University Field Station (Delta Marsh)

1993 personnel

Group photo

Regular Staff

Director: Gordon G.C. Robinson
Manager: Russell Mead
Office Assistant: Pat Gutoski
Resident Maintenance Person: Dick Convery
Cooks/Housekeepers: Doreen Greening & Shirley Dinwoodie

Summer Assistants

Biological Assistant: David Ingleson
Maintenance Assistant: Mark May
Cook/Housekeeper Assistants: Ardith Hamilton, Brenda Howe & Heidi Mead

Faculty

Dr. Mark Abrahams (Department of Zoology, University of Manitoba)
Dr. Tom Booth (Department of Botany, University of Manitoba)
Dr. James Briskie (Department of Biology, Queen's University)
Dr. Reinhart Brust (Department of Entomology, University of Manitoba)
Dr. H. Lisle Gibbs (Department of Biology, McMaster University)
Dr. Gordon Goldsborough (Department of Botany, Brandon University)
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

Robert Anderson *(Ph.D. candidate*, Department of Entomology, University of Manitoba)
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)
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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)
Krista Copeland (Department of Botany, University of Manitoba)
Victor Fazio (Canadian Wildlife Service, Ohio, USA)
Colleen Flynn (Co-op Workterm, Environmental Science Program, University of Manitoba)
Doug Froese (Department of Zoology, University of Manitoba)
Gloria Goulet (Department of Zoology, University of Manitoba)
David Jones (NSERC summer student, Department of Biology, McMaster University)
Tom Pratt (Department of Zoology, University of Manitoba)
Lisa Zdril (NSERC summer student, Department of Zoology, University of Manitoba)

Director's Report

Gordon G. C. Robinson

1993 was perhaps the most successful year for the University Field Station in recent history. Overall use of the facility was increased by 18% over the previous year and by 40% over the average use during the past eight years. Generated income was the highest in the history of the Station. Before getting into the body of this report, I would like to acknowledge with gratitude the various sources of this success. The administration of the day to day activities of the Station, the maintenance and security of the physical plant and property, the provision of comfortable accommodation and excellent cuisine, and the careful attention to the seemingly increasing masses of paperwork requires a particularly dedicated and flexible staff, and the Field Station is fortunate to have such. I would like to thank them all for their efforts, and I would also like to thank the various family members of staff, whose entirely voluntary participation in the operation of the Field Station is much appreciated. It sometimes seems that we tend to neglect the fact that the Field Station is not an 8:30 to 4:30, five-days-a-week operation. Rather it is a 24 hour-a-day, 365 days-a-year operation; this requires considerable dedication. The support of the University through the Faculty of Science, the Faculty of Science Endowment Fund 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 support of the Friends of the Field Station is also gratefully acknowledged. The first executive of that support organization (Nora Losey, Richard Orlandini, Linda Chartier, Barbara Lindsay, Darlene Chimka, Jorunn Hansen and Terri Roy) is to be congratulated for getting the organization off the ground as an effective self-sustaining fund-raising participatory group. The cooperation of our neighbours at the Portage la Prairie Country Club and the Delta Waterfowl and Wetlands Research Station, the Atmospheric Environment Service of Environment Canada, The Manitoba Department of Natural Resources and the merchants, contractors and interested residents of Portage la Prairie should all be acknowledged with sincere thanks. At the root of our successes are, of course, the Station users - the researchers, the graduate students, the undergraduates, their instructors, the student assistants and the myriad of others who use the Station for one reason or another throughout the year. Of these I would particularly acknowledge the dedication of Spencer Sealy, Gordon Goldsborough, Norman Kenkel, Brenda Hann, Lisle Gibbs, Mark Abrahams, James Briskie, Keith Hobson, Tom Booth, Jack Gee, Maria Zbigniewicz and Isobel Waters. I should also like to thank those who supported the Field Station through monetary gifts, and I gratefully acknowledge the ongoing support of our library by the Stevens and Lindquist families through their additions to the Todd Stevens Memorial Collection. Congratulations are due to Marlene Gifford upon the successful completion of her M.Sc. degree. I sincerely thank Gordon Goldsborough for his editorial work on this report, and indeed for all of his electronic wizardry.

For the body of this report I would like to re-state some of the overall objectives and goals of the Field Station, report the statistics on station use, and provide some analysis of Station activities in the areas of Research, Teaching and Service.

Objectives and Goals

The principle research objective of the Field Station is to facilitate, accommodate and equip field-oriented research projects of senior undergraduates, graduate students and faculty from the University of Manitoba and other institutions. The provision of a supportive data base (consisting of meteorological, water-level and water chemistry information) is a component of this objective. An on-going goal is to stimulate integrated and cooperative research initiatives in the strategically important wetland environment that comprises most of the Field Station property. The promotion and communication of research conducted at the Station is facilitated by the publication of an annual Research Pamphlet and a formal ISSN-numbered Annual Report, but also by hosting an Annual Public Seminar on current Station research. It is clear that the promotion of research at the Station will have to take a more pro-active approach to include the actual generation of at least some funding (from within the University, from Granting Agencies and through the Friends of the Field Station).

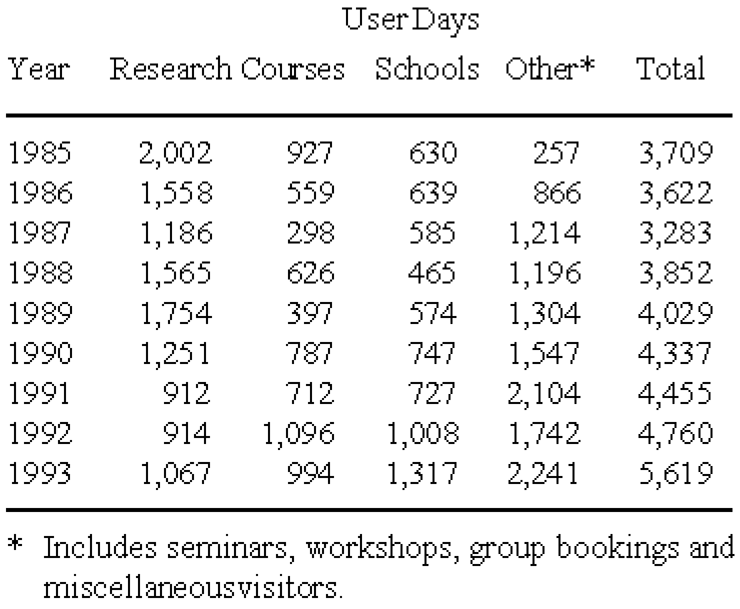
The primary teaching objective is to solicit, encourage and facilitate the presentation of field-oriented credit courses at the Field Station. This is done by simple solicitation of the participation of Departments and coordination through Continuing Education. It is also done by the provision of high quality infrastructural support which includes functional and well equipped teaching laboratories, modern and functional equipment to meet the needs of a variety of courses, annotated and accessible reference collections of local biota, study and library facilities, comfortable accommodation, and support personnel. A related goal is to provide opportunity and some small financial assistance to a small number of young people in the form of "apprenticeships" in field teaching and research methods. An ancillary objective is the provision of a conducive environment for specialized seminars, conferences and workshops for the University of Manitoba, but also for other constituencies.

Service objectives are in the form of outreach activities in four areas: (1) the provision of instructional facilities, staff and formal programs for school classes, (2) the provision of environmentally oriented residential workshops to the community at large, (3) the provision of a public seminar series during the summer months, and (4) the provision of Elderhostel residential courses. An ancillary service-related goal is to offer the Field Station facilities to various "educational" groups at times when the Station is not fully occupied by the above. Whereas this is primarily a fund raising activity to subsidize the above activities, it does at the same time offer a service to the public. The Station also offers the use of its facilities to bona fide members of the organization of Friends of the Field Station.

The ideal balance of the teaching, research and service activities of the Field Station is primarily determined by the seasons. Research and teaching activities are almost exclusively restricted to the period from May 1 to October 31, with most service activities occurring in the remaining six months of the year. The net result of this is that a balance of 25% research, 25% teaching and 50% service would appear to be ideal, and particularly so if the fund-generating aspect of the service component can adequately subsidize the teaching and research functions.

Facility use

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



	User Days				
Year	Research	Courses	Schools	Other*	Total
1985	2,002	927	630	257	3,709
1986	1,558	559	639	866	3,622
1987	1,186	298	585	1,214	3,283
1988	1,565	626	465	1,196	3,852
1989	1,754	397	574	1,304	4,029
1990	1,251	787	747	1,547	4,337
1991	912	712	727	2,104	4,455
1992	914	1,096	1,008	1,742	4,760
1993	1,067	994	1,317	2,241	5,619

* Includes seminars, workshops, group bookings and miscellaneous visitors.

Research

Criteria that can be used to assess the Field Station's research activity are: (1) The number of projects undertaken in a single year, (2) the number of publications that have arisen in a single year from work conducted at the Field Station, (3) The number of theses completed in a single year that have emanated from work conducted at the Field Station, and (4) the user days/year that can be attributed to research activity. Ancillary measures which may also be used are (5) NSERC infrastructural funding, (6) presence/absence of research conferences/workshops in any single year, and (7) the presence/absence of collaborative integrated research undertakings in any year. Good performance would be considered to be numbers greater than the running average for criteria 1-4, and presence of activities numbered 5-7.

The number of projects conducted in the past period was 17 (mean=15); the number of publications was 9 (mean=13); the number of theses completed was 1 (mean=3); and the number of user days associated with research activity was 1,067 (mean=1,374). $25,000 was provided in the form of an NSERC Infrastructure Grant. This was the last installment of a three-year grant. $25,000 per year for each of the next three years was, however, obtained in the most recent NSERC competition. The 12th North American Diatom Symposium was hosted by the Field Station in the early fall of 1993. The symposium was generally considered by the participants to have been the best yet. Although no distinctly collaborative enterprises were undertaken, a considerable effort was expended by Field Station users in the preparation of a re-submission of a Tri-Council Eco-Research proposal, the results of which are as yet unknown.

Although in most categories performance was better than in the previous period it still remains in most categories below an eight year running average. It is difficult to know why this should be, although it is very likely that increased difficulty in acquiring research funds, diminished graduate enrollments and a very low turnover rate of faculty members may all contribute to the situation. One difference between this period and the previous one was that funds were obtained from the Faculty of Science to support three co-operative education work terms for environmental science students at the Field Station. This certainly did permit the commencement of two research projects that would not otherwise have taken place.

Teaching

For the Field Station, assessment can be based on the number of courses offered and the user days associated with teaching each year, with additional assessment being available from specific user evaluation forms.

I suspect that the maximum number of courses that could be accommodated during a single season at the Field Station is six 3CH courses, and a maximum number of user days would be in the order of 2,000. A good performance would be three courses and 1,000 user days.

In 1993 four courses and parts of three others were conducted at the Field Station, generating a total of 994 user days. This represents an increase of one course over the previous year but a decrease of some 9.3% in user days. The number of students registering for field courses was therefore somewhat decreased over the previous year. This may, however, be a single year anomaly for the use (in terms of user days) was 47% greater than the eight year mean for the Station. Nonetheless, under-utilization still prevails to a degree. An encouraging aspect of 1993 was, however, the fact that Continuing Education seemed a great deal more receptive to the concept that "break-even" enrollments in field courses are often unrealistic, and in fact "break-even" enrollments are generally too high for effective field instruction. There does still remain a difficulty in the supply of teaching assistants for field courses. Field courses clearly, by their very nature, require TA's for lesser numbers of students than do other courses, but as it presently stands the enrollments in field courses do not generally meet the universal formula for the provision of TA's.

In 1993-94 some significant strides were made in the provision of equipment. This was made possible by capital equipment funds from the Faculty and also from the Endowment Fund. The Field Station now has a rather well equipped Macintosh/IBM microcomputer facility, enhanced night-vision equipment for the study of nocturnal behavior and global positioning systems for the exact location of sites. Two inshore boats with motors were purchased and the bicycle fleet will be increased by the beginning of the next season.

Student evaluations of the facility were distinctly positive, with the exception of the recurring criticism of the inadequacy of the teaching facility, study space and library access.

Service

Principal service activities include the provision of instructional facilities and programs for school classes, provision of environmentally oriented residential workshops, and the delivery of a public seminar program.

Methods of assessment available are annual user days associated with school activities and with seminars, workshops and other miscellaneous Station activities. These can be compared with running averages, and any value equal to or greater than the running average may be interpreted as being indicative of good performance. Unfortunately our data base does not permit distinction between seminars, workshops and other miscellaneous activities.

For this period, user days associated with school activities were 1,317 (mean=675), and user days associated with other activities were 2,241 (mean=1,309). My interpretation of these numbers is that the Field Station is doing exceptionally well in the area of Service. Activity in our school program increased by 31% over the previous period. Additional school activities over the past year included "Ecoscope", a three day exploration and investigation of the Marsh sponsored by the Winnipeg Adult Education Centre, and a two day visit from the Young Scientists of Canada from Sarnia. Six public seminars were presented at the Station and five residential workshops were conducted. A new and successful venture was the hosting of two Elderhostel courses during the year. The Station also hosted an extremely successful "Day at the Marsh" for Friends of the Field Station.

