Nesting Ecology of a Population of Red-necked Grebes in Northwestern Ontario

© By Tanya Wheeler

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Declaration

The research presented in this thesis was carried out by the author, and has not been previously submitted for credit toward any degree or diploma. The work of others, where included, has been appropriately cited.

May 2001

Abstract

One of the largest, documented breeding populations of Red-necked Grebes (*Podiceps grisegena holboelli*) in the world was studied at Whitefish Lake, Ontario in 1993 and 1994. Whitefish Lake (WFL) represents a unique area compared to other study sites that show mostly solitary nesting Red-necked Grebes or a few pairs/lake. The population of nesting Red-necked Grebes at WFL is large for this species. It is also exceptionally dense (mean 1.01 pair per hectare) for this territorial species and could be considered a semi-colonial situation. The mean number of pairs nesting on the lake for 1993 and 1994 was 49 (range 59-39).

The objective of the study was to expand on the limited information available on the Red-necked Grebe and to acquire data on nest and nest-site characteristics, egg measurements, clutch size, egg laying period, incubation period, hatching success, and young produced. Census results for 1993 show that peak nesting occurred on 21 June with 59 nests with eggs. Total number of eggs reached a maximum for 1993 at n = 202 for 21 June. Total nests with eggs peaked n = 39 on 22 June, 1994 while total eggs (n = 135) peaked on 30 June, 1994.

The population is strongly associated with uncultivated wild rice (*Zizania palustris*) stands in shallow bays of the lake. Shallow, uniform water depth, and the high productivity of Whitefish Lake provide abundant food and vegetation for grebe breeding activities. Eighty-five percent of 121 nests in 1994 were constructed primarily of wild rice, the most abundant emergent species in the study area. One hundred and

six of the 121 (88%) of the nests at Whitefish Lake were floating nests attached to the lake substrate by a column of sub-surface vegetation and detritus.

Nest-site selection in Red-necked Grebes is influenced by underwater characteristics such as water depth, availability of nest material and anchors for the nest. Early evidence of future plant emergence, (future) shelter from wind and waves and protection/concealment from predators and some form of anchorage (debris, sticks or logs) evident only from underwater searches.

A factorial ANOVA revealed significant differences between nest and non-nest sites for depth and vegetation density. Water depth at nests (57.4 ± 35.3 cm, n = 180) was significantly shallower than non-nest sites (86.9 ± 27.9 cm, n = 120). Overall vegetation density was higher for nest sites than non-nest sites.

Mean distance for nearest neighbour for 148 nests at Whitefish Lake was 27.2 ± 30.0 m (range 1.5-185). Aggregation indices calculated from study area indicated that clumping occurred and a simple test of significance for deviation from randomness revealed significant differences for all of eleven sections sampled.

Water depth and vegetation density must be considered when evaluating the quality of territory selected by grebes. A study investigating all variables potentially associated with breeding success is recommended. Since aggregations of this size and density are so rare for this grebe species. Whitefish Lake represents a suitable site for future research.

There are over 50,000 lakes in Ontario (OMNR) in which only a handful of have been identified to have nesting Red-necked Grebes. Regional and provincial surveys could provide additional data for comparison with Whitefish and other lakes. It is

important to establish more specific hypotheses on the habitat and nest site selection of this Grebe and perhaps determine the variables that can be attributed to their breeding success in Ontario.

Acknowledgements

I wish to thank my supervisor, Dr. J. P. Ryder for his support throughout this study and for sharing his expert advice gained from many years of valuable fieldwork on the Ring-billed Gulls and Ross's Geese and Dr. Gary Nuechterlein for his time and valuable insight as a Grebe expert. I would also like to thank my committee members Dr. W. Momot and Dr. S. Hecnar for their excellent advice and the time they spent discussing with me the various factors involved in this study from their own perspective and expertise.

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I would like to thank P. and B. Seidel of Artesian Wells Resort for their friendship and generosity, and for their keen interest in the birds they continue to monitor every spring and summer.

I am grateful to Dr. K. Abraham and A. Harris of the Ontario Ministry of Natural resources for their initial input, financial support and especially to A. Harris for identifying the Grebes of Whitefish Lake as a significant population worth investigating.

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1. Introduction

The Red-necked Grebe (*Podiceps grisegena holboellii*), also known as Holboell's Grebe, is a holarctic species that occurs in North America and Eastern Asia (Storer 1979, DeSmet 1982, Del Hoyo et al. 1992, Stout and Nuechterlein 1999). The Red-necked Grebe is a distinct subspecies and has a slightly larger bill and body size than it's counterpart *Podiceps. g. grisegena* in Europe and Western Asia (Stout and Nuechterlein 1999).

The breeding distribution of *P.g. holboelli* reaches the northern limit of the tree line in Alaska, Yukon and Northwest Territories and extends south through the interior of British Columbia, northern and western Alberta, north-central Saskatchewan, central Manitoba and northwestern and central Ontario and east into south-western Quebec (DeSmet 1982, Godfrey 1986, Stout and Nuechterlein 1999) (Fig. 1).

Red-necked Grebes typically nest in shallow freshwater lakes, ponds and marshes, or in bays of larger lakes with some emergent vegetation (Palmer 1962, Stout and Nuechterlein 1999). The presence or abundance of vegetation is not a requirement in small ponds (Munro 1941) but in secluded bays of larger lakes, cattails *(Typha spp.)*, sedges *(Carex spp.)*, and reed beds (*Scirpus spp.)* provide concealment for birds, and nest material.

Red-necked Grebes winter along the marine waters of the east and west coasts of North America (Fig. 1). Along the Pacific coast, it winters from the Aleutian Islands and southeastern Alaska south to central California. On the Atlantic coast, it winters

Figure 1. Breeding distribution and wintering range of the Red-necked Grebe in North America (from Stout and Nuechterlein 1999).

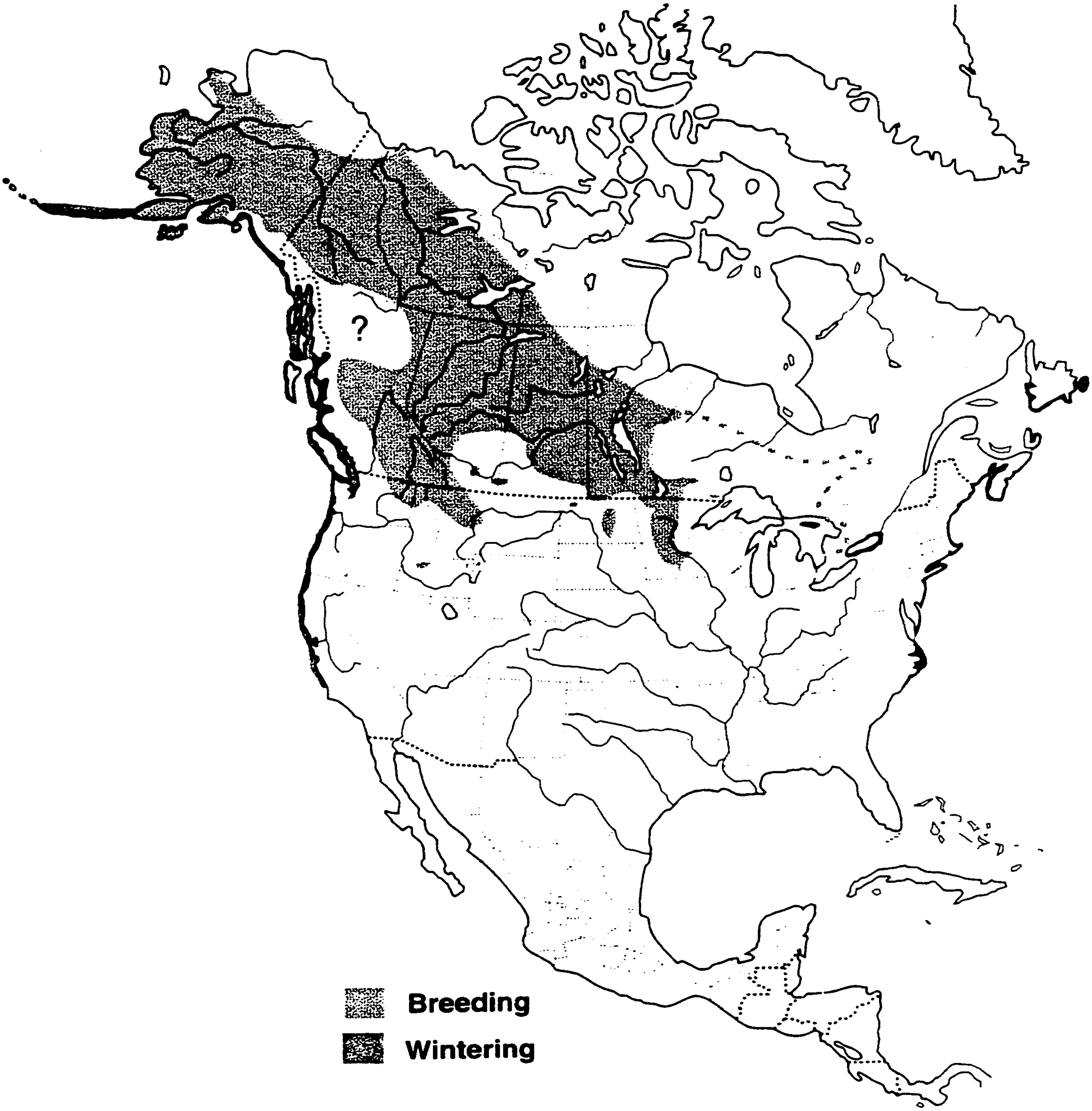


Figure 1

in Newfoundland and south to North Carolina and occasionally to central Florida (DeSmet 1982, Godfrey 1986, Stout 1995, Stout and Nuechterlein 1999) (Fig. 1). Fall migration of eastern-wintering migrants is principally via the Great Lakes from eastern breeding populations. Pacific-wintering migrants may represent breeding populations from the west. Red-necked Grebe migration has been poorly documented other than a recent unpublished M.S. thesis by Stout (1995).

The main food source for mature Red-necked Grebes consists of aquatic and terrestrial invertebrates and small fish (Palmer 1962, Cramp and Simmons 1977). The North American race, *P. g. holboelli*, is thought to eat more fish than invertebrates unlike its' European counterpart, *P. g. grisegena* (Wetmore 1924, Palmer 1962, Stout and Nuechterlein 1999). Tadpoles (Anura), salamanders (Urodela), crustaceans (Crustacea) mollusks (Mollusca), aquatic worms (Annelida) and some vegetation were found in the stomach contents of 46 Red-necked Grebes (Wetmore 1924).

The young are fed mostly insect larvae including dragonflies (Anisoptera), damselflies (Zygoptera) and caddis fly larvae (Trichoptera) in the first week and gradually take on larger food items such as crayfish, tadpoles, aquatic and terrestrial invertebrates and small fish (2-6 cm) (Munro 1941, Palmer 1962, Stout and Nuechterlein 1999).

Published literature on the Red-necked Grebe in North America is limited. Palmer (1962) summarized much of the existing breeding biology from short papers that include observations from very few breeding pairs. Studies of the Eurasian race are more extensive (Wobus 1964). Vlug and Fjeldsa (1990) have compiled a "Working Bibliography of Grebes of the World" in which there is a bibliographical section for

Holboell's Grebe consisting primarily of general accounts in short papers on behaviour, habitat and feeding ecology, range and populations.

Available studies of Red-necked Grebes are for the most part, unpublished masters theses (Kevan 1970, Riske 1976, DeSmet 1983, Ohanjanian 1986) with few published exceptions (Chamberlin 1977, Fournier and Hines 1998, Stout and Nuechterlein 1999). Kevan (1970) studied factors affecting nest dispersion of a population of Red-necked Grebes on Astotin Lake, Alberta. Riske (1976) presented 6 years of data on 5 grebe species, including the Red-necked Grebe. He looked at human and environmental impacts on distribution and abundance, and reproductive success. A two-year study of the breeding biology and productivity of the Red-necked Grebe at Turtle Mountain Provincial Park, Manitoba, provides the most recent account of a breeding population of Red-necked Grebes (DeSmet 1983).

One of the only publications on the breeding ecology of individual pairs of Red-necked Grebe was conducted in the Yellowknife region of the Northwest Territories (Fournier and Hines 1998). More recently, the "Birds of North America" paper on the Red-necked Grebe completed by Stout and Nuechterlein (1999) is the most complete report to date.

In all studies, the data on the breeding ecology of the Red-necked Grebe came from a number of breeding pairs on separate small lakes or potholes in the study area. They are usually described as solitary nesters (Palmer 1962), however aggregations can produce semi-colonial conditions (Stout and Nuechterlein, 1999) and are sometimes referred to as 'loose colonies' (Palmer 1962). Whitefish Lake provided a unique opportunity to compile baseline data on the largest (reported) nesting population of Red-necked Grebes in the world. Whitefish Lake (WFL) presents a unique situation as compared to other studies that are mostly on solitary nesting Red-necked Grebes or a few pairs/lake. The breeding population at WFL is not only large for this species, it is also exceptionally dense (pairs/ha) for this territorial grebe.

In Ontario, the species is restricted to breeding areas in the west; Abram Lake, Pelican Lake, Whitefish Lake, Sandy Lake, Trout Lake, Lillabelle Lake, Mildred Lake and counties north and west of Lake Ontario (Palmer 1962, Godfrey 1986, Armstrong 1950 in Cadman et al. 1987, Dobos and Edmondstone 1998, Stout and Nuechterlein 1999) (Fig.2). Until recently, Lillabelle Lake (near Cochrane, Ontario) had the largest reported number of nesting pairs of Red-necked Grebes in Ontario: approximately 15 breeding pairs for the past 30 years. These numbers however, have declined over the past 5-10 years and now rarely exceed 2-3 pairs (Cochrane Field Naturalists, pers. comm.). A resulting loss of habitat from changes in water levels from a nearby dam project has caused a disappearance of nests reported on Steeprock Lake, Atikokan Ontario (D. Elder, pers. comm.).

