate species maintains a competitive advantage for a sufficient period of time to become the dominant species permanently (Hutchinson 1961; Hall *et al.* 1970). Environmental conditions in Blind Channel often exhibit rapid temporal changes, resulting in greater habitat variability when compared to Crescent Pond. Consequently, there was temporal instability in the zooplankton community with the dominance of any one cladoceran species in Blind Channel switching frequently, in contrast to the seasonal shift in dominance of cladoceran species in Crescent Pond, with *Daphnia rosea* dominant for the first half of the summer and *Ceriodaphnia dubia* dominant for the last half. Lynch (1978) explained a similar *Daphnia*-*Ceriodaphnia* species substitution in a fishless pond by seasonal changes in competitive abilities for a shared algal resource.

Hanson and Riggs (1995) conducted a study in a series of wetlands to examine the potential effects of fish predation on wetland invertebrates. They determined that the presence of fathead minnows in particular had an inverse relationship with indices of abundance, biomass and taxon richness of crustaceans and insects. While their observation of elevated abundance (and indirectly biomass) of invertebrates in the absence of planktivorous fish paralleled that found in our study, the pattern for taxon richness was in contrast with our results. However, Hanson and Riggs (1995) did not take into consideration the indirect effect that reduced vertebrate predation on macroinvertebrate predators (insects) has ultimately on the microinvertebrates (crustaceans), or the direct effect invertebrate predation alone has on zooplankton. In addition, the degree of taxonomic resolution used by Hanson

and Riggs (1995) is not directly comparable to our study. Their placement of taxa into only two groups (i.e. crustaceans and insects) precludes any interpretation of the response of individual species to varying levels of predation pressure and to differential predation by planktivorous fish and invertebrates.

Densities of cladocerans and copepods in the early spring show different patterns due largely to different evolutionary strategies for adapting to a seasonally variable habitat. Cladocerans overwinter as resting eggs in the sediments, while the copepods tend to overwinter as immature copepodite stages in the water column and/or sediments (Pennak 1978). The strategy of the copepods to overwinter as immature copepodites gives them an initial advantage in the spring over the cladocerans. As a result, there is a time lag in the spring until the cladocerans hatch from their resting eggs during which time the copepods dominate the zooplankton community. In Blind Channel, elevated copepod densities continue throughout the summer with the cyclopoid *Diacyclops thomasi* being the dominant zooplankter almost every week, except for a brief bloom of the cladoceran *Bosmina longirostris.* However in Crescent Pond, once the abundance of phytoplankton increases to the extent that sufficient food is available for the asexually reproducing cladoceran populations to expand rapidly, they take over from the copepods as the dominant zooplankters, with *Daphnia rosea* dominant early in the season and *Ceriodaphnia dubia* becoming most abundant as the summer progresses.

Although community analyses are informative, analysis of body size, which ignores behavioural, taxonomic, and trophic characteristics, provides very valuable insights into community response to predation. The size-frequency distributions assembled document the shifts in modal sizes for the zooplankton community over the sampling period. The most consistent difference in size distributions is that CP exhibits a bimodal pattern in contrast to the largely unimodal pattern in BC (except in week 8). The second peak of larger organisms is generally absent from BC. At week 1 the measurements obtained for organisms from both areas show a peak at 450 µm, each corresponding to cyclopoid copepods. By week 4 the histograms appear quite different with the peak for Crescent Pond still occurring at 450 µm, but now corresponding to cladocerans and the peak for Blind Channel shifting to a smaller size. This peak at 250 µm in Blind Channel is composed of the small cladoceran *Bosmina longirostris* and the rotifer *Asplanchna* sp., in addition to the cyclopoids. It may be inferred that selective fish predation on larger zooplankton has shifted the size distribution to smaller-sized organisms in Blind Channel. The dominance of large cladocerans in Crescent Pond is probably attributable to their superior rapid reproductive capabilities when compared to the copepods, the abundance of algal food and the lack of vertebrate predation pressure. The presence of early instar insect larvae selectively feeding on smaller zooplankton may also be contributing to the maintenance of the peak at a larger size.

The modal size of the cladocerans in Crescent Pond declined slightly at week 8 to 300 µm. The predatory insect larvae may now be larger, feeding on larger prey, and thereby releasing the smaller cladocerans from invertebrate predation. A distinctly bimodal size-distribution is seen in Blind Channel in week 8 only with a cyclopoid peak at 400 µm and a calanoid/larger-sized cladoceran peak at 1150 µm. The occurrence of these two peaks may be the result of the activity of primarily invertebrate predators if planktivorous fish abundance is indeed greatly reduced at this time in the season (Schneider 1983), thereby releasing the large zooplankton from predation. Maximum abundances of planktivores occur typically in May and June in Delta Marsh, then benthivores (e.g., bullheads) migrate into the marsh in August (Schneider 1983).

Submersed macrophytes, at peak biomass in Blind Channel at this time, may also provide a refugium for the large zooplankton (Diehl 1992), while superior swimming skills could allow escape by the cyclopoids from the macroinvertebrate predators. Thus, release from fish predation and increased habitat complexity can result in a bimodality of size-classes of zooplankton, similar to that observed throughout the season in fishless CP.

Predation pressure exerted by fish on zooplankton is typically considered to be more significant than that exerted by invertebrate predators (Diehl 1992) especially in pelagic communities. However, predatory invertebrates may play a more substantial role in zooplankton community dynamics in shallow or littoral ecosystems such as wetlands. Our study has shown that the presence of planktivorous fish does exert a strong degree of predation pressure on the zooplankton community, producing a unimodal size distribution. Strong pressure is also exerted by invertebrate predators, but the higher abundance of zooplankton in a waterbody subject to invertebrate predation alone substantiates that vertebrates are more effective predators than invertebrates (Hall *et al.* 1970).

This study has focused attention on the roles of both vertebrate and invertebrate predation in zooplankton dynamics in a wetland. Much more now needs to be known regarding seasonal distribution of these predators, and their dietary preferences in order to fine-tune the food web dynamics.

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