Manager's Report

Russ Mead

When viewed from a future perspective, 1993 will be seen as the year that the station "jumped" from a moderate yearly increase in Station utilization to an impressive 18% overall increase in use. Certainly, the expansion of the user base can be credited to the Station's importance as an educational and research resource, the need to access this resource and the improved and organized facility and programs.

Without the combined co-operation of the Station's many users and the dedicated efforts of the staff to provide the multitude of needs, the results of the year would not have been possible. I sincerely thank all those users and staff for their support. In particular the students' interests and requests continue to drive the improvements and fine tuning of all aspects of the Station. Doreen Greening and Shirley Dinwoodie deserve special recognition for their dedication and competence. It was more than once they were called upon to provide room and meals for more users and faster turnover times than ever before. I know I speak for everyone when they say thank you and we appreciate you. Additionally, Brenda Howe, Ardith Hamilton and Heidi Mead "pitched in" when two pairs of hands were not enough to handle the load. Thank you for your many capable efforts. Summer Assistants again provided much assistance throughout the summer. David Ingleson provided the necessary components for the school groups, summer courses and all the various users. Mark May capably filled the position of maintenance assistant helping with all the aspects of interior and exterior improvements and groundskeeping. Dick Convery once again proved "it ain't easy" but entirely possible keeping up with the many improvements and repairs a large facility requires. 1993 also represents a year in which many areas of the physical plant were vastly altered and upgraded. Lastly, recognition and thanks is extended to Pat Gutoski and Gordon Robinson who make up the other two-thirds of the administration "team". From making bookings, billings, to advertising, all aspects of communication and promotion have been made possible by Pat and Gordon's efforts.

Facility and Property Improvements

The most notable improvement of the year was the conversion of the iron filters from a chemical oxidation method to more efficient and chemical free air oxidation filters. The water system now approximates the quality found in most cities and towns, thanks to Ray Goetz and Physical Plant for their continued participation in the improvements made to the Station. Even though the summer was a very wet season much painting was accomplished with the PMQ's and cottages all receiving new treatments. Thanks are due to Lloyd Syvret and the Human Resources group from Portage. The Bell House also received a face lift with a new concrete floor and painting inside and out.

Meteorological Station

This year will be remembered as one with more than usual amounts of precipitation, especially in the summer months. The students and instructors of summer courses are to be commended for their persistence in the field and resistance to constant rains. With increasing demands on the environment with runoff via the diversion and development proposed around the marsh, monitoring and data collection becomes more important. All parameters continue to be assessed; participation in the Crop Network Program continues to assist monitoring and prediction of growing conditions in the vicinity.

School Program

School group use and programs increased in number and diversity. Two Portage and one Brandon High School utilized the station for peer counselling/student match workshops. School groups which stayed for more than one day totalled 11. Thanks to the many dedicated teachers and organizers for their interest and support of the Station. "Ecoscope", a three day exploration and investigation of the marsh, sponsored by the Winnipeg Adult Education Centre, was a welcome addition to existing programs. Young Scientists of Canada from Sarnia, Ontario conducted a two day visit in early July. Teachers and schools participating in multi-day programs included: Brent Poole - Fort Richmond Collegiate (2x), Lois Quesnel - St. Adolphe School, Debbie Romeyn, Kathy Innes, and Henry Fast - Kelvin High School, Karen & Ron Watson - St. Rose Collegiate, Barbara Kehrstephan - Arthur Meighan High School (2x), Hazel Hewitt - Vincent Massey High School (Brandon), Catherine Fillis - Lord Selkirk Regional Secondary Comprehensive School, Mike James - St. James Collegiate.

Seminars, Workshops, Elderhostels

Six seminars were presented over the summer:

- **Dr. Isobel Waters** *(Department of Botany, University of Manitoba)* "Phenotypic plasticity in hybrid cattail stands *Typha glauca* Godr. along a water depth gradient"
- **Dr. Barrie Webster** *(Department of Soil Science, University of Manitoba)* "Soil organic matter and chemical ecology: environmental transport"
- **Dr. Bruce Ford** *(Department of Botany, University of Manitoba)* "Pollination biology of Manitoba orchids"
- **Dr. Bill Turnock** *(Insect Ecologist, Agriculture Canada)* "The invasion of Manitoba by an introduced Lady Beetle"
- **Dr. Eva Pip** *(Department of Biology, University of Winnipeg)* "Cycling of heavy metals in aquatic systems"
- **Dr. Keith Hobson** *(Research Scientist, Canadian Wildlife Service)* "Using stable isotopes in ecological research"

Dr. Spencer Sealy gave a special topic seminar at the Friends of the Field Station picnic on July 10th entitled "Bird species decline and population status in North and Central America". Dr. Gordon Robinson presented a seminar to the May and September Elderhostels titled: "Environmental crises that should concern us all".

Five workshops were held over the course of the year. These included: "Winter Survival" with Rick Riewe and Jill Oakes, "Spring Photography" and "At the Waters Edge" (fall) with Mike Grandmaison and Dick Toews, "Spring Bird Migration" with Bob Jones and "Fall Migration" with Jean Horton. Many thanks to all the instructors for their fine presentation. The public has benefitted greatly from the exchange of knowledge and expertise on these topics.

Two Elderhostel courses were held, one in May and one in September. The Chamber of Commerce, Portage la Prairie, was co-host to the events. Three topics were presented: Photography, birding and history-architecture. The Chamber provided registration and history topic. Lorraine Rae, director, deserves many thanks for initiating and promoting these events. New educational opportunities were realized for many people from across North America. Their enthusiasm was genuine and it was we who benefitted from their shared wisdom and wit.

Noteworthy Happenings

- July 10th, Friends of the Field Station open house/seminar/fundraising picnic.
- September 23 - 25, 12th North American Diatom Symposium.
- November 19-21, CUEW Conference.
- Visitors and interest (request from BBC for filming) from all over the world.
- Second year of migrant bird banding by Canadian Wildlife Service. In one 90 minute interval on August 23, Paula Gieef and Victor Fazio counted 1,300 night hawks; also August 6, recorded a peak of 120 ruby-throated hummingbirds in migration.
- T-shirt and sweatshirt design was courtesy of Heather North, a true marsh representative - the Great Blue Heron.

- Mange seen and recorded in many of the foxes in the area.
- Hantavirus possibility in Deer Mice leading to small mammal trapping being suspended in the Fall.
- Dr. Jennifer Shay officially retired this year. Congratulations on her Senior Scholar status. Everyone wishes her the best in the years to come.

Twelfth North American Diatom Symposium

NADS group photo (811K)

From the 23rd to the 25th of September, 1993, the Field Station hosted the Twelfth North American Diatom Symposium (NADS). This meeting was the first in the 25-year history of the biennial event to be hosted in Canada. It attracted 85 scientists from across Canada (18), the USA (60), México (3), England (1), Sweden (2), and The Netherlands (1), and it was considered by many to have been one of the most successful NADS in recent memory.

The program consisted of presentations on all aspects of diatom biology. Diatoms (pronounced die-ah-toms) are single-celled algae that are encased in an ornately patterned siliceous shell or frustule. There are hundreds of diatom species, each with a characteristic frustular shape and pattern. Although invisible to the naked eye, diatoms are abundant in most aquatic environments and are important as the base of aquatic food webs. They are ubiquitous in the Delta Marsh, being found on the surfaces of submerged plants, suspended in the water column and inhabiting the soft sediments on the bottoms of marsh channels and bays. In addition to their ecological importance, diatoms are valuable indicators of past environmental change because their frustules persist in sediment deposits. As such, they preserve a record of changes in the overlying water through time. Diatoms have been used throughout the world as bioindicators of the occurrence and progression of water pollution by acids, nutrients and salts. Diatoms have numerous industrial uses as well. Diatomaceous earth, a grayish powder composed of pure diatom frustules, is widely used in filters and abrasives (including toothpastes) and as a natural insecticide.

Keynote addresses were given at NADS by two distinguished diatomists, Drs. Eileen Cox (British Museum, London, England) and Hannelore Håkansson (Lund University, Sweden). In addition, 33 papers and 29 posters were presented during the formal program, and enthusiastic gatherings in Murray's Cottage each evening fostered the informal exchange of information, the development of contacts and the renewal of friendships. Dr. Charles Reimer (Academy of Natural Sciences, Philadelphia), co-author of an important book on the diatoms of North America, was honoured for his continuing contributions to the field via a "roast" conducted by his friends, colleagues and former students. Another highlight of the meeting was the Scum Run, in which relay teams of three diatomists were required to run along the beach wearing chest waders, identifying diatoms shown in photographs along the way. The meeting was preceded by a successful field trip to Riding Mountain National Park, organized by Sharon Gurney of the Manitoba Department of Environment. Following NADS, a productive trip to the Experimental Lakes Area in northwestern Ontario was organized by Hedy Kling of the Freshwater Institute, Winnipeg.

The success of NADS would not have been possible without the contributions of numerous persons and agencies. We were fortunate to receive an NSERC Conference Grant, which enabled Drs. Cox and Håkansson to attend the meeting. The Dean of Science at Brandon University provided additional financial aid. Corporate sponsorships were generously provided by Abitibi-Price (Pine Falls Division), Hoechst Canada Inc., the Canadian Museum of Nature, Leica Canada Inc., Simplot Canada Ltd., Fisher Scientific, Monsanto Canada Inc., Agassiz North Associates Ltd., NorWest Labs (Winnipeg), Labatt's Manitoba Brewery, Robin's Donuts (Portage la Prairie), the Manitoba Department of Environment and the Environmental Youth Corps, Coca-Cola Bottling (Brandon), Manitoba Hydro, Tourism Winnipeg, the Portage la Prairie & District Chamber of Commerce, and Travel Manitoba.

I thank the other members of the NADS Organizing Committee (Sharon Gurney, Hedy Kling and Gordon Robinson) for their help in planning and running the meeting. Help was also provided by Dr. Dave Czarnecki (Loras College, Iowa), Tom Henderson (Brandon University), Kelly-Anne Richmond and Dr. Jim Teller (University of Manitoba) and the staff of the Field Station and the Delta Waterfowl Station. Particular thanks are due to Rhonda McDougal and Maria Zbigniewicz for their help "above and beyond the call of duty", including late nights on shuttle service between the Field Station and satellite accommodations at the Delta Waterfowl Station. I am proud to say that we have set a high standard for the organizers of the 13th NADS, to be held in autumn 1995 at Lakeside Lab, Iowa.

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The function of Yellow Warbler alarm calls

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Introduction

Predators pose the greatest threat to the nesting effort of most avian species (e.g., Goossen and Sealy 1982). Approximately 55% and 66% of egg and nestling losses, respectively, are due to predation (Rickelefs 1969). Many passerine nests are also threatened by brood parasites, birds that lay their eggs in the nests of other species, the hosts (Friedmann 1929). The Brown-headed Cowbird (*Molothrus ater*) is a widespread North American brood parasite (Mayfield 1965), that is known to have laid eggs in the nests of over 200 species (Friedmann and Kiff 1985). Brown-headed Cowbirds usually remove a host egg around the time of parasitism (Sealy 1992). In addition, cowbird nestlings often outcompete host nestlings for food (Friedmann 1963). Whereas predators threaten nests throughout the nesting cycle (Andersson *et al.* 1980), cowbirds threaten host nests mainly during the hosts' egg-laying and early incubation stages, which is when cowbirds lay most of their eggs (Rothstein 1975).

When defending their nests against predators and brood parasites, nest owners typically utter alarm calls (e.g., Nice 1937; Edwards *et al.* 1949, 1950; Smith and Hoskings 1955; Seppa 1969; Greig-Smith 1980; East 1981; Knight and Temple 1986a; Hobson and Sealy 1989; Duckworth 1991; Neudorf and Sealy 1992; Mark and Stutchbury 1994). Cowbirds and avian nest predators, such as Common Grackles (*Quiscalus quiscula*), commonly elicit the same alarm calls from nest owners (e.g., Neudorf and Sealy 1992). Cedar Waxwings (*Bombycilla cedrorum*) uttered 'disturbance' calls with equal frequency to cowbird and grackle models presented at their nests. In some species, predators may elicit other alarm calls, in addition to those elicited by cowbirds. Gray Catbirds (*Dumetella carolinensis*) emitted 'mew' calls to both cowbird and grackle models, but primarily gave 'screams' to grackles (Neudorf and Sealy 1992). Few species give unique alarm calls in response to brood parasites (Edwards *et al.* 1949, 1950; Smith and Hoskings 1955; Seppa 1969; Duckworth 1991; Hobson and Sealy 1989). Most species that do so are hosts of Common Cuckoos (*Cuculus canorus*).