Red-necked Grebes nest on shallow lakes or ponds rarely less than 2.0 ha (Stout and Nuechterlein 1999) however they also inhabit ponds as small as 0.1 ha adjacent to other surrounding ponds (Fournier and Hines 1998). Nesting also occurs on large lakes in discrete sheltered bays along shorelines. This habitat type is typical of Whitefish Lake, near Thunder Bay, Ontario.

At present the largest number of nesting pairs in Ontario occurs on Whitefish Lake near Thunder Bay, Ontario. Breeding birds were first noticed in small numbers at

Figure 2. Breeding distribution of the Red-necked Grebe in Northwestern Ontario.

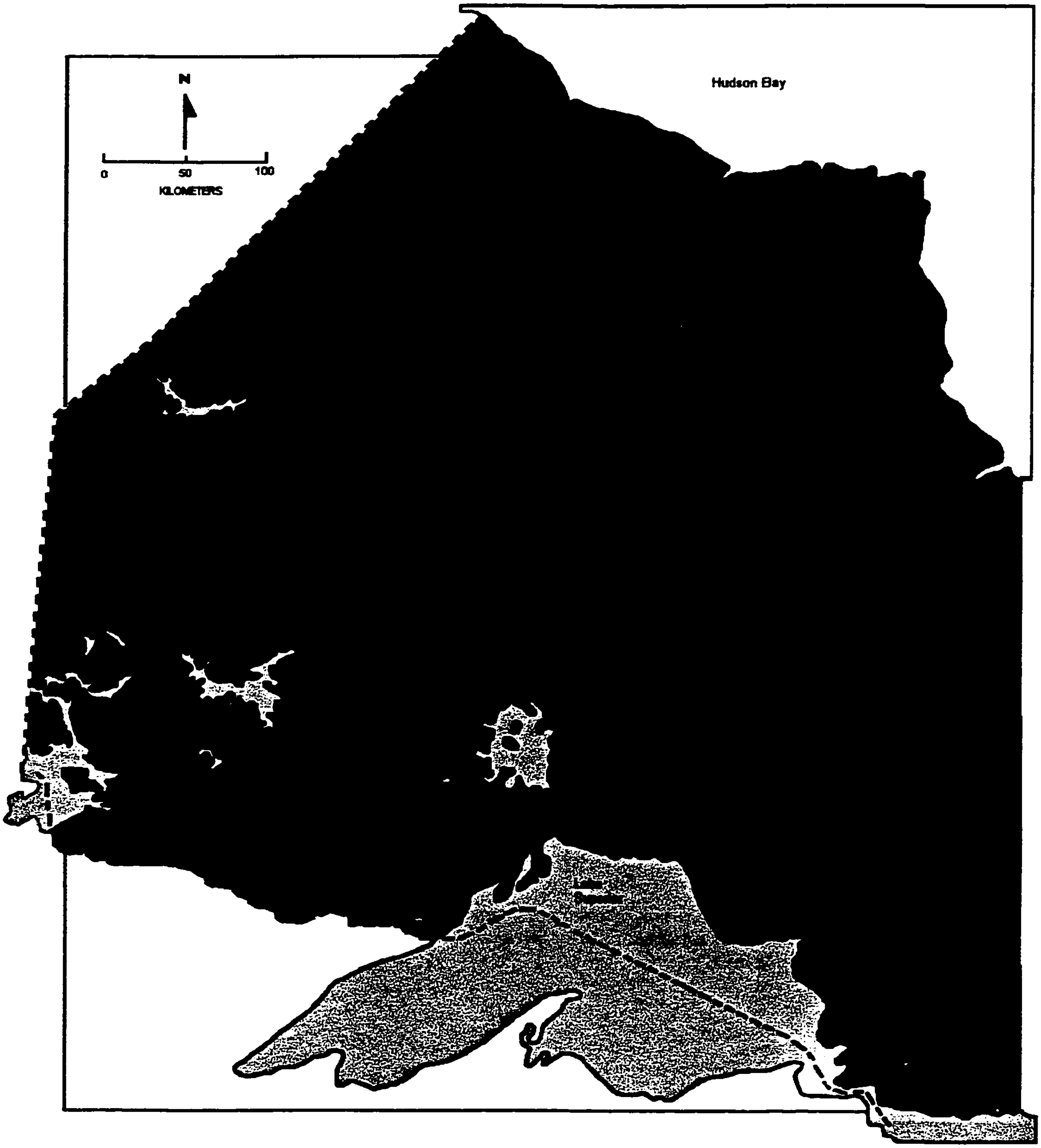


Figure 2

Whitefish Lake in the 1930's; 1-6 pairs reported from 1932-1961 (A. Harris pers.comm.).

From 1988 to 1992, A. Harris of the Thunder Bay Field Naturalists conducted an annual Red-necked Grebe census at Whitefish Lake during the second week of June (Table 1). In 1992, he found a nesting population of approximately 40-50 pairs of Red-necked Grebes (A. Harris pers. comm.). The population now consists of more than 50 breeding and non-breeding pairs, larger than any reported by DeSmet (1982).

This population is associated with wild rice (*Zizania palustris*) stands in shallow bays in the west end and northwest shoreline of the lake. Wild rice stands on Whitefish Lake and discrete bays situated along the shoreline provide concealment from predators, adequate shelter from the wind and high waves, and provide abundant nest material for the 'loose colony' described in this study.

Shallow, uniform water depth, and the high productivity of Whitefish Lake provide abundant food and vegetation for Red-necked Grebe breeding activities. Uncultivated wild rice stands in many bays along the west, northwest and south shores permit greater numbers of breeding pairs to nest with a reduced need for competition for prime nest sites and habitat resources. It is the lake's glacial history and its shoreline geography combined with food and nesting resources that have led to the high numbers of nesting Red-necked Grebes in one location compared with other reports. This lake provides an ideal habitat for Red-necked Grebes.

I conducted this study to expand on the limited information available on the Red-necked Grebe and to acquire data on nest and nest-site characteristics, egg measurements, clutch size, egg laying period, incubation period, hatching success, and

Table 1. Whitefish Lake Red-necked Grebe nest survey results, Ontario Ministry of Natural Resources, 1988-1992.

Date	Notes
26 June 1988	40 adults, 10 nests*, 6 adults with young. Incomplete survey.
9, 22 July 1989	23 nests*, 3 adults with young. Complete survey.
21 May 1990	20 pairs, some nests* started. Incomplete survey before peak nesting.
23 June 1991	58 nests*, 3 adults with young. Complete survey.
20 June 1992	40-50 pairs, 45 nests*. Complete survey.

*Some may be platforms without eggs (see text).

young. Whitefish Lake represented the exclusive source for study and data collection for this paper in the 1993 and 1994 field seasons.

The purpose of the present study was to investigate factors related to the high number of breeding pairs of Red-necked Grebes at Whitefish Lake. Wild rice stands, sheltered bays, shallow uniform water depth, high productivity and an abundance of food sources make Whitefish Lake desirable for breeding pairs of Red-necked Grebes. Dense wild rice stands, where the breeding population concentrated, were thought to provide ideal nest sites, i.e.) abundant vegetation for nesting and nest construction, protection from wave action and predators and a significant nursery for aquatic food sources.

2. Study Area

Whitefish Lake (48 17' N., 90 11' W.) is located in Hardwick and Strange townships 72 km south west of the city of Thunder Bay, Ontario. It is a shallow, mesotrophic lake with an average mean depth of about 1.8 m, a maximum depth of 6m and an area of 3015 ha.

Whitefish Lake's glacial history makes it one of the most productive lakes in the Thunder Bay district. The lake is rich in minerals and sediment attributed to its basin shape that is thought to have trapped deposits from glacial activity in the region. The lake rests on a sedimentary surface and is not derived from granite. This feature makes it unique and contributes to high calcium release into the lake (R. Ryder, pers. comm.).

Whitefish Lake has high nutrient availability in the form of high levels of dissolved solids, particularly phosphorous (Total P = 0.027mg/l) and nitrogen (0.522) that increase lake productivity. Utilizing Ryder's Morphoedaphic Index (MEI) (Ryder 1965) as a crude measure of lake productivity (total dissolved solids/mean depth), Whitefish L. has an MEI of 33 -1 exceeding most other lakes in the district (Appendix 1). Whitefish Lake is considered to be one of the most productive lakes in the Thunder Bay district (M. Freutel, pers. comm.).

Water level is regulated by a dam on the Whitefish River; the single outlet from Whitefish Lake. The lake is surrounded by hills with three small in-flow streams. Adjacent forest consists of poplar (*Populus spp.*), willow (*Salix sp.*), white spruce (*Picea* *glauca*) balsam fir (*Populus balsamifera*) and some white cedar (*Thuja occidentalis*). On the northwest shore is a peat bog dominated by black spruce (*Picea mariana*).

Significant features of this lake include: its shallow uniform depth, gradually sloping shoreline and abundant aquatic vegetation. The latter includes large stands of wild rice (*Zizania palustris*), cattail (*Typha latifolia*), common burreed (*Sparganium emersum*) and spike-rush (*Eleocharis sp.*), water lily (*Nymphaea odorata, Nuphar variegatum*), pondweeds (*Potamogeton spp., Sagitaria spp., Spirodela sp., Lemna minor*) horsetail (*Equisetum spp.*) and sedges (*Carex spp.*). Submergent vegetation includes milfoil (*Ceratophyllum demersum*), bladderwort (*Utriculatum vulgaris*), coontail (*Myriophyllum sp.*) and a detritus layer composed mainly of decaying wild rice stalks.

The three predominant fish species in Whitefish Lake are yellow perch (*Perca flavescens*) walleye (*Stizostedion vitreum*) and northern pike (*Esox lucius*). Walleye, introduced in 1943, have established a self-reproducing population. Perch and cyprinids were not recorded in early studies (Armstrong 1950) and to date, there is no evidence that cyprinids occur. Commercial fishing in the 1940's, and the introduction of walleye may have significantly affected the decline of whitefish (*Coregonus clupeaformis*) and eventually led to its extirpation in the 1960's and 70's (W. Momot pers. comm.).

Though little quantitative data are available on macroinvertebrates in Whitefish L., it is has exceptionally large annual emergence of dragonflies (*Odonata*) as well as early spring emergence of mayflies (*Ephemeroptera*) stoneflies (*Plecoptera*) and caddisflies (*Trichoptera*) (pers. obs.).

The Red-necked Grebe population at Whitefish Lake occupies two distinct areas of uncultivated wild rice: an area along the northwest shoreline and a disjunct section off the south shore. Aerial photos show whitish-grey areas along the shoreline that represent uncultivated wild rice (*Z. palustris*) stands (Fig. 3). The edge of the west and northwest shore consists of a floating, vegetated peat mat, parts of which are dominated by cattail. Location of the colony along the described shoreline has remained consistent since 1992 and shows signs of eastward expansion.

Figure 3. Aerial photographs (1992) representing the west end, northwest shoreline and south shore of Whitefish Lake, Ontario. (Ontario Ministry of Natural Resources 1992 photos, serial numbers; 92-4808 18-249, 92-4807 19-44, 92-4808 18-25).

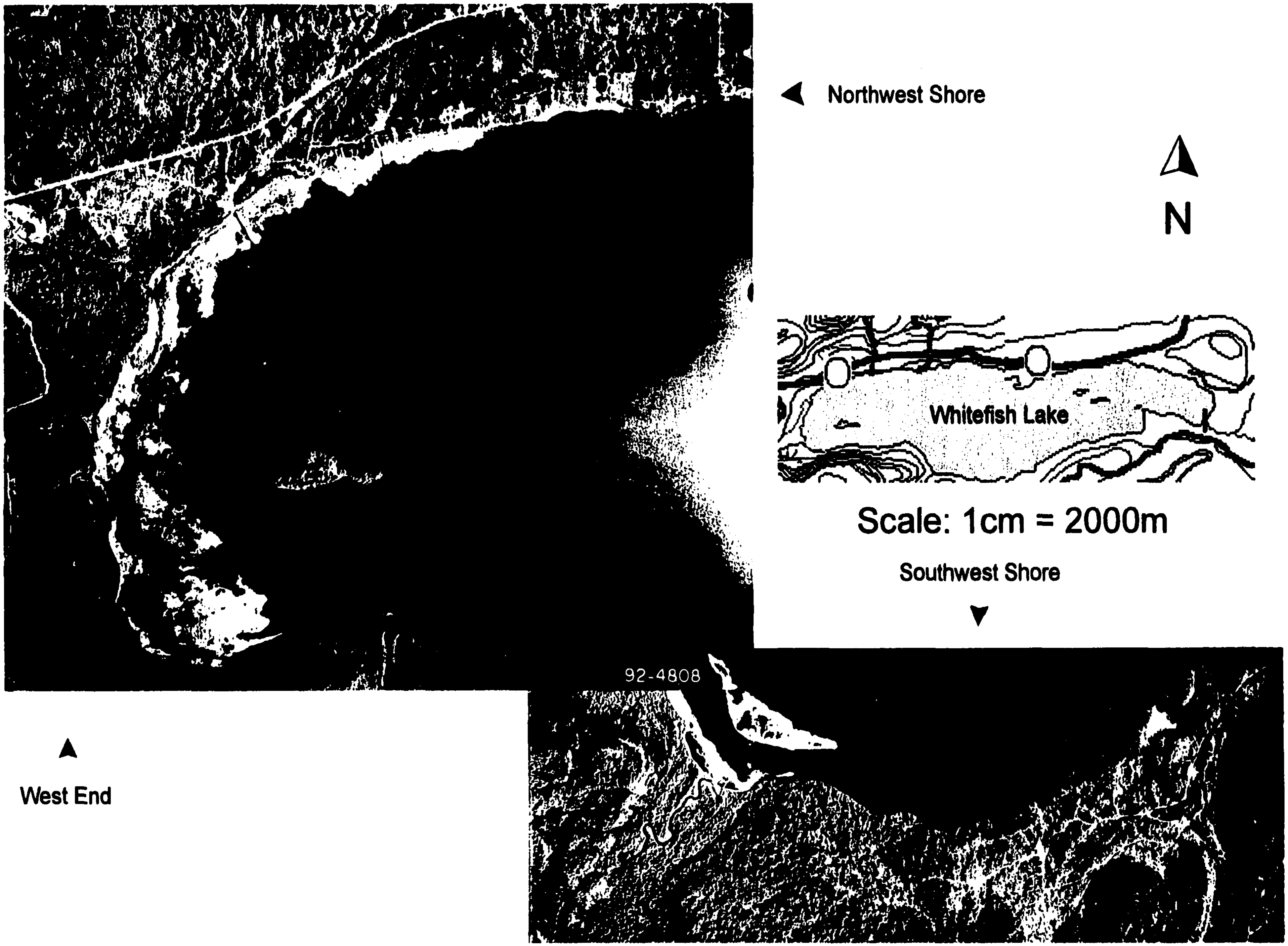

Northwest Shore
N
Whitefish Lake
Scale: 1cm = 2000m
Southwest Shore
92-4808
West End

Figure 3

3. Methods

The breeding ecology of the Red-necked Grebe at Whitefish Lake was documented in 1993 and 1994. I collected data on: arrival dates of birds to the study area; courtship; nesting; territory establishment; total numbers of nesting pairs; distribution of nests; nest and nest-site characteristics; egg laying; incubation; parental and brood behaviour; and reproductive success.