Among North American birds parasitized by cowbirds, Yellow Warblers (*Dendroica petechia*) are the only species known to respond to cowbirds with a unique alarm call, the 'seet' call (Hobson and Sealy 1989). This call is given infrequently in response to other intruders such as mammalian nest predators, humans, non-threatening intruders, and conspecific intruders, each of which primarily elicits a structurally and aurally distinct alarm call, the 'chip' call (Ficken and Ficken 1965; Reid and Sealy 1986; Hobson *et al.* 1988; Hobson and Sealy 1989, 1990). Because the response to an avian nest predator is unknown, however, the seet call may be given to all avian intruders that pose a threat to the nest, rather than being a specific call given to cowbirds.

Alarm calls given in response to a particular stimulus in the environment are called 'referential signals'. Such signals cause nearby conspecifics to react in a way best suited to avoid predation (Smith 1977). Domestic chickens (*Gallus gallus*) were more likely to look up and run to cover when 'hawk' or aerial alarm calls were played to them than when ground or mammalian alarm calls were given (Evans *et al.* 1993). Similarly, vervet monkeys (*Cercopithicus aethiops*) fled into cover and scanned the sky when an aerial alarm call was sounded, whereas they scanned the ground when a ground alarm call was given (Seyfarth *et al.* 1980a,b). Whether nest-associated alarm calls denote predators or cowbirds has never been examined. Yellow Warblers are ideal candidates for studying referential signals, because the seet call is primarily elicited by cowbirds. Moreover, Yellow Warblers perform nest-protection behaviour, described as a 'rush to sit in the nest', primarily in response to cowbirds (Hobson and Sealy 1989), such that a unique defensive behaviour is expected in response to the seet call (see Smith 1977; Seyfarth *et al.* 1980a,b).

Alternatively, so-called referential signals may simply reflect the immediacy of response imposed on the prey by the predator (Owings and Hennessey 1984). Thus, a predator elicits a specific alarm call when it is close to the caller, but elicits a different one when it is farther away. Because studies that showed that Yellow Warblers gave the unique seet call to cowbirds presented models only close to the nest, the seet call may indicate response urgency rather than intruder class (see Pereira and Macedonia 1991).

Several hypotheses have been formulated to explain the function of nest-associated alarm calls. To maintain contact and coordinate behaviour, mates often call when they are around their nests (Benson 1939; Slack 1976; Lein 1980; Howes-Jones and Barlow 1988). Thus alarm calls may signal to the mate the presence of an intruder, or more specifically, a cowbird if the seet call is given. Calls may also be directed towards nestlings, causing them to stop begging and crouch in the nest (Greig-Smith 1980; Knight and Temple 1986a). Chip calls are given frequently during the nestling stage, suggesting that they may function in this regard (Hobson *et al.* 1988). Seet calls are not predicted to warn nestlings, since they may denote cowbirds that threaten the nest primarily at egg-laying stage (but see DuBois 1957; Tate 1966; Beane and Alford 1990 for observations of cowbirds preying on nestlings).

Nest-associated alarm calls also may function to elicit group mobbing by con- and heterospecifics (Curio 1975; Klump and Shalter 1984; Howes-Jones and Barlow 1988; Hobson and Sealy 1989). If Yellow Warbler seet calls function to elicit group mobbing, species which are threatened by cowbirds would be primarily expected to respond (i.e. 'acceptors'). By contrast, if chip calls signal a nest predator, all individuals nesting in an area might be expected to respond.

Finally, alarm calls may function as distraction displays or may act to enhance the effectiveness of distraction displays (Greig-Smith 1980; Knight and Temple 1986a; Montgomerie and Weatherhead 1988). Yellow Warblers give conspicuous distraction displays when models are presented to their nests (Hobson and Sealy 1989). Alarm calls given during such displays may help draw the intruder away from the nest (Montogomerie and Weatherhead 1988).

The objectives of this study were to determine whether: (1) Yellow Warblers utter seet calls only to cowbirds and not to avian nest predators; (2) the seet call is a referential signal denoting cowbirds; (3) Yellow Warbler alarm calls function to warn mates and nestlings of approaching danger; (4) alarm calls function to elicit mobbing by con- and heterospecifics; and (5) alarm calls function as or enhance distraction displays.

Methods

At Delta Marsh and Portage Country Club, I located Yellow Warbler nests in the dune-ridge forest that separates Lake Manitoba from the surrounding marsh (MacKenzie 1982). These nests were monitored by G. McMaster or myself every day until clutch completion and every 2-4 days until the young fledged or the nests failed.

I performed three experiments in the 1993 field season. The first aspect of my study consisted of presenting taxidermic mounts of a Fox Sparrow (*Passerella iliaca*), a Common Grackle (*Quiscalus quiscula*), and a female Brown-headed Cowbird to nesting Yellow Warblers at the egg-laying and nestling stages. Fox Sparrows migrate through the study and, as such, present a semi-novel stimulus to Yellow Warblers at Delta Marsh. Grackles are the smallest-known avian predator of both eggs and nestlings (Sealy, unpubl. data). At the egg-laying stage, I tested nests from the second day of laying (two eggs) to the third day of incubation. I tested nests with nestlings at least two days old, but no older than seven days old. Yellow Warbler nestlings 8-10 days old will leave the nest prematurely if approached (pers. obs.). Concurrent with model testing, an assistant recorded vocalizations elicited by the model. The assistant was hidden in a blind that was positioned as close to the nest as possible without disturbing the nest owners. In most cases I was also hidden in a blind; otherwise, I positioned myself as far back as possible while maintaining a clear view of the nest. We set up the blinds 15 minutes prior to model testing to allow the nest owners to habituate to them.

After habituation time and if the nest owners were out of the area, I quickly positioned the model approximately 0.5 m from the nest. I clipped models to vegetation and positioned them facing the nest. If the nest owners were in the area after the 15-minute period, I waited to present the model until both left the area. I presented the models in a random order and separated each test by at least 15 minutes to reduce habituation or carry-over aggression (Knight and Temple 1986b). Once the nest owner responded, I started behavioural observations, while my assistant began recording any vocalizations elicited. For five minutes, I recorded the nest owners' responses on audio tapes using a hand-held tape-recorder and transcribed the tapes later. I recorded all responses displayed by both male and female nest owners, but in the present report I focus on alarm calls and nest-protection behaviour. I recorded nest-protection behaviour as the number of 10-second intervals in which it occurred, and alarm calls as the number of times they were given in the 5-minute trial. If both nest owners called during the model trial I could not assign vocalizations to one sex. Therefore, I combined male and female calling, and compiled the proportion of calling by each sex at both egg-laying and nestling stages.

Vocalizations elicited by the models were recorded by my assistant using a Uher 4000 Report-L, Sennheiser ME 88 microphone with fixed windscreen and K3 low frequency filter, and Ampex Precision Magnetic tapes. 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. Tape speed was always set at 19 cm / sec to make the best quality recording possible (Spector 1991). The filter suppresses low and high levels of noise at positions II and III, respectively. I set the filter at position II during low wind conditions, and at position III when it was windy. I recorded the filter position used in all cases.

In the second set of model trials I presented female cowbird models at three distances from the nest: 0.5, 2.5 and 4.5 m (n=22). All protocols were as above except that vocalizations were not recorded, models were occasionally positioned on poles, and nests were tested only during egg-laying stage. If poles were used I positioned them 15 minutes prior to the first trial and repositioned them at the end of each trial. If nest owners did not respond within 30 minutes, I removed the model and recorded this as no response.

The second aspect of my study consisted of playing back seet and chip calls to nest owners. Playbacks consisted of 1 minute of seet or chip calling. This length of playback is appropriate to prevent habituation (Falls 1982). Moreover, parasitism by cowbirds (Sealy *et al.,* in press), and predation (pers. obs.), occur within 1-2 mins. From the recordings made during model testing, I selected a section of calling 2-30 seconds long from which I made a one minute 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 in the length of time they spent calling. I also recorded one minute of background noise that was used as a control.

I performed the playback experiment one or two days after model testing. Accordingly, both egg-laying and nestling stages were tested. Playbacks were delayed by two days only when it rained. Sample sizes here were smaller than in model presentation because some tested nests were depredated over night (see results). 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 are 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. I randomized the order of the playbacks. Some nest owners did not utter seet or chip calls during model testing. Therefore, the sample sizes for self call playbacks vary among treatments (seet: egg-laying [n=22], nestling [n=9]; chip: egg-laying [n=18], nestling [n=19]).

One minute before playback, I began behavioural observations. I recorded behaviours directly into a field notebook in which I had delineated seven minutes into 10 second intervals. I recorded male and female behaviours using the same categorization as in model testing, and again focus on the vocalizations emitted and nest-protection behaviour. I started playbacks after one minute of observations except when the female was on the nest. If the female was on the nest, I waited until she left. For five minutes after playback, I recorded the behaviour of the nest owners. Subsequent test calls were played back after five minutes, for a total of ten minutes between successive trials.

In addition to recording the nest owners' behaviours, I attempted to determine nestling response to the playbacks. This proved more difficult than I had anticipated. Yellow Warbler nestlings that are a few days old are difficult to see in the nest. Furthermore, they do not start vocalizing until they are 7-8 days old (pers. obs.). However, nestlings at this age may also start leaving the nest when the nest is checked. Also, the position of most nests did not allow me to see the nestlings. Thus, I provide only anecdotal observations of nestling responses.

Because the data were not normally distributed, I used non-parametric tests to analyze the results. To determine whether model type (sparrow, grackle or cowbird) or distance (0.5 m, 2.5 m or 4.5 m from the nest) influenced the nest defense responses elicited, I ranked the data within each nest (blocks), and then performed a Friedman two-way ANOVA. When significant differences resulted ($p < 0.05$), I used Fisher's protected least significant difference (FPLSD) test on the ranks to determine which model(s) elicited a significantly different response(s). Because the hypotheses concerning playbacks specify the appropriate comparisons, I used x2 test of homogeneity to determine whether the proportion of females performing each behaviour was influenced by call type.

Results

Model Presentation

Yellow Warblers frequently vocalized during model presentation. Yellow Warblers uttered significantly more chip calls in response to the grackle model than the other models, but more to the sparrow than the cowbird (Table 1). Conversely, Yellow Warblers gave significantly more seet calls to the cowbird model than either the sparrow or the grackle. Most females uttered seet calls as they rushed to sit in the nest (i.e. nest-protection behaviour). Once females entered their nests they usually remained silent. Yellow Warblers gave also metallic chip calls (Ficken and Ficken 1965) to cowbird and grackle models only, although this was not significant. A previously undescribed vocalization, which I describe as a soft-pitched warble call, was elicited only by the grackle at the egg-laying stage. Warble calls were given rarely and only when the warbler was distraction displaying.

At the nestling stage, Yellow Warblers gave significantly more chip calls to the grackle than to the other models. They uttered more seet calls in response to the cowbird model than the grackle or sparrow models. Both metallic chips and warbles were elicited more by the grackle model than by the cowbird or sparrow. Nest-protection behaviour was performed more frequently by females during cowbird trials than grackle trials.

All alarm calls except the seet call increased over the nesting cycle (Table 2). The number of seet calls given towards the cowbird and sparrow models decreased significantly over the nesting cycle. Yellow Warblers gave significantly more chip, metallic chip, and warble calls to the grackle at the nestling stage than at egg-laying stage. Although rarely given towards sparrow model, the number of pink calls elicited by this model increased significantly from egg-laying to nestling stages. Time spent in the nest by females in response to the cowbird model decreased significantly over the breeding cycle.

Cowbird model at three distances

Warblers uttered chip calls more frequently when the model was farther from the nest, but this was not significant (Table 3). Seet calls were uttered at an equal rate during all trials, given primarily when the model was first sighted. Females sat in the nest more in response to the model placed closest to the nest than at the greater distances.

Playbacks

Yellow Warblers uttered significantly more seet calls in response to the seet playback than either the chip or noise playback (Table 4 and Table 5). Although Yellow Warblers sat in the nest significantly more in response to the seet playback than the chip, the proportion of birds sitting in the nest did not differ between the seet and noise playback. Accordingly, females sat in the nest more in response to the noise playback than the chip playback. The proportion of birds uttering chip calls did not differ between the playbacks. At the nestling stage, Yellow Warblers responded similarly to all playbacks.

The proportion of individuals giving seet calls and the proportion of females sitting in the nest in response to the seet call was significantly greater at the egg-laying stage than at the nestling stage (Table 6).

Discussion

Do Yellow Warblers discriminate between cowbirds and avian nest predators?

Yellow Warblers responded with four alarm calls to the three models, but each model elicited a different set of vocalizations. The cowbird model elicited primarily seet calls, particularly at the egg-laying stage. Hobson and Sealy (1989) also found that Yellow Warblers gave more seet calls to cowbirds at egg-laying than the other nesting stages. Chip, metallic chip (Ficken and Ficken 1965) and warble calls were infrequently given to the cowbird model at egg laying, but each call was given more frequently over the nesting cycle.

By contrast, the grackle and sparrow models elicited chip calls most frequently, but the number of chip calls given to the grackle model far exceeded those given to the sparrow. Yellow Warblers uttered significantly more chip calls to the grackle at the nesting stage. Metallic chip calls were rarely given at egg-laying stage in response to any model, but increased significantly over the nesting cycle in response to grackle and sparrow models. I also recorded 'warble' calls, which have not been described in the literature. These soft-pitched calls are given rarely at either nesting stages. Warble calls were given most to the grackle model at the nestling stage, and only when the nest owners were distraction displaying.

The vocal responses to the models indicate that Yellow Warblers discriminate between the cowbird and grackle, and that they recognize the unique threats each poses. Yellow Warblers gave the seet call primarily to the cowbird model, and rarely to the grackle model, indicating that the seet call is a specific response to cowbirds rather than uttered in response to any avian intruder threatening the nest. Furthermore, female warblers performed nest-protection most frequently to the cowbird model. These results corroborate previous studies that suggested unique recognition of cowbirds by Yellow Warblers (Robertson and Norman 1977; Folkers 1982; Folkers and Lowther 1985; Burgham and Picman 1989; Hobson and Sealy 1989). Few other studies have examined whether hosts respond differently to nest predators and brood parasites. Neudorf and Sealy (1992) showed that Red-winged Blackbirds discriminate between these distinct nest threats, but that three rejecter species showed little or no discrimination. Duckworth (1991) found that Reed Warblers (*Acrocephalus scirpaceus*) discriminated between nest predators (Jays *Garrulus glandularis*) and Common Cuckoos.

Is the seet call a referential signal?

Results from the model experiment provide preliminary support that the seet call is a referential signal denoting cowbirds, because the call was given primarily to cowbirds at the egg-laying stage. Furthermore, Yellow Warblers gave the same number of seet calls to the cowbird model at each of the distances it was from the nest, whereas nest-protection behaviour decreased with increasing distance. Thus, seet calls did not vary depending on whether the situation was 'high urgency' (close to the nest) or 'low urgency' (far from the nest; see Pereira and Macedonia 1991). The other alarm calls of Yellow Warblers may reflect response urgency, however. Metallic chip calls are heard mostly in the latter half of model trials, perhaps as the bird escalates the interaction because it has been unable to move the intruder (model) away from the nest. Ficken and Ficken (1965) indicated that chip and metallic chip calls may grade into each other. Similarly, the warble call may reflect an escalation in the interaction.

Playbacks

Calls that are referential signals are predicted to elicit defensive behaviours normally given in an actual encounter with the stimulus (Smith 1977; Seyfarth et al. 1980a,b). Yellow Warblers performed nest-protection behaviour and seet calling when the seet call was played to them. Thus Yellow Warbler seet calls are referential signals denoting cowbirds. This is the first study to show the existence of a referential signal in response to a brood parasite or even a nest threat.

The playback of background noise caused females to sit in the nest in 50% of trials. Because females usually uttered seet calls in association with nest-protection behaviour, I suspect that the responses of females to the noise and seet playbacks are not the same in a functional sense. Females rushed back to the nest seet calling in response to the seet playback. By contrast, females appeared to be returning to the nest to incubate or brood during noise playbacks, and never uttered seet calls during this return. Therefore seet and noise playbacks elicited two very different behaviours.

Chip call playback did not elicit intense responses by Yellow Warblers. However, females did not return to the nest during chip call playback suggesting that it might have a 'stay away' function. This was more apparent at the nestling stage, when few females approached the speaker at all. During testing with the grackle model, nest owners usually stayed over two meters from the model. Perhaps the chip calls communicate the presence of a predator, such that nest owners do not approach too closely. Cheney and Seyfarth (1982) showed that vervet monkey responses to 'grunt' calls are subtle, consisting mostly of movement to and away from the speaker.

Functions of Yellow Warbler alarm calls

I tested three hypotheses on the function of alarm calling in Yellow Warblers: (1) Alarm calls elicit group mobbing; (2) Alarm calls warn mate and offspring of potential danger; and (3) Alarm calls act as a distraction display. I will go over each hypothesis separately and present evidence gathered from my experiments.

Hobson and Sealy (1989) proposed that Yellow Warbler seet and chip calls may cause group mobbing, but conceded that they never recorded mobbing during model trials. During the playback experiment, I never recorded birds other than the nest owner(s) responding. By contrast, during 34 model trials, I frequently recorded individuals other than the nest owners responding. Most of the birds that responded were Yellow Warblers, but Gray Catbirds, Red-winged Blackbirds (*Ageliaus phoeniceus*), and Song Sparrows (*Melospiza melodia*) also were drawn to the area. Calling during the grackle model presentation drew in birds most frequently (21 / 34 cases). Furthermore, a Common Grackle I observed depredating a Yellow Warbler nest attracted four other warblers, plus a Northern Oriole (*Icterus galbula*) and Gray Catbird (pers. obs.).

Birds other than nest owners may require additional visual cues to identify the stimulus before they respond. Although the seet call will identify to Yellow Warblers that the intruder is a cowbird, other warblers did not respond to the playback and only rarely appeared during presentation of the cowbird model (2 / 34 cases). Host aggression may lead cowbirds to nests (see Robertson and Norman 1976,1977; Smith et al. 1984; Gill et al., unpubl. data), therefore other Yellow Warblers may not risk responding unless their nest is threatened directly.

Chip calls are given in a wide variety of situations, and to various intruders at the nest, both threatening and benign (Ficken and Ficken 1965; Reid and Sealy 1986; Hobson et al. 1988; Hobson and Sealy 1989, 1990). Because they are given in so many contexts, warblers may rely on contextual information to determine the meaning of the call (Smith 1977; Lein 1980). In the absence of such information, warblers, including nest owners, may not respond. Alternatively, the structure of chip calls may vary with context, such that contextual information is encoded in the call (Stone and Trost 1991). If this occurs then chip calls given to the grackle would elicit different responses than those given when foraging or leaving the nest. Whether Yellow Warblers respond differently to chip calls recorded from different contexts needs to be determined.

The second hypothesis on the function of Yellow Warbler alarm calls that I tested considered whether the calls warn the mate and offspring of an intruder in the area. I gathered only anecdotal and equivocal observations on whether the alarm calls warn nestlings of approaching danger. Some nestlings retracted their heads during chip call playbacks, but other nestlings did not. I can conclude nothing from these meager observations. However, I have suggestive evidence that the chip call may function to warn nestlings. Chip calling without apparent stimuli increases in frequency over the nesting cycle (pers. obs.). Additionally, the farther the female was away from her nest, the more chip calls she gave (pers. obs.). This suggests that calling may indicate to the nestlings that the female is not near the nest. The increased frequency of chip calling in response to the grackle model over the nesting cycle may reflect communication to the nestlings as well (see Gyger *et al.* 1986). Black-billed magpies (*Pica pica*) increased their alarm calling as their nestlings grew older and louder, presumably to keep them quiet (Buitron 1983). The seet call is not expected to communicate anything to nestlings, as cowbirds present little threat to nests with nestlings.

Alarm calls may also warn the mate of impending danger. Both seet and chip call playback attracted female and male nest owners back to their nest. Seet calls also elicited nest-protection behaviour, another response given primarily to cowbirds. Thus these alarm calls may be used by nest owners, especially females, to bring their mate back to the nest, and to solicit aid in nest defense from the mate. Small passerines may defend the nest most successfully when two parents are present (Moksnes *et al.* 1990).

The third hypothesis for alarm call function is that calls act as a distraction display, drawing the intruder away from the nest (Greig-Smith 1980; Knight and Temple 1986a), or enhancing the effectiveness of distraction displays (Montgomerie and Weatherhead 1988). Although not tested directly, this is likely to be important for Yellow Warblers. During egg-laying stage, most warblers were silent when they displayed. Nest owners stopped calling before they engaged in displaying, calling only after they stopped displaying. Similarly, warblers distraction displaying during the nestling stage were initially silent, primarily vocalizing only after displaying was unsuccessful. Yellow Warblers unable to draw the intruder (model) away, started alarm calling later in the trial. This suggests that the nest owners were attempting to increase effectiveness of distraction display by drawing more attention to themselves by calling (Montgomerie and Weatherhead 1988). The soft-pitched warble call may be especially effective in this regard. This call sounds like it is coming from an injured animal. That it was given most in response to the grackle model during the nestling stage, and only while the nest owner was distraction displaying, supports this contention. The grackle represents a greater threat to the nest than either the sparrow or cowbird model at this time (Patterson *et al.* 1980).

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Responses of marsh algal communities to controlled nitrogen and phosphorus enrichment

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Introduction

It is well known that nutrient enrichment of lakes, especially by nitrogen and phosphorus, contributes to their accelerated eutrophication. Specifically, increased nutrient levels cause increased total primary production, often by bloom-forming cyanobacteria. This observation has arisen largely from studies of deep aquatic ecosystems where phytoplankton are the predominant primary producers and pelagic invertebrates and fish are the primary consumers. There is comparatively little information on the responses of shallower, littoral-dominated ecosystems such as wetlands to nutrient enrichment, so the extent to which the above generalization applies to such systems is unknown.

There are several ways in which N and P levels in a wetland may increase. It is widely recognized that wetlands are maintained by periodic water level fluctuations (Good *et al.* 1978). During periods of climatically-induced drought or intentional drawdown, inorganic nutrients are generated via decomposition of organic materials in exposed sediments. These nutrients are subsequently released into the water column following reflooding. In addition, the feces of geese and ducks contribute significantly to the nutrient budget of lakes (Manny *et al.* 1994). It is likely that such additions are at least as important in wetlands, which are often important resting, feeding and breeding grounds for waterfowl (Batt *et al.* 1989). Benthivorous fish such as carp (*Cyprinus carpio*), introduced to wetlands from adjoining lakes and inflowing rivers, can increase sediment resuspension (Meijer *et al.* 1990), thereby enhancing efflux of sediment-bound nutrients. Finally, nutrients in fertilizers and sewage may represent significant inputs to wetlands receiving drainage from agricultural, domestic and industrial sources.

Using a series of large, littoral enclosures constructed originally for use in toxicological studies in the Delta Marsh (Goldsborough 1991), studies were initiated in 1993 to examine the responses by benthic algae (periphyton and epiplon) and phytoplankton to controlled additions of N and P. The basis for the experiment was an hypothesis that marsh plants and their epiphytes outcompete phytoplankton for nutrients under unperturbed conditions. When nutrients are added to the water column, phytoplankton may compete effectively. Thus, it was predicted that pulsed additions of N and P would cause a shift in the composition of algal primary producers, from an epiphyte-dominated system similar to that occurring naturally in the marsh to one in which phytoplankton were abundant.

Methods

Each experimental enclosure consisted of a wooden frame, 5 m by 5 m in size, with a 40 cm wide walkway around it. The frame was supported slightly above the water surface by foam blocks fastened under the walkway. A translucent plastic curtain was attached to the inner side of the frame. It extended through the water column and into the sediments. The bottom end of the curtain was fastened to metal rods embedded in the bottom, thereby preventing the direct movement of water between the inside of the enclosure and the surrounding marsh. The total enclosed water volume was about 15,000 L. Four enclosures fastened together were deployed in the center of the Blind Channel in mid-May, 1993.

Minnow traps were placed into each enclosure immediately after curtain installation to remove fish. The objective was to exclude fish as a potential consumer and, therefore, to reduce the number of variables in the experiment. However, fecund females laid numerous eggs on the inner side of the curtain prior to their removal and fry were subsequently observed in all enclosures. Traps were checked daily for the duration of the experiment.

One hundred cylindrical acrylic rods (0.64 cm diameter, 90 cm length) were positioned vertically in each enclosure on 18 May, 1993 so the uppermost 60 cm was available for periphyton (epiphyton) colonization. Prior to placement, the substrata were notched with a small saw to provide two adjacent 2.5 cm segments (27.5 to 32.5 cm above the sediment interface when *in situ*) for carbon fixation measurements. These were bracketed by two 10 cm substratum segments that were retained for algal chlorophyll analysis. The remainder of the substratum was unused. Sampling began on 1 June (designated as "week 1") and continued at weekly intervals until 17 August (week 12). At each sampling time, six colonized substrata were selected from random positions within the enclosure and subsampled segments were returned to the laboratory for analysis. At the same time, three 1 L samples of surface water (< 10 cm depth) were collected at random positions from each enclosure for analysis of phytoplankton carbon fixation and chlorophyll. Beginning on 7 June, three samples of surface sediments (circa 1-2 cm) were collected from random positions in each enclosure using a vacuum aspirator apparatus.

Substratum segments used in measurements of algal carbon fixation were placed in clear glass tubes containing filtered water from the same enclosure as the sample. Radiolabeled bicarbonate solution (1 µCi/mL) was added to each tube. The tubes were then placed in a benchtop water bath that maintained a constant temperature (25°C) and irradiance (500 µE/m2/s) over an incubation time of 3-4 hours. Following incubation, segments were collected onto filters under vacuum, fumed over concentration HCl to liberate residual inorganic radiolabel and placed into liquid scintillation cocktail. Sample radioactivity was determined by liquid scintillation counting and used, along with the pH, temperature and alkalinity of the incubation medium, to calculate carbon fixation rate during the incubation period. Substratum segments collected for chlorophyll analysis were frozen for at least 24 hours then thawed and placed in 90% methanol. Pigments eluted into the solvent were measured spectrophotometrically and chlorophyll concentration was calculated using the formulae of Marker *et al.* (1980).