In 1993 and 1994, the entire length of Whitefish Lake shoreline was searched by motorized canoe for nest activity and birds. This led to the determination of the colony limits on the west and northwest shoreline and the presence of the birds on the south shore.

Field studies began 8 May 1993, one week after the disappearance of ice from the lakeshore. A high power spotting scope (Bushnell 20x) positioned on the northwest shoreline provided good visual coverage of about half of the study area. On 10 May 1993, I conducted a Red-necked Grebe census from the northwest corner of the lake along a floating peat mat to the west end. Beginning 13 May, the census resumed by canoe until 10 August 1993. Each nest (section) was visited approximately two times per week with an average of 2-4 days between census intervals. On 12 June 1993, a whole lake census was conducted to count the number of individual pairs.

In 1994, field observations began 17 April. The first noted arrival of Red-necked Grebes at the Lake was 4 May, immediately after ice-out. Census from shore began 4 May and continued by canoe 18 May and ended 16 August 1994. In both years, presence of the birds and or vocalizations suggested possible nest sites. On 10 June 1994, a whole lake census was conducted to count the number of individual pairs.

General courtship, nesting and territorial behaviours were observed an estimated 59 and 40+ pairs of Red-necked Grebes 1993 and 1994 respectively. Changing numbers of pairs within each bay, diving behaviour and changes in platform and nest sites prevented accurate counts of the numbers of pairs in the early field season. Consistent bird counts were only possible when pairs established a nest with eggs.

The study area was divided into 16 separate sections (Fig. 4) based on the west and northwest shoreline features (bays) as well as a disjunctive section of the south shore. Computer-drafted maps that showed the shoreline features specific to each study section were brought into the field along with a census form to record nest activity. Each section consisted of a cluster of birds separated from adjacent clusters by distance or variation in the habitat such as the end of a bay, resorts/docks, volatile water, or high shorelines with strong wave action. The study area consisted of 8.4 km of western shoreline as well as parts of the northwest and south shores.

The 16 sections (Fig. 4) corresponded with the 16 aggregations of nesting birds. Section A was originally representative of the west end but further divided into A1, A2, A3 and A4 to distinguish bays and sub-groups of nesting pairs. Section F provided poor habitat in that its shoreline was marked by deeper water, high wave action with very little vegetation, thus contained no nests.

Estimates of distances between sections and total population area were established using aerial photographs of Whitefish Lake and shoreline landmarks

Figure 4. Study area at Whitefish Lake, Ontario showing the areas of 16 sections (letter designation) and estimates of total area (ha). (Ontario Ministry of Natural Resources aerial photos, 1992.) Dots represent individual nests plotted on each section.

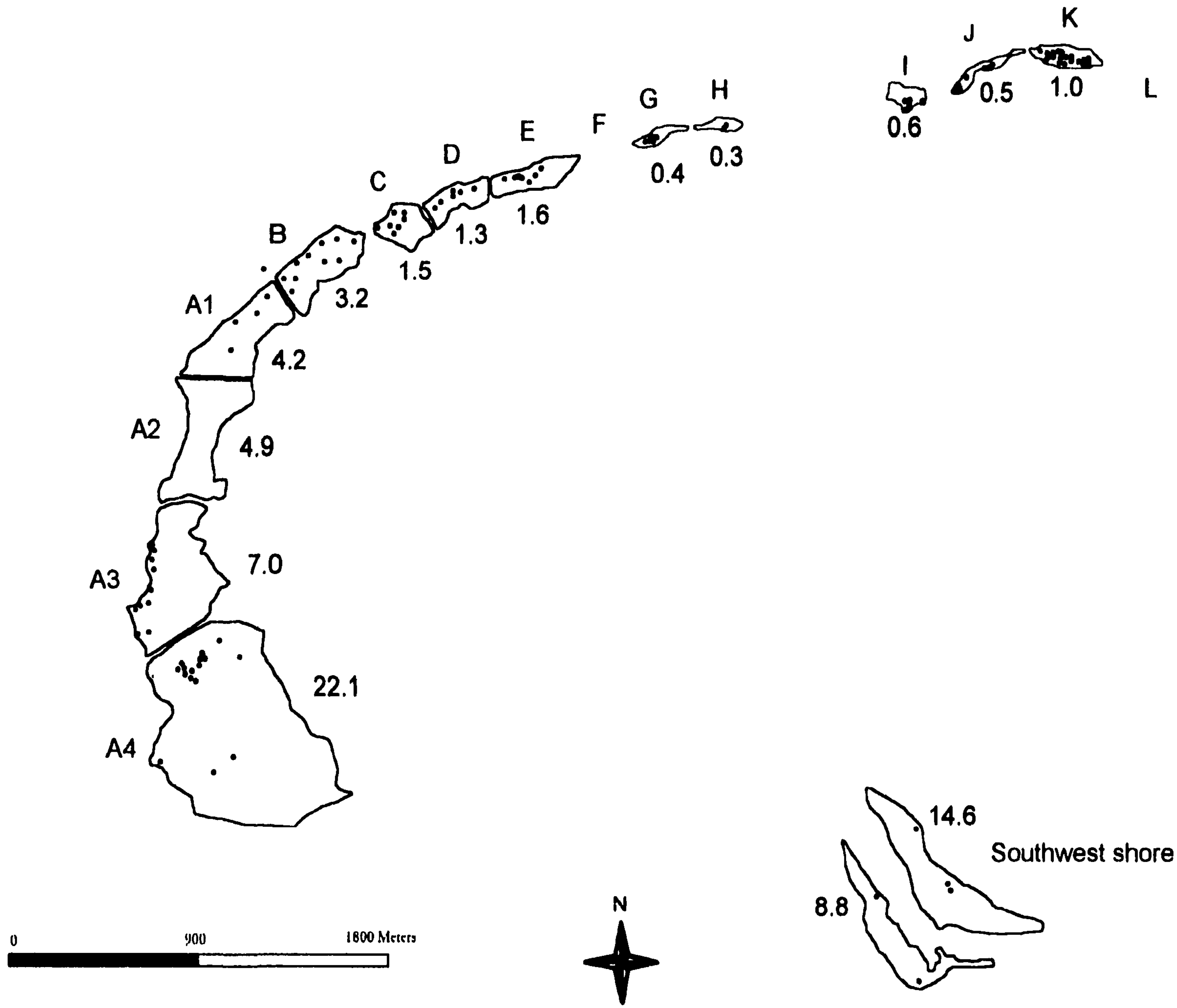

K
J
I
H
G
F
E
D
C
B
A1
A2
A3
A4
L
0.5
1.0
0.6
0.3
0.4
1.6
1.3
1.5
3.2
4.2
4.9
7.0
22.1
14.6
Southwest shore
8.8
N
0
900
1800 Meters

Figure 4

(OMNR 1992 photos, serial numbers; 92-4808 18-249, 92-4807 19-44, 92-4808 18-251)(Fig. 4). An estimate of density (pairs/ha) for each section was calculated based on peak number of nests with eggs from 1993 and 1994.

Measurements were taken of nearest neighbour distances and distance from shore for each nest in a section using a floating 50 m tape. A simple correlation analysis was performed to explore a relationship between nearest neighbour distances and distance from shore.

An index of aggregation (Clark and Evans 1954) model was used to determine whether nests were placed randomly, clumped or uniformly. Section density (based on peak numbers of nests with eggs (mean value) for 1993 and 1994) and mean nearest neighbour distances (in vegetated areas) were applied to the formula based on Clark and Evans (1954) method (see Appendix 2). An index of aggregation was calculated for each section and a simple test of significance for deviation from randomness was also determined (Appendix 2).

Censuses were conducted by canoe, traveling through the shoreline vegetation to any site which appeared to have nesting activity such as vocalizing pairs, presence of Red-necked Grebes, and evidence of platform or nest activity. During each census, nests were identified and marked on computer-drafted maps. A record was created and maintained for each nest for future analysis of overall nest success.

A wooden stake, made of 2" x 1/4" slats, was placed along the shore directly behind each nest for identification. Censuses involved a visit to nest sites (by canoe) every 2-4 days during the nest building and egg laying period, then every 4-6 days thereafter to prevent excessive disturbance. Each census consisted of a visit to as many sections as possible (time and weather permitting).

Newly constructed nests were recorded in field notes and transferred to individual nest record forms. Nest histories were compiled for nests that contained at least one egg and remained intact and stable on the water surface for at least 15 days. Due to the high frequency of platform construction and high rate of disappearance of nests, the arbitrary number of 15 days was determined for inclusion in nest history data. Plant species used in nest composition were identified and estimated percentages of specific materials used in the construction of the nests were recorded.

For each nest I recorded to the closest centimeter: maximum diameter (below the water surface), minimum diameter (above the water surface), cup diameter, cup depth, highest point above the water, and water depth at the nest (from substrate to bottom of the nest at water level) (Fig. 5).

Presence of new eggs was recorded. Individual eggs were uniquely marked indicating order of laying whenever possible. Otherwise they were marked in order of discovery. The order of laying was determined by the degree of staining that occurred from resting in the nest. Bright blue eggs were clean and free from nest staining and were considered newer than those with varying degrees of staining. Darker stained eggs were considered older. Brown or pink nail enamel marked the blunt end with a single or series of dots indicating order within a clutch.

Maximum length (L) and breadth (D) were measured to the nearest 0.1 mm using Vernier calipers. Egg volumes were calculated using the equation $\pi LD^2/6$ (Storer and Nuechterlein 1992). Egg fates for the entire population were determined on

Figure 5. Measurements of Red-necked Grebe nests at Whitefish Lake, Ontario.

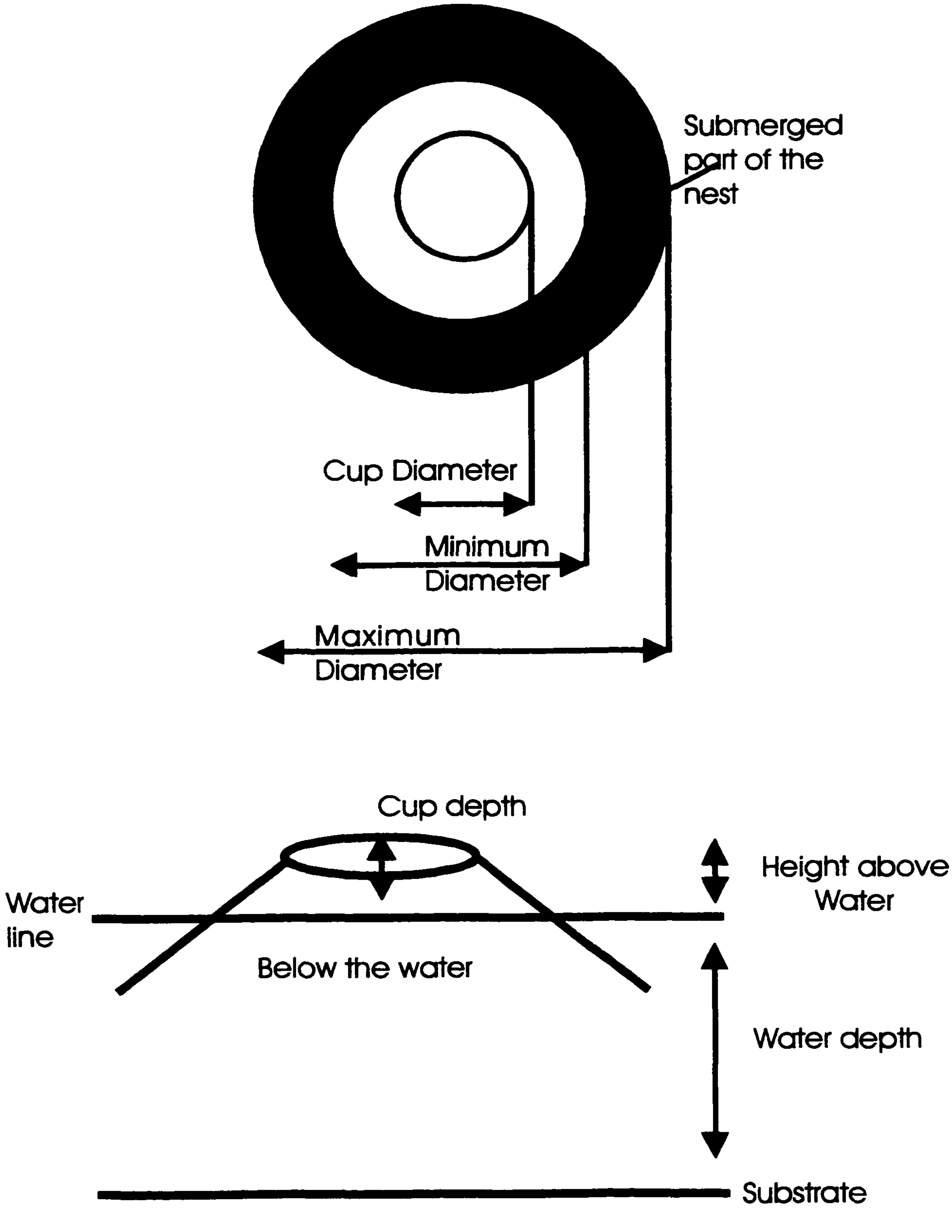

Submerged
part of the
nest
Cup Diameter
Minimum
Diameter
Maximum
Diameter
Cup depth
Height above
Water
Water
line
Below the water
Water depth
Substrate

Figure 5

the basis of viability, loss due to unknown causes, loss due to wind or waves, predation, rolled into water, cracked or broken in the nest, dumped, and hatched young.