Sediment slurry samples were transferred at the laboratory into beakers whose sides were blackened to prevent light penetrance. They were allowed to stand in a dark drawer for 24 hours then the supernatant was carefully withdrawn. The wet sediment surface was covered by a piece of lens paper and the beakers were transported to the Field Station Met Station where they received natural irradiance for circa 18 hours. The lens papers were then removed from each beaker and suspended in a sample of filtered water from the same enclosure from which the sediment samples were collected. The samples were shaken vigorously to dislodge associated epipelic algae and subsamples of the resulting suspension were dispensed into clear glass tubes for carbon fixation rate measurements. Incubation and post-incubation sample preparation conditions were identical to those used for periphyton and phytoplankton samples.

Two enclosures were arbitrarily chosen to receive nutrient additions and the other two enclosures were unmanipulated controls. The first nutrient addition took place on 20 June. An aqueous solution of NaH2PO4 and NaNO3 in a concentration sufficient to yield an initial expected concentration of 1 mgP/L and 10 mgN/L was added to the surface of each treated enclosure. The solution was mixed thoroughly in the surface waters using a paddle. Water samples were collected from all enclosures prior to the addition and at daily intervals after treatment, and analyzed for ammonia and orthophosphate. Additional samples were collected at weekly intervals from all enclosures and submitted to the W. M. Ward Technical Services Lab (Winnipeg) for analysis of nitrate+nitrite, total phosphorus, total dissolved phosphorus and total Kjeldahl nitrogen. A second spike addition of the same N and P concentration was made to the same treated enclosures on 2 August, after which water samples were collected at 12 hours intervals and analyzed for orthophosphate and nitrate+nitrite. Methods of water analyses followed Stainton *et al.* (1977).

Results & Discussion

Nitrate-N and orthophosphate-P levels in untreated enclosures, like those in the surrounding Blind Channel, were at or below detection limits throughout the experiment. There was no evidence of nutrient leakage from treated to untreated enclosures. Twelve hours after the first nutrient addition, N and P levels in treated enclosures were 6.6 mg N/L and 0.56 mg P/L, respectively. As expected, nutrient levels in surface waters decreased rapidly with time. Ten days after the addition, N and P levels were similar in treated and control enclosures. Frequent water sampling done after the second nutrient addition confirmed this rapid dissipation rate. Samples from treated enclosures collected 2.5 hours after the addition contained 9.0 mgN/L and 0.94 mgP/L (Fig. 1). First-order dissipation half lives for N and P, calculated using data collected during the first 8 days after treatment, were 108 hours (4.5 days) for N and 62 hours (2.5 days) for P. By 8-9 days after treatment, N levels were slightly above detection (0.1 mg/L) while P levels remained above detection for the remainder of the experiment (Fig. 1). The disappearance of added nutrients was likely due to the combined effects of assimilation by algae and macrophytes, and chemical transformation in the water column and sediments. The half-lives were longer than anticipated on the basis of tracer experiments done in lake epilimnia (e.g., Rigler 1956), where total phytoplanktonic assimilation within hours was the norm.

Periphyton biomass increased in nutrient-enriched enclosures, as compared to untreated controls (Fig. 2a) and remained higher throughout the experiment. On the other hand, phytoplankton biomass was lower in treated enclosures (Fig. 2b). There was no difference in epipelon biomass between enclosures (Fig. 2c). There was no apparent effect of the two nutrient additions on carbon fixation rates of periphyton (Fig. 3a), phytoplankton (Fig. 3b) or epipelon (Fig. 3c). In part, these results are due to high variability between substrata from a given enclosure, and variability between replicate enclosures. This variability arises from spatial variation in the abundance and species composition of macrophytes. Where macrophyte development is profuse, shading and competition for nutrients results in lower algal biomass.

These results are significant in the context of a conceptual model for algal communities in temperate wetlands proposed by Goldsborough and Robinson (1995; Fig. 4). By this model, most areas of the Delta Marsh are "open marshes" in which epiphytes colonizing the surfaces of submersed macrophytes are the predominant algae. This dominance is maintained, in part, by physical disturbance caused by wave action and carp, and invertebrate herbivory, all of which ensure that epiphyton biomass remains sufficiently low that it does not eventually eliminate macrophytes via shading (cf. Phillips *et al.* 1978). When this stable state is perturbed through nutrient enrichment, the system may evolve either into a "sheltered marsh" where mats of filamentous green algae (metaphyton) predominate, or to a "lake marsh" dominated by phytoplankton. In either case, increased nutrient loading initially leads to increased epiphyton biomass which, in turn, leads to increased shading and bacterial nectrophy of macrophytes. If macrophytes are reduced to the extent that their stabilizing influence on the sediments, and ultimately the water column, is lost, competitive stress on phytoplankton for nutrients may be alleviated, causing them to flourish. The resulting phytoplankton blooms can lead to the eventual elimination of macrophytes, thence to the stable "lake marsh" state. Such a progression has occurred in wetlands such as those in the prairie "pothole" region of western Manitoba, North Dakota and Minnesota that have undergone nutrient loading (Hanson and Butler 1994). Alternatively, if macrophytes remain in enriched areas of the wetland, providing substratum for the initiation of metaphyton, a "sheltered marsh" persists. The latter alternative occurred in experiments comprising the Marsh Ecology Research Program (MERP), which were conducted at the Delta Waterfowl and Wetlands Research Station in the 1980s. During MERP, flooding of drawn-down areas of the marsh were observed to produce massive floating meadows of metaphyton (Hosseini and van der Valk 1989).

Results of this study contradict the prediction that marsh phytoplankton would respond positively to nutrient enrichment. Instead, increased epiphyton biomass and the persistence of macrophytes in all enclosures may explain the net reduction in phytoplankton. This indicates that the systems within treated enclosures were progressing to the "sheltered marsh" state. The absence of conspicuous metaphyton, contrary to model expectation, may relate to the nature of the experimental treatment. Although N and P levels were high immediately following spike additions, their rapid dissipation precluded a high ambient nutrient environment needed to cause such a shift. It would be interesting to determine if different results could be obtained by adding the same cumulative nutrient load at more regular intervals. Such an experiment is planned for the summer of 1994.

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Location and selection of Clay-colored Sparrow nests by Brown-headed Cowbirds

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Introduction

The Brown-headed Cowbird (*Molothrus ater*) is an avian brood parasite that lays its eggs in nests of other birds, the hosts. The hosts then raise the offspring. Parasitism often incurs a cost in lost reproductive effort and is considered an important cause of nest failure (Ricklefs 1969). Cowbirds have been known to parasitize 216 species, although only 139 have successfully raised young cowbirds (Friedmann *et al.* 1977). These numbers show that although many species are potential hosts, for various reasons, some are better than others. In fact, several studies have shown that cowbirds do not parasitize hosts in proportion to their abundance and actually preferentially parasitize a few species (Fleischer 1986; Wiley 1988).

Before laying their eggs, cowbirds must first choose an appropriate host. Many host characteristics have been discussed by several authors: diet, egg size, breeding synchrony between host and parasite, and whether hosts accept or reject cowbird eggs (Rothstein 1975; Payne 1977; Wiley 1988). Once a cowbird has chosen an appropriate host, it must then locate nests and choose a suitable nest from among those found. In the present study, I am examining three cues that cowbirds might use to locate and select a host nest: (1) host activity, (2) host aggression, and (3) nest concealment.

Host activity may be used by cowbirds to locate nests (Buech 1982). I am testing this by placing out nests and simulating different amounts of host activity (Thompson and Gottfried 1981). Host aggression was used to test if the nest-cue hypothesis could operate. This hypothesis states that cowbirds use host aggression to locate nests. It predicts that the more aggressive individuals should be parasitized more frequently because their nests are easier to locate (Robertson and Norman 1977; Smith 1981). It also requires that hosts be aggressive at distances farther from their nests in order to attract cowbirds. This is the aspect that I am testing. Nest concealment will be used to determine if cowbirds actually choose nests, rather than parasitize them at random. Predation is a major cause of nest failure for most passerine species (Ricklefs 1969). It has been shown that better-concealed nests suffer less predation (McLean *et al.* 1986). Cowbirds should therefore lay in the better-concealed nests because they will also benefit from a decreased predation rate (Gates and Gysel 1978).

This study involves a grassland species, the Clay-colored Sparrow (*Spizella pallida*). Knapton (1978) found that better-concealed nests were more successful because they were preyed upon less frequently. He also stated that nest defense appears to be ineffective in preventing predation. This may also apply to parasitism as it's sometimes considered as a form of predation.

Methods

This study was initiated at the University of Manitoba Field Station at Delta Marsh (50°10'N, 98°22'W) during the spring and summer of 1993. A second field season is planned for 1994. The area is an old-field succession dominated by snowberry (*Symphoricarpos occidentalis*) and wild rose (*Rosa* sp.).

I located nests by searching the habitat daily. For each nest found, I took a concealment value in eight directions by assigning a value of 0-5 corresponding to decreasing visibility of the nest, 0 = 100% visibility, 1=80% visibility, etc. (see Holway 1991). I averaged these values and compared them for each nest. I monitored each nest for signs of predation and parasitism. I considered a nest successful if, three days after the last egg was laid, the complete clutch was still intact. I chose a three-day cutoff because I wanted a comparable time frame for both parasitism and predation. Parasitism does not usually occur after the first few days of incubation (Sealy 1992).

The host-activity experiment consisted of placing out old Clay-colored Sparrow nests for eight days. Nests received one of five treatments: no eggs, full clutch (four eggs), one egg per day, one egg per day + model Clay-colored Sparrow or one egg per day + model + song (Thompson and Gottfried 1981). The first three treatments were part of the 1993 field season. Treatments four and five will be part of the 1994 field season. The five treatments simulate different amounts of host activity. I monitored nests daily for eight days for signs of predation and parasitism. I conducted comparisons between treatments and between nest failure types. The artificial eggs used were made of plaster-of-Paris (Rothstein 1970) and painted to resemble Clay-colored Sparrow eggs.

To quantify host aggressiveness, I used models placed 0.5 m, 2.5 m or 4.5 m from the nest to determine at what distance Clay-colored Sparrows react to a model. I recorded the responses of the Clay-colored Sparrows and later transcribed them (see Smith *et al.* 1984; Hobson and Sealy 1989), classifying them as follows: distance from model, vocalizations, attacks, foraging, perching and incubating. In 1993, I used a female cowbird as the model to seek support for the nest-cue hypothesis. In 1994, I will use a visual predator and an olfactory predator as models to determine if aggressive behaviour may function to deter or attract predators. If the sparrows are equally aggressive at all distances then the behaviours may have a deterrent function. If on the other hand, the sparrows are more aggressive closer to the nest then the behaviours may inadvertently attract predators. A third set of model testing will also be conducted using four models at 0.5 m to determine if Clay-colored Sparrows recognize various nest threats to their productivity.

Results

During the 1993 season, I found 62 Clay-colored Sparrow nests. Of these nests, 6 were parasitized (9.7%), 6 were predated (9.7%) and 50 were successful (80.6%). There was no significant difference for all concealment values taken at both eye-level and nest-level for the three possible outcomes. The majority (> 56%) of nests fell into a concealment value range of 4.01-5.00, i.e. highly concealed. Nest outcome was not related to either nest height (Fisher's exact test, $p = 0.769$) or supporting vegetation (Fisher's exact test, $p = 0.710$). Snowberry was the dominant plant species with 74% of nests built in this species.

I conducted two runs of nest placements (the first from 2 to 10 June and the second from 10 to 18 June) to increase sample size. I was able to combine the two runs because there was no difference between them (Fisher's exact test, $p = 0.917$). None of the three treatments (no eggs (N = 33), full clutch (N = 33) and one egg/day (N = 34) affected the nest outcomes (Chi-square test, $p = 0.787$). It is interesting, however, to note that none of the nests was parasitized. Concealment also had no effect on outcome for any treatment at both nest-level and eye-level.

With the female cowbird model, I tested 17 nests at the three distances. Only four behaviours recorded were significant, distances 2 m and 2-5 m, chips, and perch changes (Table 1). None of the more aggressive behaviours, such as close passes was significant. This is perhaps because they occurred rarely.

Discussion

The non-significant findings suggest that there is no relationship between nest concealment and nest outcome. The major predator in this area in the Franklin's ground squirrel (*Spermophilus franklinii*), an olfactory predator. Due to this fact predation rates are not expected to be related to concealment. Because host species do not benefit from a decreased predation rate with increasing concealment a cowbird egg also would not benefit. It then follows that cowbirds should lay in any nest regardless of its concealment. Indeed, this is what I found. There was no significant trend of increased parasitism rates with increasing concealment values.

The three levels of host activity simulated did not appear to be enough to elicit parasitism, as no parasitism was observed. Predation, however, did occur and seemed to be independent of the level of host activity. One possibility is that perhaps a critical level of activity or a critical type of activity was not simulated. It is this critical point that must be reached before cowbirds cue in on the hosts and their nests.

Host aggression towards a female cowbird at three distances was used to test if the nest-cue hypothesis could operate. Aggressive behaviours were infrequent and therefore probably cannot be used as a cue for cowbirds. Cowbirds may, however, be able to use the distance of the host from itself, the frequency of chips, and the number of perch changes as cues to the presence of a nest. Clay-colored Sparrows spend more time closer to the model and perch-change and chip more frequently when the model is closer to the nest. There is also a gradation in responses for < 2 m, chips and perch changes; all three increase in frequency as the distance from the nest decreases. These three cues may be used by cowbirds to locate nests. It is these three behaviours that may allow the nest-cue hypothesis to operate because they occur at the furthest distance. They are not, however, highly aggressive behaviours. These behaviours may also give the cowbird an indication of host quality. If sparrows can spend more time near the nest and not be away foraging, this might indicate a better quality host, i.e. the sparrows may be superior at foraging in a shorter time frame and can therefore spend more time near the nest (Arcese and Smith 1988). Cowbirds may be able to detect this and select these nests because their young may have a better chance of surviving.

Summary

This study has examined some of the possible cues used by cowbirds to locate and select host nests. Three of six objectives of the project were met in the 1993 field season. I looked at host activity using nest placements, and host aggression using a female cowbird model to discover their role in nest location. I also looked at nest concealment to see if it had a role in nest selection. I needed to do more research to further isolate the cues that may be used individually or in combination by cowbirds. Two of these cues will be further examined in the 1994 season; host activity will be further investigated by adding two treatments to the nest placements, and host aggression will be looked with respect to predators using a visual and an olfactory predator. I will also test enemy recognition using four models.

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Neotropical migrant banding program at the University Field Station, Delta Marsh, 1993

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Neotropical migrant songbirds, those species that winter in the American neotropics (including primarily Central America, northern South America, and the islands of the Caribbean), and breed in temperate North America, appear to be declining dramatically. However, despite growing concern over the plight of neotropical migrant passerines breeding in Canada, little information exists on population trends of these species, particularly throughout the western provinces. Indeed, much of our current concern is based on population declines documented for migrants that move through and breed in the hardwood forests of the eastern United States and it is not known to what extent these trends may be valid throughout the continent (Askins *et al.* 1990; Robbins *et al.* 1989). This paucity of data on populations of neotropical migrants occurring in the Prairies has prompted the Canadian Wildlife Service and the Long Point Bird Observatory to establish or support monitoring stations at Last Mountain Lake in Saskatchewan and Beaverhill Bird Observatory in Alberta. Routine mistnetting and banding at these stations will help us establish 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 in this region. Fortunately, a banding study conducted in the early 1980s has provided an excellent opportunity to monitor possible declines of warblers moving through south-central Manitoba.

From 1982 to 1984, Heidi den Haan, under the supervision of Dr. Spencer Sealy of the Department of Zoology, University of Manitoba, conducted 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 the breeding or wintering grounds. The recent interest in the status of neotropical migrants by CWS and the willingness of Dr. Sealy and Heidi den Haan to collaborate in a follow-up study has provided the necessary impetus for our recent three-year program established at the University Field Station (Delta Marsh) in 1992. This report summarizes banding results for the 1993 field season.

Methods

In July of 1993, eleven mistnet sites were established at the same positions as used previously in 1992 and by den Haan and Sealy in the early 1980s. These sites are located between the Station and the Assiniboine River Diversion. All mistnets are 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 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. 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 Estimated 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 summaries and trend analysis will be performed following the three-years of data collection. From 14 July through 30 September 1993, 4021 captures were recorded representing 76 species (Table 1). Dramatic increases in the numbers of captured Ruby-crowned Kinglet, Tennessee Warbler and Yellow-rumped Warbler were found in 1993 compared with 1992.

Comments

Following the research component of this project it is hoped that a permanent banding station will be established at the University Field Station (Delta Marsh). Currently, there is ample opportunity for volunteer help at the Station between mid-July and the end of September and all interested individuals are encouraged to contact the author.

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Demography of clonal ostrich fern (*Matteucia struthiopteris*). I. Year one of a long-term study

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Introduction

Plant population ecology involves the study of the number of individuals of a plant species, and how and why a population size changes over time. Plant demography is the study of such populations changes, and the causes of change, throughout the life cycle of the species (Silvertown 1987). Demographic information can be obtained either by following the fate of individuals over time (practical for relatively short-lived species), or by estimating age-specific mortality probabilities from the age structure of a population at a given time (commonly used for forest trees).

In the majority of plant species, recruitment through the production of vegetative offshoots (clonal growth) predominates over recruitment by diaspore germination. Clonal growth can be defined as the "horizontal extension of a plant by the addition of ramets which develop their own roots" (Silvertown 1987: 108). In established clonal populations, there may be controlling mechanisms to ensure that the number of ramets produced does not exceed the carrying capacity of the habitat (Kenkel 1993). Once a clonal plant has become established and has reached the carrying capacity of the habitat, there is a regular annual pattern of ramet birth and deaths. Clonal plants typically have a pool of dormant buds (analogous to a pool of dormant seeds), which can be 'recruited' following disturbance (Noble *et al.* 1979).

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. However, it has also been argued that individual ramets are largely independent even if they remain physically attached (Kenkel 1993).

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). Turkington and Harper (1979) have demonstrated that 'fine-scale biotic differentiation' may occur, with different genets occurring in different micro-environments within the same general habitat.

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 long-term study, I use a spatial approach to examine the 'fate' of individual ramets of the clonal ostrich fern (*Matteucia struthiopteris*). Specifically, I will relate individual ramet productivity (ramet size), reproduction (production of fertile fronds), and longevity to spatial configuration of the stand (i.e. the size and proximity of ramet 'neighbours').

Matteucia struthiopteris (L.) Tod. var. pensylvanica (Willd.) Mort.

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. 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. Vegetative fronds die back in the fall, while fertile fronds persist for at least 2 years.

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 2 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 pensylvanica*). 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 assininboinensis*, *Rhus radicans*, *Osmorhiza longistylis*, *Actaea rubra* and *Rudbeckia laciniata*. Löve (1959) characterizes most of these species as having 'eastern' floristic affinities.

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.

Site Selection and Field Mapping

The location of the 5 x 5 m study plot was based on the following considerations: (a) dense, monodominant population of ostrich fern with very few other species present; (b) perceived uniformity of abiotic conditions, including soils and degree of shading by trees in the area; (c) absence of trees within the plot. The study plot selected is near the 6 x 12 m plot described in Kenkel (1991, 1992).

All ramet rootstocks within the 5 x 5m study plot were numbered with a small red 'flag' and mapped. Mapping was accomplished by measuring the distance (± 1 cm) to each of the four corner posts of the study plot. The law of cosines was then used to obtain the spatial coordinates of each rootstock. For each rootstock, the size (three classes: 'full', 'half' and 'small' size) and number of vegetative fronds were recorded. For rootstocks with fertile fronds, the number of current (this year's) and older (previous years) fertile fronds were also recorded. Mapping and recording of rootstocks was performed in early August, 1993. A total of 235 rootstocks were mapped, corresponding to a density of 94,000 rootstocks/ha.

Data Analysis

A map of the study plot was obtained, showing the locations of all sterile and fertile rootstocks. In addition, simple summary statistics were computed, and the distribution of the number of sterile fronds per rootstock was plotted.

Results

Spatial Map

A map of rootstock locations within the study plot is shown in Fig. 1. The spatial pattern of the rootstock distribution has not been examined in detail, but it appears to be random (a complete analysis is planned; note that Kenkel (1992) found that the pattern was random for a nearby 6 x 12 study plot). There is some suggestion of a lower density of rootstocks on the western side of the study plot, but this has not been confirmed statistically. Rootstocks with one or more fertile fronds are distributed relatively evenly throughout the study plot.

Number, Distribution and Size of Vegetative Fronds

There were a total of 1033 fronds (from 235 rootstocks) in the study plot, of which only 31 (3.00%) were fertile. The number of vegetative fronds per rootstock ranged from 1 - 8 (mean = 4.264). The distribution of number of vegetative fronds is approximately normal (Fig. 2), though this has not been statistically tested. The majority of the rootstocks (171, or 72.77%) were classified as being 'full-sized'. Of the remaining, 55 were classified as 'half-sized', and 27 as 'small-sized'. Most 'small-sized' rootstocks had a fewer than average number of fronds (range 1 - 6, mean = 2.704), and these fronds were often brown-coloured and unhealthy looking.

Production of Fertile Fronds

Only 21 of the 235 rootstocks (8.94%) had one or more fertile fronds. Of these, 15 had both older and current fertile fronds, indicating that they have remained fertile for at least two years. An additional 7 rootstocks had older fertile fronds, but did not produce any fertile fronds in 1993. All rootstocks producing fertile fronds were large, and generally also produced a large number of vegetative fronds (range 4 - 8, mean = 6.43). An average of 1.476 fertile fronds were produced per fertile rootstock (distribution: 13 produced one fertile frond, 6 produced two, and 2 produced three). These results suggest that the production of fertile fronds may be energetically costly, with only the most robust rootstocks producing fertile fronds, and even then in small numbers.

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Response of whitetop meadow vegetation to disturbance: a five-year experiment

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In prairie marsh ecosystems, disturbance plays an important role in the maintenance of floristic and landscape diversity. At the scale of the whole marsh, water level fluctuations are of critical importance (van der Valk and Davis 1978; van der Valk 1981). The prairie regions of North America are characterized by alternating cycles of high and low annual precipitation, which in turn results in a cycle of alternating flooding and drawdown periods in prairie wetlands. High water levels in the marsh kills emergent macrophyte vegetation, but vegetation regeneration from the seed bank and surviving underground parts occurs when water levels fall again. Van der Valk hypothesized that such periodic disturbance is essential to the regeneration of prairie wetlands. In recent years, concerns have been raised that anthropogenic control of water levels in wetlands may permit highly competitive species to competitively exclude less competitive ones, resulting in lowered species and habitat diversity (Kenkel 1993).

More localized disturbances may also be important in maintaining species and habitat diversity in prairie wetlands. Examples included muskrat 'eat outs' of macrophyte vegetation, and the 'trampling' effects on vegetation by deer and humans. While the effect of such localized disturbances on prairie marsh vegetation has not been extensively studied, they may be very important. Prairie marshes are characterized by a few dominant emergent macrophytes that, through clonal growth, form extensive monodominant stands. Associated 'understory' species in such stands are generally opportunistic, non-clonal annuals and short-lived perennials. These 'understory' species usually occur at low frequency and abundance, but may be locally abundant in small disturbed patches within an extensive monodominant stand.

An example of the possible importance of small-scale disturbance in whitetop meadows is given by Neill (1990a,b). While his study was designed to examine the effect of nutrient addition (N and P) on emergent macrophyte productivity, an important secondary effect related to local disturbance was observed. The author found that nitrogen limited growth of both *Scolochloa festucacea* and *Typha x glauca* at the Delta Marsh, Manitoba. In whitetop meadows, nitrogen significantly increased productivity in the year following application. However, a quite different effect was observed in the second year, as whitetop biomass decreased dramatically while biomass of other species (particularly the annual *Atriplex patula*) showed a dramatic increase. Neill hypothesized that whitetop growth in the second year was inhibited by a mat of fallen litter from the previous year. Thus a disturbance (in this case, nutrient addition) caused a 'mulching' effect of litter that in turn resulted in a localized increase in species diversity. Neill also hypothesized that this effect would be short-lived, as whitetop was expected to quickly spread back into these 'mulched' patches through vegetative propagation. This was not verified, however, as his experiment was terminated after two years.

In this study, I investigate the long-term effects of small-scale patch disturbance on productivity and species diversity in a whitetop meadow at Delta, Manitoba. I used different levels of salt (sodium chloride, NaCl) addition to 'simulate' a gradient of increasing disturbance in a controlled, replicated experiment.

Study Area

The Delta Marsh, a large (21,870 ha) lacustrine prairie wetland at the south end of Lake Manitoba, is one of the largest remaining natural marshes on the North American prairie. The marsh is connected to Lake Manitoba by a series of channels crossing a sandy dune ridge. The dominant macrophyte species in the marsh include *Scirpus* sp., *Typha* sp. (mainly the hybrid cattail *T. glauca*, *T. angustifolia* x *T. latifolia*), *Carex atherodes*, *Scolochloa* *festucacea*, and *Phragmites australis*. A complete description of the vegetation is given by Löve and Löve (1954) and Walker (1965). Soils are variable, but are predominantly silt loams, sand loams, and silty clay loams overlain by a poorly to moderately decomposed organic layer. The substrate is somewhat basic, and generally slightly to moderately saline. Water levels in the marsh typically drop over the growing season, typically between 20 and 50 cm.