A record of laying dates, first and last eggs, clutch size, egg laying period (ELP, from first egg laid to final clutch), incubation period (IP, according to date of first egg laid), losses due to weather, predation and/or other causes, and hatching dates. Clutch size was determined for total recorded eggs reported for each nest, including eggs lost. This information was transferred from census forms to a specific nest record for each nest.

A transect-plot method was used to determine possible differences in water depth and vegetation density between nest and non-nest sites (Fig. 6). At radii of 5, 10, and 15 m extending out from the center of the nest, (north, south, east and west), water depth and vegetation density were recorded within a 1x1 m plot. Corresponding non-nest sites were selected randomly by drawing cards from 2 paper bags containing distance values (5, 10, 15...,100 metres) and orientation values (N, S, E, W, NW, NE, SW, SE). Random distances and directions selected were measured from the corresponding, known nest-site. Cards were replaced after each draw. Independent t-test (between nests and non-nests) was used to determine whether there was a significant difference in water depth at the nest for nest and non-nest sites.

Analysis of variance was used to determine significant main effects and where significant differences occurred in vegetation density and water depth for nest and non-nest sites. A 2x3x4 ANOVA factorial design tested the null hypothesis of no difference

Figure 6. Measurements of water depth and vegetation density inside 1m x 1m plots, north, south, east and west, taken for Red-necked Grebe nest and non-nest sites at Whitefish Lake, Ontario 1994.

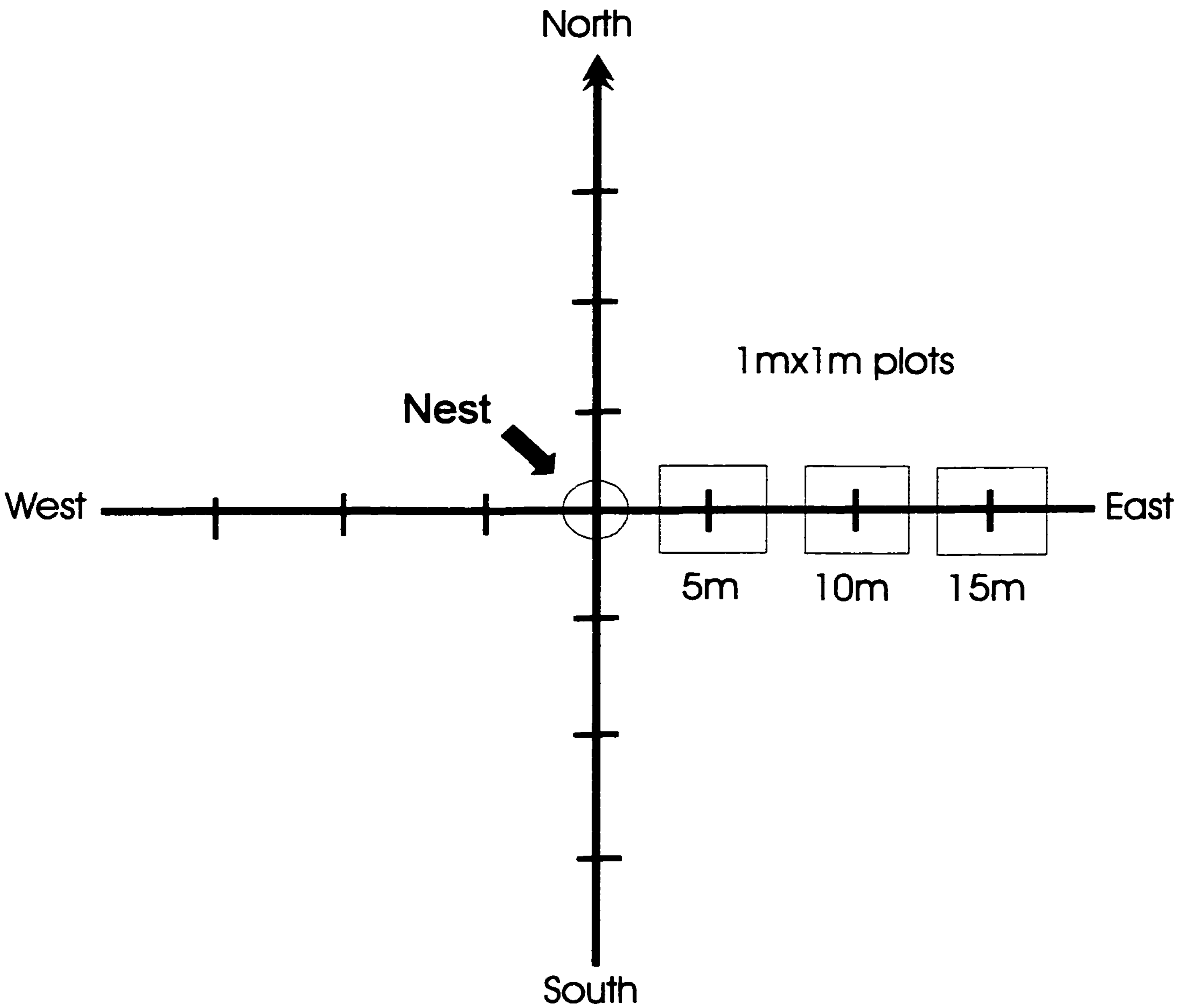


Figure 6

in water depth and vegetation density at all directions and distances extending from the nest, between nests and non-nests. All statistical procedures were performed on SPSS/Windows 9.0.0 Standard version software.

4.0 Results

Methodological Complications and Challenges

Red-necked Grebes are diving birds. They represent a significant challenge for accurate counts since they can submerge and surface only a few metres or many metres away. Hence they can be counted twice or even excluded from a count. Therefore, the numbers reported in this paper are only best estimates for adult birds and later for those mobile young that moved into open water with their parents.

Nest histories completed for pairs posed a significant problem because of the high number of re-nesting attempts and platform construction within an unmarked population. For this reason, there are higher numbers (n) of nest measurements, egg-laying periods, hatching periods, total nests (pairs) reported in the final results than there were actual nesting pairs. The appearance of duplication represents the result of re-nesting attempts that were estimated to be at least 2 nests (average) per unmarked pair in each field season.

4.1 Arrival

1993

Grebes arrived in the study area at or on approximately 28 April 1993 according to local camp owners (P. and B. Seidel, pers. comm.). This arrival date was consistent with camp owners from the furthest section K, on the northwest shore (J. Biloski, pers. comm.) who reported that grebes arrived to this part of the lake at ice-out (28 April).

Air temperature at the lake was 20° C and the sky was partially overcast. Lake water in the study area was filled with partially decayed wild rice litter from the previous years.

I arrived at the west end of the lake on 8 May 1993. I was able to count roughly 28 Red-necked Grebes, from the dock at Artesian Wells Resort (located between section A4 and B, Fig. 4). Approximately 75% appeared to have already established pair bonds by demonstrating consistent association and frequent "Greeting Ceremonies" as described in detail by Stout and Nuechterlein (1999). There was extensive vocalization among pairs and between adjacent conspecifics. At least 2 pairs appeared to engaging in "Discovery Ceremonies" indicating courtship and early pair formation.

1994

In 1994, reports from Thunder Cape Bird Observatory (located on the Sibley Peninsula beneath a major migratory flyway) indicated that nearly 100 Red-necked Grebes had flown overhead on 3 May (Al Harris, pers. comm.). The grebes are suspected to have arrived that evening at the west end of Whitefish Lake (B. Seidel, pers. comm.)

I arrived at Whitefish Lake on 5 May 1994 to find that the ice was only 20-30 metres from shore. The arrival of the grebes corresponded with the ice moving off of the lake two days earlier on 3 May 1994.

4.2 Courtship

In both 1993 and 1994, most arriving birds had already paired and were performing courtship ceremonies or building 'platforms', early nests and copulating. Pairs engaged in highly vocal displays erupting in "Whinney-Braying" to reunite separated pairs (Stout and Nuechterlein 1999). Courtship and pair bond activities were similar at least in part to those described by Storer (1963).

Red-necked Grebes at Whitefish Lake frequently displayed a "Greeting Ceremony" (Stout and Nuechterlein 1999). This greeting could be described as a recapitulation of the pair bond that served to strengthen the bond and to let others know that the individuals performing the ceremony were officially paired. A defensive display would frequently occur when intruders entered a pair's territory and might lead to aggressive behaviour or attack toward the intruder. The "Greeting Ceremony" was also triggered by the vocalizations of nearby pairs. Pairs would follow the "Greeting Display" with "Parallel Barging" as described by Stout and Nuechterlein (1999).

On 5 May 1994, fourteen clearly paired grebes (seven pairs) were collecting decaying vegetation from below the water surface and carrying this material back to a central location which often appeared to be nothing more than an accumulation of debris. Closer inspection of these accumulations revealed that these were indeed accumulations of weeds, decaying wild rice stalks from previous year, sticks, twigs and other matter which proved of some use as nest material.

Trees or branches embedded in the lake substrate often served to anchor the debris (Fig. 7a). Grebes seemed to detect these branches and accumulations from

Figure 7.

a. Red-necked Grebe nest with branches that acted as anchorage for nest material.

b. Underwater photograph beneath a nest. Branches were embedded in the lake substrate.

Figure 7a

Figure 7b

their aquatic activities (Fig. 7b) and utilized them as suitable for the construction of a platform or nest.

Pairs began the construction of what appeared to a nest but this often resulted in the creation of a 'platform', a structure similar to a nest in early appearance but serving instead as a location for important courtship ceremonies such as "Inviting", "Rearing" and "Wing Quivering" and "Weed Ceremonies".

The "Weed Ceremony", (Stout and Nuechterlein 1999), was part of the establishment of a platform but was not nearly as elaborate or intricate as that described for the Western Grebe *Aechmophorus occidentalis* (Nuechterlein and Storer 1982). Nearly all copulations took place on these platforms, consistent with the observations of others (Storer 1963; Wobus 1964; Kevan 1970). On two occasions, copulations took place on muskrat mounds which may have been intended nest-sites. Accumulations of decaying wild-rice stalks attracted both grebe and muskrat activity that included piling mounds of mud and decaying rice stalks to the lake surface.

Once platform construction was completed to a stage where it was possible for a grebe to mount the platform and remain above the water, one of the pair (sex unknown) would solicit the other by "inviting" the other to copulate by resting on the platform with the neck outstretched and the body in a low profile position parallel with the surface of the water (Stout and Nuechterlein 1999).

Frequently, these invitations resulted in solicitations and nothing more. This may have had more to do with the detected presence of human observers.

Occasionally, the wings on the back of the soliciting bird would appear to be shifting or "Quivering" as described by Storer (1963). On many other occasions, "Inviting Displays" resulted in copulation on the platforms followed by "Ecstatic Posture" displays by the mounted bird. "Postcopulatory Water-treading" also occurred following copulation (pers. obs.)

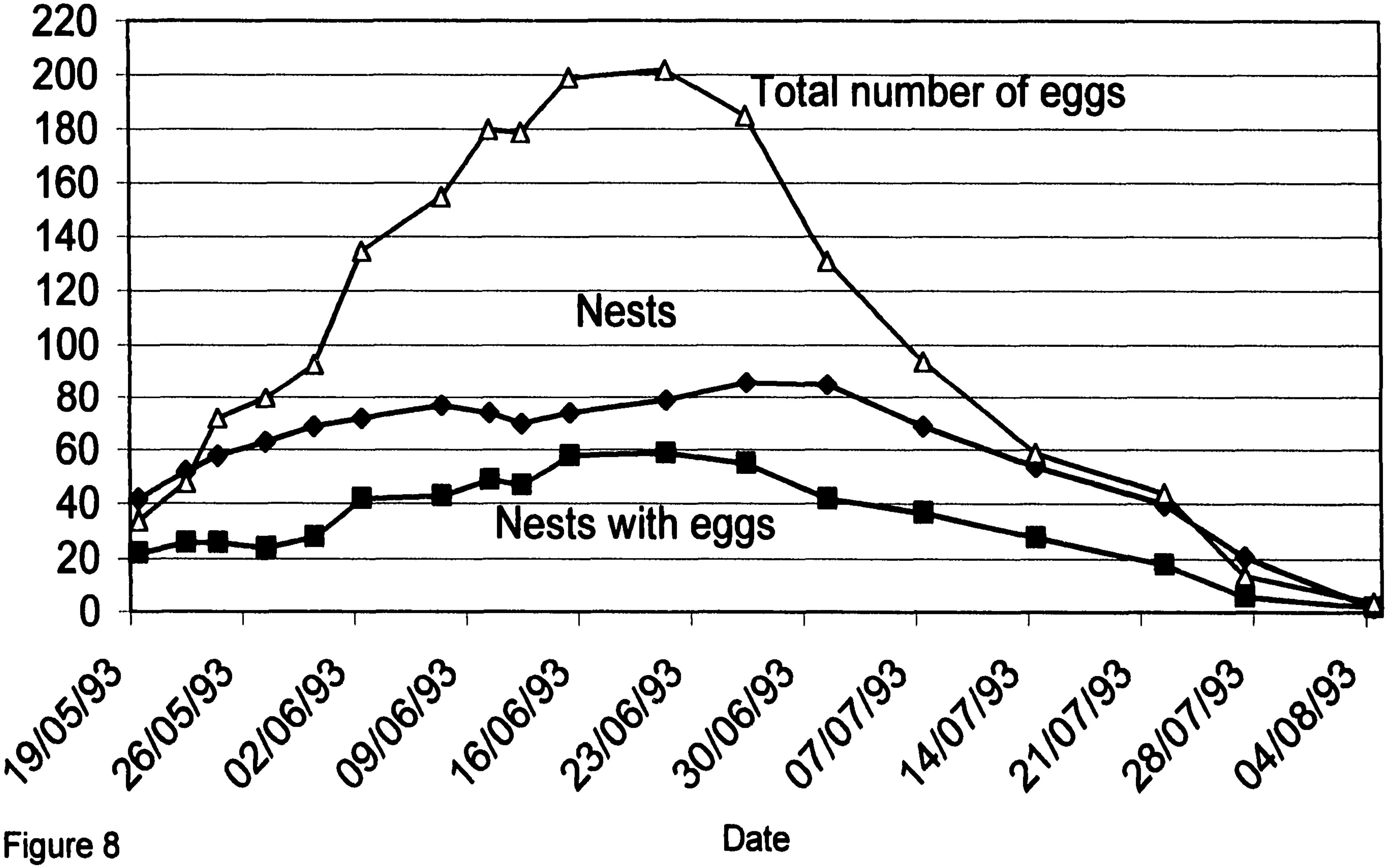
4.3 Census

Nest censuses for 1993 indicated there were 59 pairs nesting at Whitefish Lake between, 8 May and 10 August (based on peak number of nests with eggs for 21 June 1993). The first nest was initiated in early May. Whole lake census at the first part of the breeding season (8 May), and 2 more whole lake censuses, (mid June and mid July) concluded that the birds were only nesting along the west end and a portion of the north west and south shorelines which constituted 8.4 km of shoreline. Nests were not discovered past section L (Last Chance Resort) in 1993 or in 1994.

Regular censuses of the population in 1993 showed that nesting peaked in mid to late June. The total number of eggs reached a maximum of 202 on 21 June 1993. Total nests with eggs peaked (n=59) on 21 June also. Total nests (included those without eggs) reached a maximum of 86 on 26 June 1993 (Fig. 8).

Census results for 1994 showed that peak nesting and maximum eggs (n = 135) occurred on 30 June. Total nests with eggs (n = 39) peaked on 22 June while total nests (n = 56) peaked on 18 July 1994 (Fig. 9). Therefore, the total number of pairs nesting at Whitefish Lake in 1994 was estimated to be 39, based on the peak number of nests containing eggs in that year.

Figure 8. Total number of nests, nests with eggs, and total eggs from 1993 censuses of breeding Red-necked Grebes.



220
200
180
160
140
120
100
80
60
40
20
0
Total number of eggs
Nests
Nests with eggs
19/05/93
26/05/93
02/06/93
09/06/93
16/06/93
23/06/93
30/06/93
07/07/93
14/07/93
21/07/93
28/07/93
04/08/93
Date

Figure 8

Figure 9. Total number of nests, nests with eggs, and total eggs from 1994 censuses of breeding Red-necked Grebes.

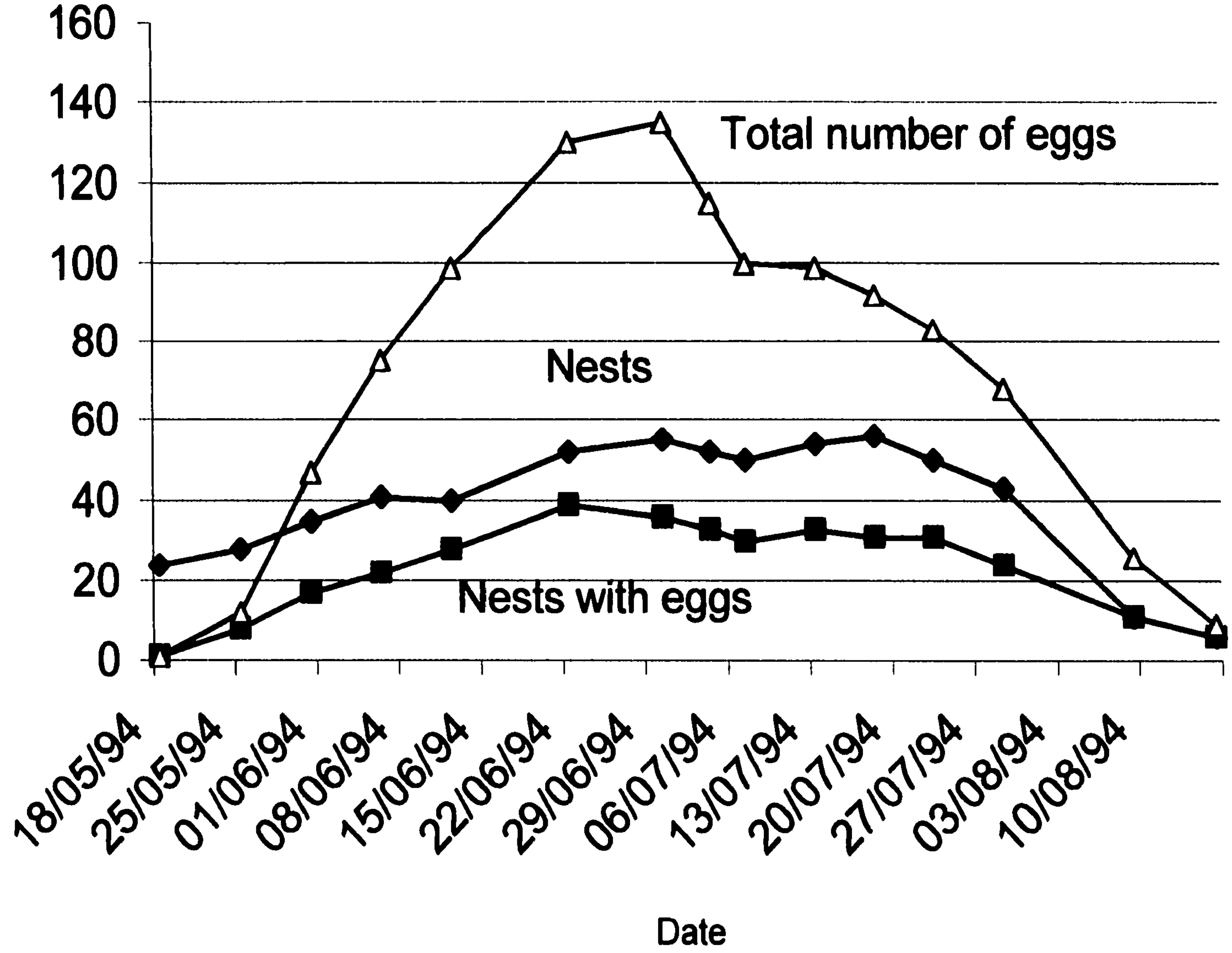

160
140
120
100
80
60
40
20
0
Total number of eggs
Nests
Nests with eggs
18/05/94
25/05/94
01/06/94
08/06/94
15/06/94
22/06/94
29/06/94
06/07/94
13/07/94
20/07/94
27/07/94
03/08/94
10/08/94
Date

Figure 9

Only 14 of the 16 sections examined at the start of the 1993 season, ever contained a nest. Section F was completely devoid of any nesting activity in both years. Section L contained two grebe pairs, only one of which ever constructed a nest. The first nest attempt was discovered 10 June, and second attempt 1 July. No eggs were recorded for either of the nests. While the mean number of breeding pairs on the lake for 1993 and 1994 was 49 (range 59-39 for 1993 and 1994 respectively) based on peak periods of nests with eggs, the mean number of pairs for 1993 and 1994 was 53.5 based on bird counts on the lake (range 58-49 pairs for 1993 and 1994 respectively). Discrepancy in numbers reveals the complicated nature of bird counts in an unmarked population.

4.4 Nest Measurements and Inter-nest Distance

Figure 10. shows that 84% of 121 nests investigated in 1994 were constructed primarily with wild rice, the most abundant emergent species in the study area. Major components of the remaining nests included water lily (*Nymphaea sp.),* buttercup (*Ranunculus aquatilus*), horsetail (*Equisetum fluviatile*) and bulrush (*Scirpus sp*). Early in the breeding season, late May – early June, most of the nests and platforms were constructed of old, decaying wild rice stalks from the previous year, and fewer with new wild rice stalks as they came available.

The old wild rice nests were typically very densely packed, compact and contained large amounts of mud. From the middle of June through the remainder of the nest-building period, nests consisted primarily of new growth wild rice. These nests

Figure 10. Vegetative composition of 121 Red-necked Grebe nests at Whitefish Lake, Ontario, 1994.

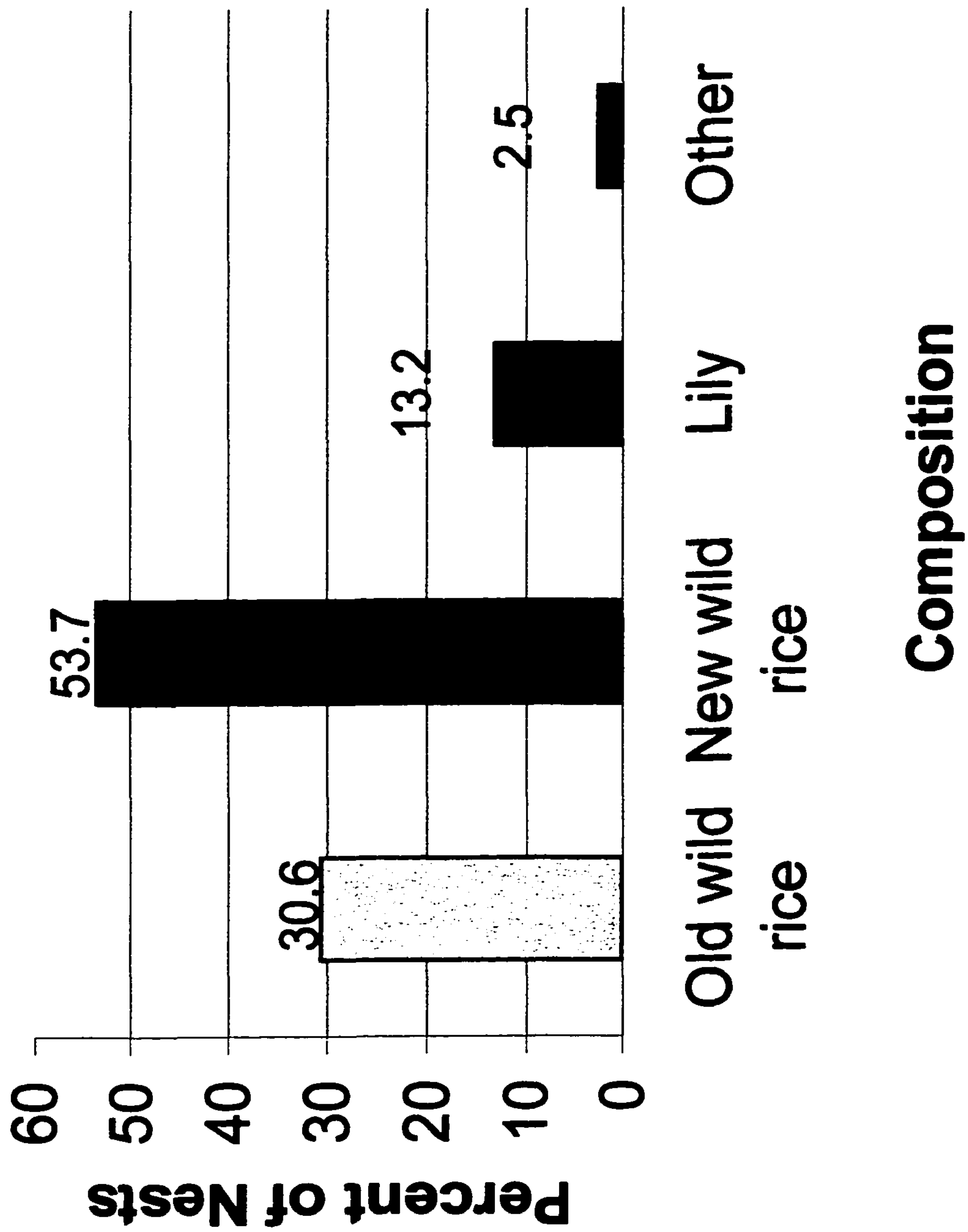

Percent of Nests
60
50
40
30
20
10
0
30.6
53.7
13.2
2.5
Old wild rice
New wild rice
Lily
Other
Composition

Figure 10

were characteristically larger than old wild rice nests and much looser in construction. In all cases, the plant species that was predominant in the nest was also the most abundant species immediately adjacent the nest site.

One hundred and six of the 121 (88%) of the nests observed at Whitefish Lake were floating nests attached to the lake substrate by a column of sub-surface vegetation and detritus. Closer investigation revealed that some underwater fixture, log, twigs or significant rise in the lake substrate served as an anchor for these nests (Fig. 7b).

Table 2. shows mean values for nest dimensions. Mean water depth at the nest for 67 nest sites was 50.4 ± 18.8 cm, range 26-108 cm (Table 3.). Mean height above water for 68 Red-necked Grebe nests was 7.0 ± 2.8 cm (Table 4).