The study site used in the experiment is located on the property of the University of Manitoba Field Station (50°11'N, 98°19'W, elevation » 250 m), just south of the main lodge. The site is a vegetatively homogeneous wet meadow dominated by whitetop (*Scolochloa festucacaea*). Associated 'understory' species, which occur at much lower abundance, include sow thistle (*Sonchus arvensis*), Canada thistle (*Cirsium arvense*), smartweeds (*Polygonum* sp.), and various mints (mainly *Teucrium occidentale*, but also *Mentha arvensis*, *Lycopus asper* and *Stachys palustris*). Opportunistic annual species (mainly *Chenopodium rubrum*, *Atriplex patula* and *Aster simplex*) occur on exposed substrates.

Biology of Whitetop

Whitetop (*Scolochloa festucacea*) is a rhizomatous, emergent hydrophytic grass. It is especially common in Manitoba, Saskatchewan and North Dakota, where it occurs in seasonally flooded meadows. It may be found at the centers of small basins (prairie 'potholes'), and along the shallow edges of larger marshes in areas inundated by snowmelt water. The species tolerates a wide range of conductivities, but does best in moderately saline habitats (Neill 1990a,b). On the prairies, vernal growth is initiated between mid-April and mid-May. Smith (1973) suggests that litter accumulation is detrimental to whitetop productivity, since burning or mowing after a season without disturbance results in an increase in productivity. He suggests that *Carex atherodes* will eventually outcompete whitetop in areas where significant amounts of litter accumulate.

Methods

Experimental Setup

In the fall of 1988, a 22 x 22 m study area was delineated within a homogenous whitetop meadow. Elevation varied slightly within the study area, with the north side of the region being the least flooded. Elevation dropped by 7 cm between the NE and NW corners, by 34 cm between the NE and SE corners, and by 27 cm between the NE and SW corners. To effectively block for this variation in elevation (which affects duration of flooding), a 6 x 6 latin square experimental design was established within the study area. The design consisted of 2 x 2 m plots spaced 2 m apart (Fig. 1). Between June 14 - 16, 1989 each plot was lined with 135 µm polyethylene film to a depth of 20 cm.

Experimental Manipulation

Different levels of disturbance were simulated by adding saline (NaCl) water, of varying concentrations, to the plots. There were six treatment levels: (1) control, unmanipulated; (2) procedural control, water only added; (3) 8 ppt saline water; (4) 16 ppt saline water; (5) 24 ppt saline water; (6) 32 ppt saline water. Salt (commercially available sodium chloride, Sifto® natural/no additive 'pickling salt') was dissolved in 20 L of wellwater and carefully added to each treatment plot using a siphon hose. An attempt was made to add the solution directly to the soil. Following salt addition, a few liters of water was used to carefully 'wash' any salt solution from plant leaves.

Salt solutions were added during the mid-summer of 1989, after water levels had dropped to the point that plots were no longer flooded. By this time, aboveground vegetative growth of whitetop was largely completed (Smith 1973). The salinity levels, while not high enough to kill the whitetop, were chosen so as to have a demonstrable negative effect on whitetop productivity. The highest salt level was well below that of halophyte-dominated salt pans in the vicinity. Salts were incrementally added over a two month period (June 14 - August 14, 1989), as summarized in Table 1.

A soil core (4 cm diameter, 15 cm deep) was taken from the center of each plot on June 7, 1989 (prior to the treatment applications) to measure soil pH, conductivity and percent water content. Additional soil cores were taken on July 5, 21 and 26 and August 16, 1989 to monitor changes in conductivity during 1989 (when salts were added), and on July 5, 1990 and August 12, 1993 to monitor conductivity and percent water content.

Aboveground biomass was harvested in 1989 (August 14 - 18), 1990 (August 21 - 23), and 1993 (August 3 - 5). In 1989 and 1990, harvesting was done in four 35 x 35 cm subplots within the central portion of each 2 x 2 treatment plot. All plants rooted within each subplot were harvested. Different subplots were used in the two years. In 1993, all plant material rooted within the central 1 x 1 m portion of each plot was harvested. Aboveground biomass was expressed on a per meter square basis. Harvested plant material was sorted into species, dried at 80°C, and massed to the nearest gram. Whitetop litter was harvested in 1989 and 1993.

Statistical Analysis

Community species diversity for each plot was measured based on the familiar Simpson's index (1- S), where:

$S = S pi^2$

and pi is the proportion of total biomass accounted for by species i in a given plot. In this study, a variant of S known as the 'odds' index (Kvalseth 1991) was used:

$K = (1/S) - 1$

Analysis of variance (ANOVA, latin square model) was used to compare whitetop biomass, and community diversity, between treatments. Separate analyses were conducted for each of the three harvest years. Graphical presentation of the results used boxplots, which summarize the data in terms of the median and ranges.

Results

Soil Factors

(a) Soil pH

Soils were slightly basic in all plots. For the July 21, 1989 sample, the mean pH = 8.121 (range 7.66 - 8.36). Values for the August 6, 1993 sample were similar (mean = 8.07, range 7.72 - 8.39). No significant differences in soil pH were found between the experimental treatment levels.

(b) Soil Water Content

Percent water content of the soil was relatively high, reflecting the relatively high organic content of the soils and the proximity of the water table in these wet meadow sites. Values in the summer of 1989 were: July 5, 1989: mean = 58% (range 38 - 65%), and August 16, 1989: mean = 55% (range 37 - 60%). Values in 1990 were somewhat higher (July 5, 1990: mean = 64%, range 58 - 72%), reflecting the wetter spring and summer weather in 1990. In 1993, values were similar to those of 1989 (August 6, 1993: mean = 56%, range 43 - 62%). No significant differences in soil water content were found between the experimental treatment levels for any of these dates.

(c) Soil conductivity

Soil conductivity trends over time are summarized in Table 2. During the summer of 1989, when salt solution was added to the plots, soil conductivity increased over the course of the summer. However, this increase occurred over all plots regardless of whether they received salt solution. The summer of 1989 was unusually hot and dry in southern Manitoba. In prairie marshes, salts in the soil may move to the substrate surface during drought as water is drawn to the surface through evapotranspirative processes. There were no significant differences in soil conductivity between treatments at any time in 1989, though values tended to be slightly higher in the high salt treatments. I hypothesize that the salt solution percolated to soil depths greater than 10 cm soon after application, and were therefore not detected by the soil cores. That the salt solution was effective in 'disturbing' the environment is evidenced by the productivity result (see below).

Conductivity values on July 5, 1990 were similar to those of June 7, 1989. This was a more typical cooler and somewhat wetter year. In 1990 soil conductivity values were highest in the most 'disturbed' plots, though this difference was not statistically significant. Values on August 6, 1993 were similar to those of 1990 and June of 1989. Note that 1993 was an unusually cool and wet summer. Even in August, the soil was saturated. As in the other time periods, there were no significant differences between treatment levels.

Whitetop Aboveground Biomass

Whitetop aboveground biomass values (years 1989, 1990 and 1993) across treatments are summarized as boxplots in Fig. 2, and the corresponding ANOVA (latin square design) results are presented in Table 3.

(a) 1989 harvest

For the 1989 harvest, no significant differences in whitetop aboveground biomass were observed between treatments. Salt solution was added in the summer of 1989, but not until the majority of the aboveground biomass had already been produced (in whitetop, shoot emergence occurs in late April, and a full developed shoot system is established by mid-June; Smith 1973). There was no significant difference in whitetop litter biomass between treatments (Table 4), but there was a significant inverse relationship between whitetop litter and aboveground biomass in the 36 plots (Fig. 3).

(b) 1990 harvest

A statistically significant decrease in aboveground biomass with increasing salinity was seen in 1990. This probably reflects the effect of salinity on disruption of physiological processes related to rhizome production. As in many temperate species, whitetop stores photosynthates in the rhizome/root system in the fall for use the following spring. Rhizome production in whitetop occurs in August and September (Smith 1973), which is after the addition of salt solution in 1989. Salinity 'stress' likely limited rhizome production in 1989, which had a carry-over effect in the 1990 growing season. However, it should be noted that the salinity levels used in this experiment, while high enough to reduce whitetop biomass, did not lead to local (plot) extinction of the species - it was present in all plots. Also, the experimental results demonstrate that there is no difference between the two control treatments. This shows that the addition of water alone (a procedural effect) had no influence on biomass accumulation in whitetop.

(c) 1993 harvest

By 1993, the plots receiving the highest salinities had significantly greater aboveground biomass compared to the control plots. Litter biomass was significantly less in the disturbed (higher salinity) plots (Fig. 4). As in 1989, there was a significant inverse relationship between whitetop litter and aboveground biomass (Table 4, Fig. 5).

Species Diversity

Species diversity values (years 1989, 1990 and 1993) across treatments are summarized as boxplots in Fig. 6, and the corresponding ANOVA (latin square design) results are presented in Table 5.

(a) 1989

No significant differences between treatment levels were seen, but the plots were quite variable. Species composition of plots also varied.

(b) 1990

A decrease in whitetop biomass at higher salinities, combined with an increase in the abundance of 'understory' species (particularly the opportunistic annual *Atriplex patula*), resulted in a statistically significant increase in species diversity with increasing salinity by 1990.

In the control plots, species diversity in 1990 was lower than in 1989. This was attributable both to a decrease in 'understory' species biomass, and an increase in whitetop biomass, in 1990. The study area was flooded for a considerable period in the spring and early summer 1990, which may have inhibited germination and establishment of 'understory' species while favouring whitetop growth (Neill 1990 a,b).

(c) 1993

In 1993, species diversity was significantly lower in the higher salinity (more highly disturbed) treatments. This was the result of both higher biomass of whitetop, and lower biomass of 'understory' species, in the high salinity plots. Higher whitetop biomass apparently inhibits the establishment and growth of 'understory' species.

Discussion

This study offers strong empirical support for the notion that long-term environmental studies are necessary to obtain a complete understanding of ecological patterns and processes occurring in nature. Long-term experiments are particularly important in perturbation studies, since the short-term effects of ecosystem disturbance may differ fundamentally from effects in the longer term. In this study, the short-term effect of disturbance (1990 results) was to reduce aboveground biomass of whitetop, while increasing biomass of ruderal species. This is the 'classical' disturbance-response effect seen in many communities, including inland marshes (van der Valk 1978). Based on this result, one might conclude that disturbance in detrimental to whitetop meadow productivity. However, the long-term effect (1993 results) indicates that the opposite is the case, as the most disturbed plots accumulated more than twice the biomass of control plots by 1993.

In an earlier study of meadow vegetation at Delta Marsh, Neill (1990a,b) hypothesized that decreases in whitetop biomass in the year following nutrient addition were attributable to litter accumulation. He suggests that litter accumulation has a strong influence on marsh productivity. The importance of litter in lacustrine wetlands was also recognized by van der Valk (1986), who stated that litter accumulation may reduce species richness. In a recent review of the ecological effects of plant litter, Facelli and Pickett (1991) point out that only recently have studies focused on the effects of litter on vegetation community structure and dynamics. In marsh ecosystems, the ecological effects of litter are complex. A litter mat intercepts light, shading seeds (and seedlings) and reducing surface evaporation. Litter also acts as a physical barrier to seedling emergence, and may prevent seed from reaching the soil surface. Through interception of the light and rain, litter affects heat and water transfer between soil and atmosphere.

The litter of the major emergent macrophyte species at Delta Marsh, including whitetop, remains standing for some time. Furthermore, the community dominants accumulate considerable quantities of litter, since all aerial biomass is transformed to litter at end of the growing season and biochemical decomposition is limited by low oxygen levels (Polunin 1984). Decomposition rates may be greater when litter contacts the ground (through, for example, snow-packing or trampling by animals).

In *Phragmites communis* stands, Haslam (1971) concluded that litter accumulation helps prevent invasion by other species, and as such is an important adaptive strategy. More generally, Grime (1979) hypothesizes that dominance of some plant species in productive habitats is attributable to their ability to accumulate litter. The idea that plant species accumulate litter to deter competitors (through physical and/or chemical means) is only partially supported by this study. The results do, however, suggest that litter accumulation has a strong intraspecific effect; decline in litter accumulation in the most disturbed sites actually resulted in an increase in whitetop biomass. This of course does not negate the possibility that litter accumulation also has a strong interspecific effect. Note, however, that the study by Neill (1990a,b) suggests that excessive litter accumulation by whitetop may actually be detrimental to the species. In *Phragmites communis* stands, removal of litter increased winter bud mortality, resulting in the release of apical dominance and an increase in density (Haslam 1971). The strong insulative effect of litter may also delay growth in the early spring, however.