The mean distance between nearest neighbour for 148 nests (for 1993 and 1994) was 27.2 ± 30.0 metres, while the mean distance from shore for 155 nests was 48.3 ± 6.0 meters (Table 5). Figure 11 shows the frequency for variable inter-nest distances (range) between nearest neighbours for 156 Red-necked Grebe nests (1993 and 1994). A substantial range for minimum and maximum inter-nest distances and distances from shore suggest that a table comparing the mean values by section would be informative (Table 6). A strong correlation (r=.83, p =0.001) between mean nearest neighbour distance and mean distance from shore (data from Table 6) suggests that nearest neighbour distances are less when closer to shore.

Results from the Clark and Evans (1954) aggregation model indicated a strong tendency away from randomness and toward clumping for eleven (data from Table 6) sections in the study area (Appendix 5). Scores revealed significant deviation from a

Table 2. Red-necked Grebe nest measurements (cm) at Whitefish Lake, Ontario for 1993 and 1994.

Dimension	n	Mean (cm)	s.d.	Minimum (cm)	Maximum (cm)
Outside diameter	48	98.6	34.8	57.0	235.0
Inside diameter	69	53.2	8.4	36.0	85.0
Cup diameter	68	16.4	0.6	0.0*	22.0
Cup depth	64	4.2	1.9	0.0*	7.0
Height above	68	6.9	2.8	1.0	14.0
Water depth	67	50.4	18.8	26.0	108.0

* Cup diameter and cup depth were often underdeveloped in newly constructed nests.

Table 3. Mean water depth (cm) by section for n = 67 Red-necked Grebe nests at Whitefish Lake, 1993 and 1994.

Section	n	Mean	s.d.
A1	9	36.4	7.8
A3	5	54.6	14.4
A4	12	59.1	16.6
B	11	48.4	16.4
C	1	74.0	-
G	1	108.0	-
I	3	87.0	3.5
J	3	67.3	17.2
K	22	40.5	10.0
Total	67	50.4	18.8

TABLE 4. Mean height above water (cm) for n = 68 Red-necked Grebe nests by section, at Whitefish Lake, Ontario 1993 and 1994.

Section	n	Mean	s.d.
A1	9	7.6	2.5
A3	5	8.0	2.7
A4	13	4.8	2.9
B	11	8.3	2.0
C	1	9.0	-
G	2	4.0	2.8
I	3	8.7	2.3
J	2	5.0	2.8
K	22	7.2	2.6
Total	68	6.9	2.8

TABLE 5. Inter-nest distance (m) for nearest neighbour and distance from shore (m) for Red-necked Grebe nests at Whitefish Lake, Ontario for 1993 and 1994.

	n	mean	s.d.	minimum	maximum
Nearest nest	148	27.2	30.0	1.5	190.0
Distance from shore	155	48.3	6.0	0.0	385.9

Figure 11. Frequency of (range) inter-nest distance between nearest neighbours for 156 Red-necked Grebe nests at Whitefish Lake Ontario, 1993 and 1994.

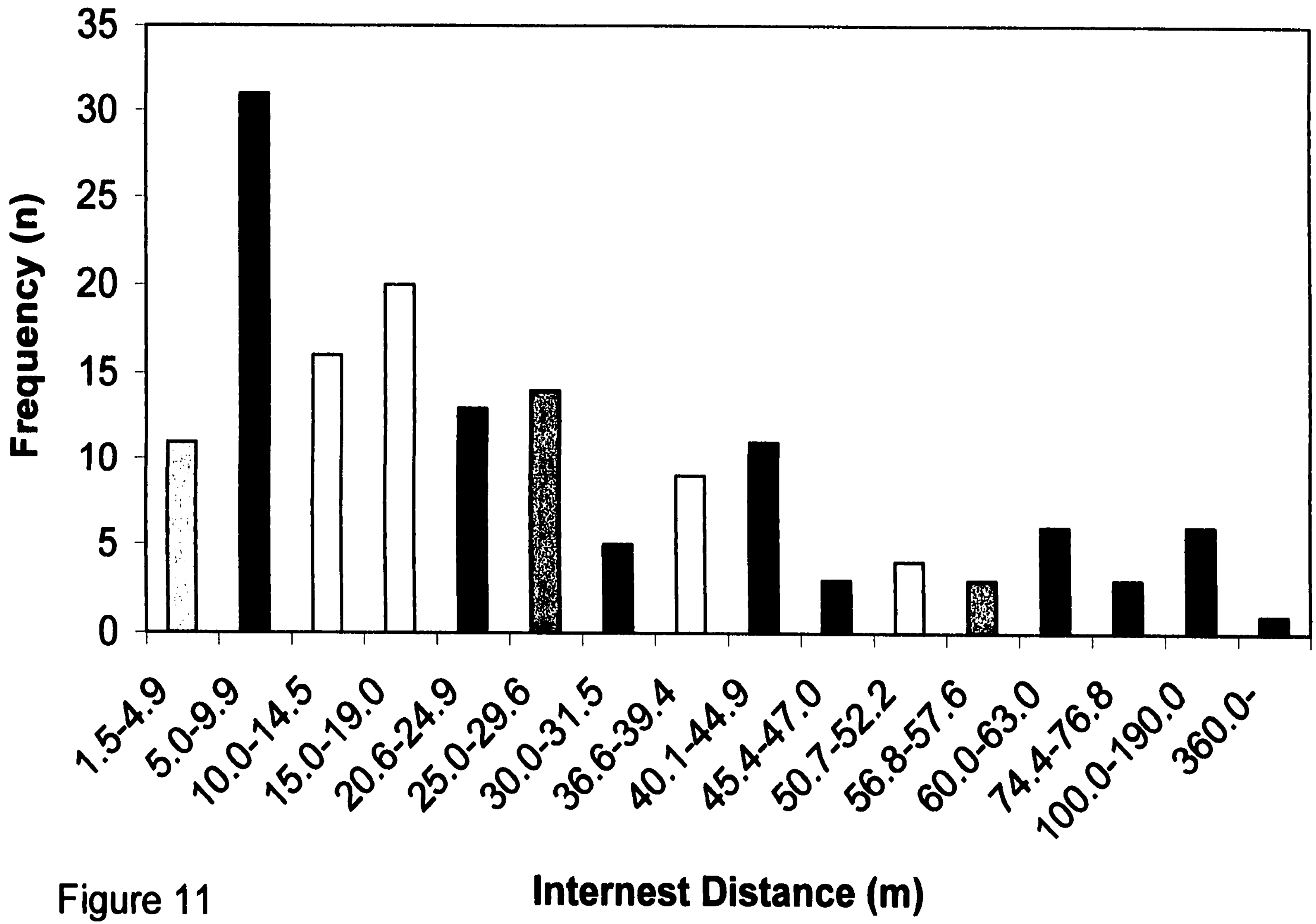

Frequency (n)
35
30
25
20
15
10
5
0
1.5-4.9
5.0-9.9
10.0-14.5
15.0-19.0
20.6-24.9
25.0-29.6
30.0-31.5
36.6-39.4
40.1-44.9
45.4-47.0
50.7-52.2
56.8-57.6
60.0-63.0
74.4-76.8
100.0-190.0
360.0-
Internest Distance (m)

Figure 11

TABLE 6. Inter-nest distance (m) and distance from shore (m) for nesting sections of a population of Red-necked Grebes at Whitefish Lake, Ontario for 1993 and 1994.

Section	n	Nearest nest (± s.e.)	n	Distance from shore (± s.e.)
A1	10	19.7 (4.6)	14	13.7 (3.2)
A2	3	4.2 (2.7)	3	0.0 (0.0)
A3	19	30.2 (3.7)	19	18.1 (3.9)
A4	27	52.9 (10.1)	28	185.1 (15.9)
B	14	32.1 (3.7)	14	22.4 (5.8)
C	10	25.3 (7.2)	10	43.6 (8.5)
G	14	19.1 (4.5)	14	14.1 (1.9)
H	3	9.1 (0.4)	3	11.7 (3.3)
I	9	14.5 (2.9)	9	19.7 (4.5)
J	13	22.3 (9.1)	14	10.1 (1.6)
K	24	15.8 (1.8)	25	18.3 (2.8)
L	2	6.3 (0.0)	2	1.9 (0.1)
Total	148	27.2 (2.5)	155	48.3(6.0)

random pattern for all sections indicating clumping behaviour in the population (Appendix 5).

Total population area comprised 48.6 hectares including the disjunctive section on the south shore. Mean population density for the study area was 1.01 pair per hectare (mean of 49 pairs/48.6 hectares, range 59-39 for 21 June1993 and 22 June 1994 respectively based on peak nests with eggs from census data). Estimates of density for each (n = 13) section (pairs/section based on peak numbers of nests with eggs for 1993 and 1994) are presented in Appendix 3.

4.5 Egg Laying, Incubation, and Hatching

The first egg in 1993 was observed on 13 May and on 18 May in 1994. The mean values (length and diameter) for 327 eggs for 1993 and 1994 are shown in Table 7. Egg fates recorded in Table 8 show that 41.3% of 789 eggs were potentially viable (laid within an acceptable incubation period 21-35 days) but whose fate was undetermined. A certain proportion of those eggs that were viable (41.3%) may have hatched to produce hatchlings but could not be confirmed so were deemed possible young. Of the remaining eggs, 31.6% were lost to unknown causes, 6.5% were inviable (had been in the nest for over 35 days), 4.2% were lost to bad weather resulting in high winds and wave action disturbing the nest, 8.1% were predated, and only 4.1% of the total eggs censused in this study, were confirmed to have hatched and therefore resulted in hatchling young.

TABLE 7. Measurements of 327 Red-necked Grebe eggs at Whitefish Lake, Ontario, 1993 and 1994.

Dimension	n	Mean	s.d.	Minimum	Maximum
Length (mm)	327	5.4	0.2	4.5	5.9
Diameter (mm)	327	3.5	0.2	2.4	3.9
Volume (cc) *	327	35.2	3.9	15.1	46.1

* Egg volumes were calculated using $\pi LD^2/6$ (Storer and Nuechterlein, 1992).

Table 8. The fates of 789 Red-necked Grebe eggs for 1993 and 1994.

Egg Fate	Frequency	Percent
Possible (viable but fate undetermined)*	326	41.3
lost to unknown causes	249	31.6
inviable	51	6.5
lost to bad weather**	33	4.2
predation	64	8.1
rolled into water	21	2.7
cracked or broken in the nest	8	1.0
dumped	5	0.6
resulted in hatched young	32	4.1
Total	789	100

*Viable within an acceptable incubation period (21-35 days) but whose fate was undetermined.
** Lost to bad weather resulting in high winds and wave action disturbing the nest.

The mean egg laying period for 214 pairs was 10.4 days ± 6.2 s.d. (range 1- 32 days). The mean value for incubation period (IP) was 29.8 ± 6.5 s.d. days (range 1-48 days). The average clutch size for 1993 and 1994 for 177 pairs was 4.3 ± 1.7 s.d (range 2-12) for nests containing 2 or more eggs. The average clutch size for 1993 and 1994 for 214 pairs was 3.7 ± 2.1 s.d. (range 1-12) including nests containing single eggs. Single eggs in a nest were included in the second analysis because many final clutches resulted in only one egg for the bulk of the incubation period. Figure 12 illustrates the frequency for various clutch sizes for 214 Red-necked Grebe clutches at for 1993 and 1994.

Results were calculated based on nest history data for an estimated 59 and 39 nesting pairs for 1993 and 1994 respectively. Nest histories for 214 apparent pairs represent the occurrence of re-nesting for unmarked birds, therefore suggesting a ratio of 2.18:1 (nests: for every pair).

4.6 Nest Site Selection

An independent sample t-test showed a significant difference in water depth between nest and non-nests. Water depth at nests (57.4 ± 35.3 cm, n = 180) was significantly shallower ($t = -7.69$; 1,298 df; $p < 0.05$) than non-nest sites (86.9 ± 27.9 cm, n = 120).

Figure 12. Clutch size frequency (%) for 214 Red-Necked Grebe clutches at Whitefish Lake, Ontario, 1993 and 1994.

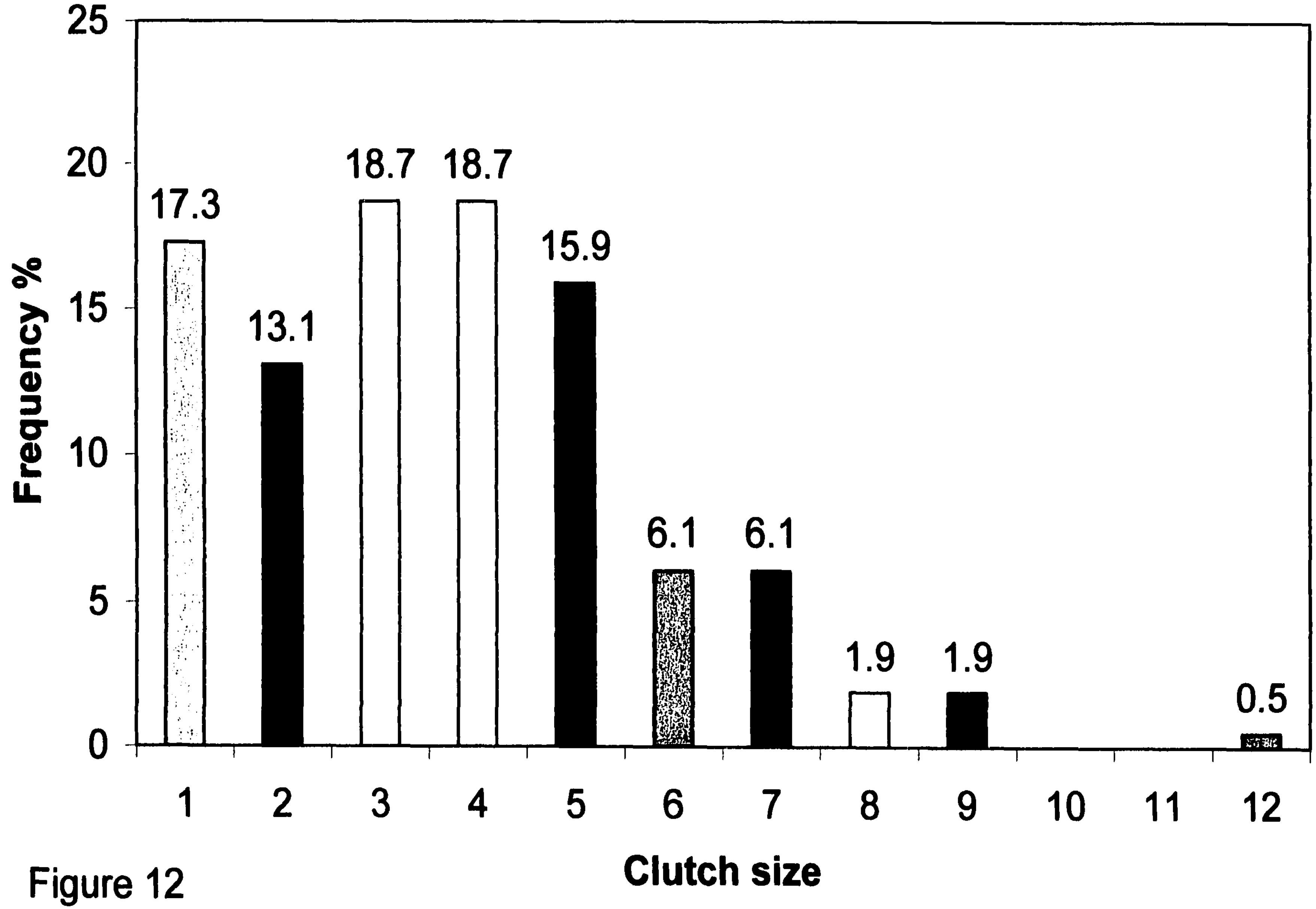

25
20
15
10
5
0
Frequency %
17.3
13.1
18.7
18.7
15.9
6.1
6.1
1.9
1.9
0.5
1
2
3
4
5
6
7
8
9
10
11
12
Clutch size

Figure 12

The factorial ANOVA revealed significant differences between nest and non-nest sites for depth (F = 56.6; 1,276 df; $p<0.001$) and vegetation density (F = 6.9; 1, 276 df; p = 0.009). No other main effects were found and there were no significant interactions. Overall, mean depth was significantly lower for nest sites than non-nests sites. Overall vegetation density was higher for nest sites than non-nest sites (Table 9).

TABLE 9. Overall mean depth, and density of vegetation for nest and non-nest sites.

	Density Index (high , med, and low)	Depth (cm)
Nest n = 180 records	2.1 ± .9 s.d.	57.4 ± 35.3 s.d.
Non-nest n = 120 records	1.8 ± .9 s.d.	86.9 ± 27.9 s.d.

5.0 Discussion

The nesting population at Whitefish Lake is associated with uncultivated wild rice stands in shallow bays of the lake. Early in spring, the lake provides an abundance of nest material in the form of decaying wild rice stalks from the previous year. When the birds arrive, little or no emergent vegetation is evident. The presence of emergent vegetation is less significant in selecting a nest site than factors evident from underwater exploration.

Later in the growing season, nests at Whitefish Lake that appeared to be floating became surrounded by thick vegetation that provided concealment and protection from high winds and wave action. Since emergent vegetation is not evident at the time of nest-site selection and early nest construction, grebes are selecting nest-sites based in part by evidence of emergent vegetation just beneath the surface or material embedded in the substrate that will act as an anchor for the new nest.

Nests in this study were almost always anchored to the bottom with unidentified twigs, branches, sticks or stalks of emergent vegetation. DeSmet (1983) suggested pairs seek suitable nest sites by peering underneath the water for accumulations of existing debris or anchorage. Nests described in the literature as "floating" are likely anchored to the lake bottom with sticks, twigs, branches or logs.

Nest site selection in the Red-necked Grebe is influenced by water depth, vegetation density and composition, protection from wind and wave action, distance from shore to provide protection from predators, and proximity to open water (Kevan 1970, DeSmet 1983, Ohanjanian 1986, Fournier and Hines 1998, Stout and

Nuechterlein, 1999). The literature suggests that nests are normally floating and attached to emergent vegetation such as *Carex spp., Scirpus spp.* and *Typha spp.*. (Kevan 1970, DeSmet 1983, Fournier and Hines 1998). However, Kevan (1970) reported that many of the nests in her study area were found in open water and not always surrounded by emergent vegetation. Kevan (1970) may have been referring to nests built early in the season that may have changed later on.

In nest-site selection, Red-necked Grebes in this study are influenced by underwater variables such as water depth, nest material and anchors for the new nest. Presumably, underwater investigation by grebe pairs permits them to evaluate the sites potential to anchor nest material and therefore rests on some existing debris already grounded in the lake substrate. Early beginnings of future plant emergence, (future) shelter from wind and waves and protection/concealment from predators or some form of anchorage (debris, sticks or logs) is evident only from underwater searches. Although above water variables such as distance from shore and nearest neighbour also affect nest-site selection (DeSmet 1983, Ohanjanian 1986, Stout and Nuechterlein, 1999), a closer evaluation of preferred territories is necessary to determine the above water variables and their relative importance with respect to underwater variables.

I concluded that water depth is significantly shallower at nest sites than non-nest sites. Water depth at the nest varies (rarely <20 cm) and is dependent on availability of emergent vegetation for nest material and cover, and varies with submerged anchorage for maximum depths and swimming access for shallower depths (Stout and Nuechterlein, 1999). In larger lakes (>30 ha), DeSmet (1983) reported nests were found in shallower water (mean 50 cm) than more exposed nests on smaller lakes (mean 60 cm).

Mean nearest neighbour distance for 148 nests at Whitefish Lake was 27.2 m and doesn't reflect high variability in absolute minimum and maximum distances between nests in specific sections or bays on the lake. Inter-nest distances as low as 1.5 metres and as high as 185 metres represent actual ranges for nearest neighbour and reflect the nature of the section they were taken from (Appendix 4). Section A4 had a distinct island of floating vegetation that resulted in very high distance from shore records and thus affected the mean value.

DeSmet (1983) was careful to present nearest neighbour distance and distance from shore according to their location; along band of emergent shoreline vegetation, within open water emergent clumps, anchored to a log or branches in open water, etc. Mean nearest-neighbour distance on Lake Osakis was 20.7 ± 17.8 m (range 2-87, n=58) for nests clustered in emergent vegetation islands and 101.3 ± 53.9 m (range 10-182) for shoreline nests (GLN and D. Buitron unpubl. From Stout and Nuechterlein 1999).

It is important to make this distinction in reporting nearest neighbour and distance from shore for Red-necked Grebe nests since it becomes obvious that distance from shore is a relevant factor but that nest-site selection is more dependent on water depth, and available nest material. Underwater characteristics such as a rise in substrate (therefore shallow water) due to emerging weed mats, logs and sticks embedded in the lake bottom that act as an anchor of some sort to collect nest material and possibly stimulate pairs to build in what appears to be open water.

Nest depth was significantly lower for nest sites than non-nest sites in this study and vegetation was more dense at nest-sites than non-nest sites. Although this comparison does not demonstrate the significance of these factors with respect to overall nest success and breeding success, it provides evidence that water depth and vegetation density play a critical role in the selection of nest sites over other sites.

Distance from shore may be a significant factor for nests located along shoreline bands of vegetation and not be significant for islands of emergent vegetation or weed mats located far out in open water as mentioned earlier and noted by DeSmet (1983). It would appear that Red-necked Grebes, although very territorial, are willing to sacrifice high nearest neighbour distances if habitat is rich and nest-sites are abundant.

Nest construction

Red-necked Grebes are opportunistic when selecting nest material. Arrival at the lake in spring provided the grebes with an abundance of decaying wild rice stalks to begin immediate nest construction and floating collections of debris. A regional survey (part of this overall research) of areas reported to have had Red-necked Grebe nests in past years revealed nests in Sioux Lookout, Eagle Lake, Abrams and Pelican Lake near Sioux Lookout. Nest composition for nests in lakes noted other than Whitefish Lake consisted primarily of the most abundant material available.

Following this study, a selection of lakes known to contain uncultivated wild rice were also surveyed and did not contain evidence of Red-necked Grebes. A comparison of total area and MEI values for lakes containing Red-necked Grebes and of lakes containing uncultivated wild rice is presented in Appendix 6. Results indicate that neither wild rice nor MEI are predictors independent of one another but suggests that further investigation of the relationship between suitable nest sites and food production is necessary.

A positive correlation (r = .73) between nest composition and nearest vegetation rather than with most predominant species in this study indicates a preference for vegetation nearest the nest. While most of the nests at Whitefish Lake were made from wild rice, the profile changed from use of old wild rice to new wild rice and lilies, emergents, submergents and other available material close to the nest-site, and changed as they became available in the growing season.

Platform building

Pairs will often build more than one nest before a final nest is established in which the clutch is laid (Wobus 1964, Kevan 1970). The previous nest attempts result in a number of platforms where courtship and copulation occasionally take place but where eggs are normally absent.

Platform behaviour, which is similar for all grebe species (Storer 1963) causes confusion for the researcher but however, has been identified as an important part of courtship and pair bonding (Stout and Nuechterlein 1999) and should be considered so. Nest counts on similar lakes may have included platforms therefore counts might be more accurate if nests were only counted when they contained at least one egg.

Platform behaviour serves many important functions; as an activity which facilitates many of the courtship and pair bonding behaviours (Inviting, Rearing, Weed ceremonies); as an activity that facilitates the nest-site selection whether that occurs from underwater scrutiny or above water nest-site selection; and finally as an activity which ultimately leads to nest construction. There is some danger that the inexperienced observer would evaluate platform behaviour as nest building activities exclusively. Platform behaviour might also be useful to observe in studies of nest-site selection. This is because it is unclear exactly what underwater characteristics might stimulate platform activity, such as collections of debris or decaying nest material caught up on submerged logs, branches or twigs.

Clutch Size, Incubation period, Hatching and Egg Fate

In this study, total numbers of nests with eggs peaked on 21 June in 1993 and 22 June 1994 which is somewhat later than that reported by laying peaks in others studies; (late May DeSmet 1983; late May, Kevan 1970; Between 24 May and 5 June (Fournier and Hines 1998). Since arrival at the lake seems to match other reports, one possible suggestion for the later peak laying period might be the higher numbers and dense population of Red-necked Grebes that contribute to a longer period of territorial feud and territory establishment. Kevan (1970) suggested that territorial skirmishes may delay the onset of clutch initiation.

The time that first eggs were laid (13 May in 1993 and 18 May in 1994) at Whitefish Lake is somewhat later than other reports (4 May, Kevan 1970) and similar to clutch initiation dates in the Northwest Territories (21 May, Fournier and Hines 1998) and so may also result in late peak laying period. Destruction of early nests and platforms by high winds and waves, 24 May 1994, is likely to be the largest reason to have contributed to later peak periods at Whitefish Lake in that year. Differences in climate among study areas may also be a contributing factor for later nesting peaks and first eggs laid.

The fate of many eggs was unknown, partly due to the long intervals between census periods. However, the method used to calculate egg fates was to determine the viability of that egg to hatch or to lead to hatched young. Only young that were seen for certain were counted in this study. The size and nature of Whitefish Lake did not allow accurate bird counts and once young were hatched since adults moved into open water within the first 2-3 days with young on their backs. The difficulty in conducting a census was limited by the large size of Whitefish Lake, unlike the small ponds, potholes and marshes described in other studies.

Egg losses due to predators in this study were 8.1% of 789 eggs and are consistent with those reported by DeSmet 1983 (6.6% of 834 eggs). Egg losses from unknown causes were likely lost either during agonistic interactions with neighbouring pairs resulting in eggs rolling into the lake and settling on the lake bottom, or lost to high wind or wave action loosening less developed nests and resulting in nest destruction or egg losses.

Eggs that were considered viable but whose fate was undetermined, had either hatched and were not discovered or, were lost to unknown causes. Many eggs that were added to partial clutches after partial losses were later abandoned when first eggs hatched. Stout and Nuechterlein (1999) suggested that these eggs may potentially contribute to production if earlier eggs are lost or become inviable (from Riske 1976, DeSmet 1983).

Clutch initiation generally begins within 2 weeks of the nest construction (Kevan 1970, DeSmet 1983) for early clutches and may extend into July or August for late clutches or when renesting (Kevan 1970). Copulation usually takes place mid-way through nest or platform construction (Palmer 1962) and often will have occurred prior to establishment of the final nest (Wobus 1964, Kevan 1970). The average clutch size is 4-5 eggs (Stout and Nuechterlein, 1999) with larger clutches assumed to be the result of joint laying (Palmer 1962). Clutches of 2-4 eggs could be the result of late nesting (Munro 1941), renesting, or clutches of young females.

Average clutch size is highly variable (Stout and Nuechterlein 1999) but results from this study (4.3 for n = 177 pairs with nests containing 2 or more eggs) are consistent with normal clutches reported by others (4.6, Kevan 1970; 4.2, Riske 1976; 5.0, DeSmet 1983; 4.1, Ohanjanian 1986; 4.4, Fournier and Hines 1998). Supernormal clutches (>7) have been reported (25 eggs, Ohanjanian 1986) and are usually attributed to multiple females "dumping eggs" and intra-specific parasitism by other females. Large (12 eggs) clutches in this study could be attributed to the same conditions due to the high numbers of birds and territorial disputes. However, in accordance with a 9-egg clutch reported by DeSmet (1983), the pair that produced the 12-egg clutch in this study was also located in one of the more stable territories and more isolated than others on the lake. The instance of large clutches and its significance for the Red-necked Grebe, may need further attention in future studies.