This study has demonstrated that a disturbance results in a decrease in whitetop biomass, while at the same time affording the opportunity for ruderal species to germinate, establish and grow. The species invading disturbed patches are primarily opportunistic ruderals that are found in the seed bank (van der Valk and Davis 1978). In lacustrine marshes, such species may 'lie in wait' in the seed bank for considerable period of time (Welling *et al.* 1988a,b). A 'quiltwork' of disturbance patches in the landscape may be essential to the maintenance of species diversity and richness in lacustrine marshes. However, patches are soon recolonized by the dominant species, usually through clonal growth of roots or rhizomes. It is therefore important that patches are continually formed, and that the species invading such patches are fast-growing, prolific seed producers.

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Does host-egg removal increase the hatching success of parasitic cowbird eggs?

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Introduction

Avian brood parasites lay their eggs in the nests of other birds, the hosts, which then incubate and raise the young (Payne 1977). Brood parasitism often reduces the number of host fledglings produced through damage or removal of host eggs, eviction of host eggs and/or young, and nestling competition (Payne 1977). The removal of host eggs from nests by female brood parasites has been documented in many parasitic species world-wide. Parasitic cuckoos (Cuculidae), honey guides (Indicatoridae), two finch genera (*Vidua* and *Anomalospiza*), and cowbirds (Icterinae) are known to remove or damage host eggs (Friedmann 1960, 1963; Payne 1977; Sealy 1992). In cavity-nesting species where nest sites may be limiting, egg removal may be employed as an usurpation tactic designed to force resident females to desert their nests (Lombardo *et al.* 1989). Female parasites usually remove host eggs in association with the laying of their own egg in the host nest (Sealy 1992), although one instance of egg removal by a male has been observed (Lombardo *et al.* 1989). While host-egg removal decreases host reproductive success by reducing the number of host offspring that can be raised, this behaviour may benefit the parasite and ultimately increase its reproductive success (Rothstein 1990).

Female Brown-headed Cowbirds (*Molothrus ater*) remove eggs from nests of many of the host species parasitized (Friedmann 1963), but removal varies in terms of number and timing. In fact host eggs are not removed from all parasitized nests but, on the other hand, one or more eggs are often removed (Mayfield 1961; Zimmerman 1963; Sealy 1992). Female cowbirds have been observed removing eggs on the day before, the same day, and the day after laying their own egg (Hann 1937; Norris 1944; Nolan 1978). When removing a host egg, cowbirds usually puncture it with their bill, carry it away, and sometimes eat it (Hann 1937; Scott *et al.* 1992; Sealy 1992).

Several hypotheses have been formulated to explain the function of host-egg removal behaviour (review in Sealy 1992). Enhancing the incubation efficiency of the host is one explanation given for the function of this behaviour. The incubation capacity of the host is limited by both the amount of heat that can be produced physiologically, and by the number of eggs that can physically contact the brood patch. The addition of a parasitic egg to a host clutch increases both the number and volume of eggs a host must incubate. This increase in clutch size could result in inefficient host incubation that may jeopardize the parasitic egg's chances of hatch successfully (Davies and Brooke 1988). Therefore, the incubation efficiency hypothesis states that host-egg removal by female brood parasites reduces host clutch volume to within the limits of the host's incubation capacity, optimizing the hatching success of the cowbird egg.

Methods

In 1992 and 1993, I located Yellow Warbler (*Dendroica petechia*) nests in the forested dune-ridge at Delta Marsh (50°11'N, 98°19'W) on the properties of the University of Manitoba Field Station and Portage Country Club. I monitored nests found before clutch initiation until the first egg was laid (Laying Day 1 = LD1). I assigned at random one of three treatment groups to each nest on LD1 to examine possible manipulation of host incubation behaviour by cowbirds. Treatment 1 consisted of switching a single, viable cowbird egg for a single host egg. In Treatment 2, I also added a single cowbird egg, but in this experiment, I did not remove a host egg. Treatment 3 was a control where cowbird eggs were neither added nor host eggs removed. Most cowbird eggs were added on the morning of LD1 (0700-1100h C.S.T.), although several were added later on the afternoon of LD1 (1200-1300h C.S.T.).

Viable cowbird eggs were obtained from naturally parasitized nests of 6 different species. An effort was made to use only cowbird eggs of known age, that had been exposed to minimal incubation (i.e. had been found during early egg-laying, or preferably even before the host had initiated its clutch).

An effort was made to minimize the amount of time a cowbird egg spent out of a natural nest. Any cowbird eggs found on a given day were added to a Yellow Warbler clutch that same day if possible. If no warbler clutches were available for parasitism eggs were kept overnight in a cardboard egg crate in a refrigerator at 10°C. Cool temperatures arrest embryonic development and allow the embryo to remain viable for much longer periods than would normally be possible (Drent 1975).

Five eggs is the modal Yellow Warbler clutch size at Delta Marsh (Sealy 1992). However, 4-egg clutches are also common, especially later in the breeding season. At the moment of the experimental parasitism on LD1 there is no way to predict whether the female will eventually lay 4 or 5 eggs. Therefore, in order to keep the number of host eggs constant between nests, once clutches were complete host eggs were transferred to 4-egg clutches to ensure all nests had 5 eggs. As 5-egg females may be able to incubate larger clutches more efficiently than 4-egg females, the influence of natural clutch size was investigated using the General Linear Models procedure.

In 1992 once the clutch was complete, I measured all eggs, and calculated egg volume using the formula V=kLB2 (k is a constant, k=0.515 for cowbird eggs and k=0.497 for Yellow Warbler eggs; L=egg length; B=egg breadth) (Hoyt 1979; Mills 1987).

Nests were revisited 1-2 days before they were predicted to begin hatching. When possible, the identity (cowbird or warbler) of the first egg to hatch was noted. In nests where cowbird eggs did not hatch, hatching order was not recorded as only Yellow Warbler eggs would be available to hatch first. The incubation period was defined as the day after the last host egg was laid (the first day of full incubation) up until the first egg in the clutch hatched. Therefore a single incubation period was recorded for the clutch as a whole. Hatching spread was defined as the date from the first egg hatching to the day the last egg hatched.

Results

In 1992 a total of 185 Yellow Warbler nests was found, of these 103 were experimentally parasitized with live cowbird eggs. Most clutches were initiated in early June, while the latest clutch initiated was on July 4. Another 37 nests were left unparasitized and monitored as control nests. In 1993 a total of 255 Yellow Warbler nests was found, of these nests 86 were experimentally parasitized with live cowbird eggs. Another 28 nests were left unparasitized and monitored as Control nests. The majority of clutches were initiated in late May or early June, while the latest clutch initiated was on June 29.

Mean ambient temperatures at Delta Marsh for the months of June and July 1992 were cooler than the average temperature for 1951-1980. The mean temperature for June 1992 was 14.88°C compared to 16.5°C ± 1.6 (SD) for the 1951-1980 average (Environment Canada data). The mean temperature for July 1992 was 15.13°C compared to 19.1°C ± 1.2 (SD) for the 1951-1980 average (Environment Canada data). Mean daily temperature at Delta Marsh for the month of June 1993 was slightly cooler (15.7°C) than the average mean daily temperature for the period of 1951-1980 (16.5°C ± 1.6 SD) (Environment Canada data). The mean daily maximum (21.4°C) and minimum (10.03°C) for June 1993 were also only slightly cooler than those from 1967-1990 (mean daily maximum = 22.3°C, mean daily minimum = 10.9°2C).

Eggs were not measured in 1993, however 1992 data showed that clutch volume differed significantly between treatments (GLM, ANOVA, F = 60.58, $p < 0.0001$, N = 69). Treatment 2 clutches (mean = 9.91 mL, N = 18) were larger than Treatment 1 clutches (mean = 8.57 mL, N = 29), which in turn were larger than Control clutches (mean = 7.17 mL, N = 22).

The majority of cowbird eggs that hatched in both 1992/1993 combined did so before (45%, N = 23) or the same day as Yellow Warbler eggs hatched (41%, N = 21). However treatment had no significant effect on the hatching order of parasitized clutches in 1992 (c2 = 2.87, p = 0.238), 1993 (c2 = 0.77, p > 0.6), or 1992/1993 combined (c2 = 1.42, p > 0.4). Therefore, the likelihood of a cowbird egg hatching before warbler eggs did not differ between Treatment 1 and Treatment 2 clutches.

In 1992 the incubation period of a clutch was not significantly affected by either treatment (GLM, ANOVA, F = 2.16, p = 0.13, N = 39) or natural clutch size (GLM, ANOVA, F = 0.34, p = 0.56, N = 39) (see Table 1). In 1993, however, although treatment did not affect incubation period (GLM, ANOVA, F = 2.19, p = 0.31, N = 42) (Table 1), the effect of natural clutch size approached significance (GLM, ANOVA, F = 3.86, p = 0.057, N = 42) due to a shorter incubation period for 5-egg clutch females (mean = 9.69 days) than 4-egg clutch females (mean = 10.22 days). However, for 1992/1993 combined, neither natural clutch size (GLM, ANOVA, F = 0.82, p = 0.45, N = 85) nor treatment (GLM, ANOVA, F = 0.04, p = 0.96, N = 85) had a significant effect on the length of the incubation period.

Mean hatching spreads of experimental clutches in 1992 and 1993 are presented in Table 2. Neither treatment nor natural clutch size significantly influenced hatching spread in 1992 (GLM, ANOVA, F = 1.18, *p* = 0.344, N = 34), in 1993 (GLM, ANOVA, F = 0.22, *p* = 0.95, N = 39) or in 1992/1993 combined (GLM, ANOVA, F = 0.36, *p* = 0.94, N = 76).

In 1992 Yellow Warbler hatching success differed significantly between Control, Treatment 1 and Treatment 2 clutches (c2 = 18.17, *p* = 0.0001). Host-egg hatching success was significantly higher in Control than Treatment 1 clutches, which in turn experienced significantly higher hatching success than Treatment 2 clutches (see Table 3). However, Yellow Warbler hatching success in 1993 did not differ significantly between treatments (c2 = 2.41, *p* > 0.20)(Table 3).

Cowbird egg hatching success in 1992 differed significantly between Treatment 1 and 2 clutches (Fishers Exact Test, *p* = 0.017, two-tailed). Cowbird eggs in Treatment 1 clutches experienced significantly greater hatching success than did eggs in Treatment 2 clutches (Table 4). However in 1993 treatment had no significant effect on cowbird egg hatching success (Fishers Exact Test, *p* = 1.0, two-tailed) (Table 4).

Discussion

In 1992 the removal of a single host egg on the day of parasitism had a significant impact on the hatching success of both cowbird and host eggs. Cowbird and Yellow Warbler eggs experienced significantly higher hatching success when a host egg was removed from the clutch than when no host egg was removed; findings consistent with Davies and Brooke's (1988) hypothesis. However, host egg removal in 1993 did not have a significant effect on the hatching success of either cowbird or host eggs. The discrepancy between the hatching success results of 1992 and 1993 could be explained by differences in ambient temperature during incubation between years. 1992 was a cooler summer than 1993 and was also cooler than the 30 year average at Delta Marsh. Perhaps cooler temperatures in 1992 made it more difficult for female Yellow Warblers to incubate large clutches, resulting in lower hatching success in large clutches.

Female cowbirds may derive a number of benefits from host-egg removal behaviour. Female cowbirds have been observed eating host eggs they have removed from the nest (Hann 1937; Norris 1944; Mayfield 1960; Nolan 1978; Scott *et al.* 1992). An egg could represent a valuable source of nutrition for a cowbird, as well as providing a source of calcium if the egg-shell is eaten (see Sealy 1992). Female cowbirds may require considerable calcium for egg-shell formation as they lay such large clutches (Ankney and Scott 1980). However, the frequency with which eggs are removed and not eaten by female cowbirds suggests the primary purpose of egg removal is not simply for food alone (Scott *et al.* 1992).

By removing a host egg, the female cowbird may reduce crowding and competition in the nest once the cowbird chick hatches (Mayfield 1960; Blankespoor *et al.* 1982). Parasitic nestlings hatching in the nests of other bird species must compete with host nestlings for food brought to the nest by the parents. Newly hatched nestlings of some parasitic species kill their host nestmates (honeyguides and *Tapera naevia* cuckoo) or eject them from the nest (cuckoos), thereby reducing the competition they must face (Livesey 1939; Hamilton and Orians 1965; Morton and Farabaugh 1979; Wyllie 1975; Payne 1977). Cowbird nestlings do not attack host young, instead they often crowd and outcompete host young for food (Friedmann 1963; Rothstein 1990). As cowbird nestling weight has been shown to be inversely related to the number of competitors in the nest (Hatch 1983), removal of a host egg could improve the cowbird chick's chances of survival. By removing a host egg early in the egg-laying period the female cowbird could also increase the chances the cowbird chick will hatch first, by eliminating a host embryo that may have already undergone some development (Berger 1951).

Due to conflicting results from the two summers, no firm conclusions may be made about the function of host-egg removal with regard to the incubation efficiency hypothesis. Hatching success experiments will be repeated again in 1994, in an attempt to provide clear evidence either for or against the incubation efficiency hypothesis.

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