The mean egg laying period for Whitefish Lake (8.9 ± 5.37 s.d. days) was normal and consistent with the literature while the maximum egg laying period was 35 days and accounts for the high variability. This number included first and second clutches but also included clutches which had been established but had lost eggs due to weather, territorial disputes, and other unknown causes. This was a frequent occurrence at Whitefish Lake and may contribute to part of an explanation for the adaptive significance of large clutch sizes and the protracted breeding season.

In this study, incubation periods (mean = 29.3 $\pm$ 6.44 s.d. days) were reported for 107 nests (2 or more eggs) for which at least 1 egg hatched (before abandonment) or was viable and met criteria to be determined a 'possible' egg. This is only slightly higher for those reported by DeSmet (1987) (mean = 27.6 $\pm$ 2.76 s.d.) in which the last egg hatched.

Partial clutch abandonment is common once some of the clutch has hatched, therefore, there is limited and inconsistent data available on incubation periods (Stout and Nuechterlein, 1999). The incubation period lasts for 22-23 days (Bent 1919, Heinroth and Heinroth 1926-28). However, DeSmet (1977) did not have one egg hatch in under 24 days.

Incubation period data in Red-necked Grebe studies is limited and imprecise because the last eggs to be laid are frequently abandoned (Stout and Nuechterlein 1999) once one or two eggs hatch. It was rare to see a complete hatch at Whitefish Lake and more common to see at least one and up to 4 or 5 eggs left behind if there had been a successful hatch of two or more young. Abandoned eggs were often eggs laid later in the clutch.

Mean hatching period for 66 nests of 2 or more eggs was 23.4 days with a maximum hatching period of 30 days. Hatching periods of 22-35 days (Stout and Nuechterlein 1999) are consistent with the high numbers of egg losses and attempts to complete clutches. Incubator hatches have resulted in shorter hatches (22-23 d, Bent 1919). Variability among reports can be attributed to local differences and less variation in temperature in incubators than in natural conditions (Stout and Nuechterlein 1999).

6.0 Conclusions

Whitefish Lake is a unique site that provides abundant nest material, is highly productive both for fish and invertebrates and by nature of its geography, provides smaller, shallow, sheltered bays where more than one pair can successfully nest. Abundant food resources and nest material have led to high numbers and higher density (pairs/ha) than any other population reported in the literature. This represents an opportunity to investigate significant factors relating to nest-site selection factors distinguishing more preferred over less preferred sites. Arbitrarily assigned sections and corresponding area (ha) based on vegetation boundaries from aerial photos may have skewed the results for density (prs/ha). Identifying definite boundaries a priori is recommended for further research at Whitefish Lake.

The aggregation indices from study areas at Whitefish Lake suggests that clumping occurs. Whether this is a consequence of patchy nest habitat (weed mats, vegetation, shallow water depth) along the shoreline and in open water, or whether it is evidence of a trend toward semi-colonial behaviour is unknown. The relationship between smaller nearest neighbour distances for aggregations closer to shore requires further study. Red-necked Grebes at Whitefish Lake could, as a consequence, experience some modification in territorial behaviour allowing for smaller distances if there were some reproductive benefits for higher hatching success.

Distance from shore is likely to be more significant in predicting egg losses due to land predators, potentially stranded nests and losses due to bad weather causing high winds and increased wave action. While nearest-nest distance could also be considered as a predictor for losses due to territorial skirmishes as suggested by Kevan (1970) and for competing for limited resources.

I conclude that nest-site selection however, is largely conducted underwater and dependent on water depth, (future) vegetation density, anchorage and available nest material (wild rice stalks from previous years). The availability of these factors is high in both shoreline nest sites and in vegetated mats located at a great distance from shore.

It would be useful to study the overall factors affecting nest site selection and consequences (net effect) at Whitefish Lake. It is important to note that Whitefish Lake is a recreational lake that has significant human activity associated with parts of its shoreline and none on other sections. I noted that grebe pairs with nests located next to resorts and docks exhibited less anxiety (and thus less on and off the nest activity) with human activity. Sections of shoreline with private camps presented a more disruptive environment to grebe pairs nesting along these shores. Irregular visits (on weekends and fair weather) by camp owners did not allow the grebes to become accustomed to the activity and thus caused a greater frequency of getting on and off the nest. Finally, nests located in the west end and at a greater distance from shoreline activity were less likely to be disturbed by human activity.

All of these variables must be considered when evaluating the quality of territory selected by grebes. It would be recommended that a well-designed study investigate all variables potentially associated with breeding success. Since aggregations of this size and density are so rare for this grebe, Whitefish Lake represents a suitable site for future research.

DeSmet (1982) notes that it is of particular importance to establish better "baseline data for prime breeding areas" of the Red-necked Grebe to help determine population trends. Evaluation of habitat selection with attention to limnological and feeding ecology studies are necessary to establish this baseline data for the colony of Red-necked Grebes at Whitefish Lake.

Documenting the breeding ecology of the Red-necked Grebe involved two years and provides useful data for describing a large population. It is important in establishing more specific hypotheses on the habitat and nest site selection of this Grebe and perhaps determining the variables that can be attributed to their breeding success in Ontario.

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Appendix 1. Characteristics of twenty randomly selected lakes in the Quetico Milles Lac District (Ontario Natural Resources files 2001).

Lake	Surface area (ha)	Total Dissolved Solids (TDS)	Mean depth (m)	MEI
Twinhouse	105.8	15.8	5.5	2.7
Pass	23.0	58.8	9.3	6.3
Jolly	96.9	74.0	2.1	23.4
Myrt	272.6	19.6	5.0	3.9
Dog	14804.3	45.1	29.6	1.5
Amp	92.8	40.1	2.5	16.0
Cavern	23.5	54.0	6.7	8.1
Smiley	211.4	31.2	4.1	7.6
Twining	425.7	31.6	5.4	5.5
Fork	165.6	21.5	10.2	2.1
Grouse	87.3	32.9	15.7	2.1
Cibber	426.6	23.8	3.5	7.4
Rock	4.7	36.8	3.6	7.2

Mirror	4.7	110.0	4.2	26.4
Kearns	905.9	22.4	5.4	4.2
Koss	347.6	23.3	2.0	11.7
Birch	5.7	24.0	2.5	9.6
Vivid	57.4	54.3	1.4	38.8
Hood	120.4	19.9	7.7	2.6
Webbs	12.0	21.4	0.7	30.5

Appendix 2. Clark and Evans (1954) formula for Aggregation Index and test for significance performed with nearest neighbour mean distances for eleven Red-necked Grebe nesting sections at Whitefish Lake, Ontario, 1993 and 1994.

1) Index of Aggregation formula

$$R = \frac{\bar{r}_A}{\bar{r}_E} = \text{Index of aggregation}$$

$$\bar{r}_A = \text{Mean distance to the nearest neighbor} = \frac{\Sigma\, r_i}{n}$$

$$\bar{r}_E = \text{Expected distance to nearest neighbor} = \frac{1}{2\sqrt{\rho}}$$

$$\rho = \text{Density of organisms} = \frac{\text{Number in study area}}{\text{Size of study area}}$$

If the spatial pattern is random, R = 1. When clumping occurs, R approaches zero; in a regular pattern, R approaches an upper limit around 2.15.

2) Test for significant deviation from a random pattern.

$$z = \frac{\bar{r}_A - \bar{r}_E}{s_r}$$

where z = Standard normal deviate

s_r = Standard error of the expected distance to nearest neighbor

$= \dfrac{0.26136}{\sqrt{n\rho}}$

n = Number of individuals in study area

ρ = Density of individuals in study area

If z is less than 1.96, we tentatively accept the null hypothesis at alpha = 0.05 that these nests are significantly different from a random pattern (clumped).

Appendix 3. Mean density (pairs/hectare) for 13 Red-necked Grebe, nesting sections at Whitefish Lake, Ontario for 1993 and 1994.

Section	Area (ha)	Number of pairs* 1993	Number of pairs* 1994	Mean number of pairs for 1993 and 1994	Density (pairs/ha)
A1	4.2	2	1	1.5	0.4
A2	4.9	2	-	2.0	0.4
A3	7.0	8	5	6.5	0.9
A4	22.1	10	8	9.0	0.4
B	3.2	7	5	6.0	1.9
C	1.5	7	4	5.5	0.8
D	1.3	4	2	3.0	2.3
E	1.6	5	5	5.0	3.1
G	0.4	3	-	3.0	7.5
H	0.3	2	1	1.5	5.0
I	0.6	1	2	1.5	2.5
J	0.5	1	1	1.0	2.0
K	1.0	7	5	6.0	6.0
Total	48.6	59	39	49.0	1.0

*Number of pairs based on total number of nests with eggs 21 June 1993 and 22 June 1994.

Appendix 4. Inter-nest distance (m) and distance from shore (m) for individual nests at Whitefish Lake for 1993 and 1994.

Year	Section	Nearest Neighbour	Distance from Shore
1993	A1	8.5	16.8
1993	A1	8.5	16.8
1993	A1	8.3	8.5
1993	A1	29.2	9.5
1993	A1	29.2	9.9
1993	A1	43.3	53.2
1993	A1	41.6	5.2
1993	A1	7.8	7.9
1993	A1	7.8	15.7
1993	A1	12.9	5.3
1993	A2	1.5	0
1993	A2	1.5	0
1993	A2	9.7	0
1993	A3	60.0	14.0
1993	A3	30.5	42.5
1993	A3	30.1	3.7
1993	A3	28.3	22.3
1993	A3	28.3	0

1993	A3b	13.3	5.0
1993	A3b	8.1	5.8
1993	A3b	8.1	9.2
1993	A3b	52.2	61.4
1993	A3b	22.1	30.9
1993	A3b	22.1	8.8
1993	A4	30.0	21.5
1993	A4	23.2	51.5
1993	A4	23.2	180.0
1993	A4	15.0	184.0
1993	A4	15.0	187.0
1993	A4	17.7	202.0
1993	A4	38.1	106.4
1993	A4	38.1	108.9
1993	A4	60.0	192.0
1993	A4b		46.4
1993	G	57.1	7.1
1993	G	36.6	22.3
1993	G	4.8	11.5
1993	G	4.8	12.7
1993	G	9.7	11.0
1993	G	4.9	14.9

1993	G2	10.3	11.3
1993	G2	4.7	7.5
1993	G2	4.7	10.0
1993	H	8.7	15.3
1993	H	8.7	14.7
1993	I	9.8	16.6
1993	I	9.8	15.2
1993	I	4.4	10.8
1993	I	4.4	10.9
1993	J	6.0	11.6
1993	J	6.0	14.6
1993	J	10.0	8.4
1993	J2		6.5
1993	k	14.0	13.6
1993	k	14.0	11.6
1993	k	19.0	7.3
1993	k	9.9	5.3
1993	k	9.9	8.5
1993	k		5.3
1993	l	6.3	1.9
1993	l	6.3	2.0
1994	A1		8.0

1994	A1		6.5
1994	A1		15.6
1994	A1		
1994	A1		12.5
1994	A4	60.0	174.0
1994	A4	28.0	197.0
1994	A4	28.0	190.0
1994	A4	44.0	241.0
1994	A4	190.0	63.4
1994	A4	190.0	182.3
1994	A4	185.6	275.6
1994	A4	13.1	274.8
1994	A4	102.1	385.9
1994	A4	62.4	91.7
1994	A4	60.0	174.0
1994	A4	28.0	197.0
1994	A4	28.0	190.0
1994	A4	44.0	241.0
1994	A4	30.6	188.6
1994	A4	27.2	266.2
1994	A4	20.6	286.9
1994	A4	28.3	284.7

1994	A3	39.1	163.2
1994	A3	57.6	8.2
1994	A3	25.2	4.0
1994	A3	17.0	14.1
1994	A3	18.0	19.1
1994	A3	18.0	2.8
1994	A3	43.1	23.8
1994	A3	45.4	50.0
1994	A3	45.6	18.4
1994	B	40.1	13.9
1994	B	40.1	16.0
1994	B	43.9	18.3
1994	B	50.7	11.0
1994	B	74.4	23.4
1994	B	100.0	120.0
1994	B	36.7	15.0
1994	B	24.1	15.0
1994	B	18.1	14.7
1994	B	18.1	17.1
1994	B	6.2	9.4
1994	B	24.0	18.9
1994	B	24.0	12.4

1994	B	24.9	11.0
1994	B	47.0	51.7
1994	B	76.8	172.8
1994	B	50.8	89.2
1994	C	51.0	11.7
1994	C	44.9	55.0
1994	C	44.9	99.9
1994	C	9.1	38.8
1994	C	6.4	74.6
1994	C	6.4	73.4
1994	C	63.0	79.2
1994	C	40.1	8.7
1994	C	360.0	42.4
1994	C	5.0	30.0
1994	C	2.0	15.0
1994	C	25.0	50.0
1994	G	14.5	33.5
1994	G	37.9	12.7
1994	G	37.9	7.8
1994	G	17.7	16.3
1994	G	21.4	18.0
1994	H	10.0	5.0

1994	I	56.8	107.0
1994	I	19.0	9.7
1994	I	19.0	15.2
1994	I	16.4	49.8
1994	I	31.5	15.3
1994	I	16.4	33.5
1994	J	127.2	6.9
1994	J	39.4	3.4
1994	J	12.4	12.5
1994	J	12.4	6.8
1994	J	9.1	9.1
1994	J	6.4	12.0
1994	J	7.5	27.7
1994	J	17.6	4.0
1994	J	17.6	11.4
1994	J	18.8	7.0
1994	K	7.2	14.9
1994	K	7.2	13.4
1994	K	12.4	39.6
1994	K	12.4	26.2
1994	K	15.5	30.8
1994	K	12.0	39.3

1994	K	12.0	39.3
1994	K	10.5	15.3
1994	K	29.6	38.4
1994	K	5.9	26.2
1994	K	28.8	36.0
1994	K	24.0	17.5
1994	K	2.5	39.6
1994	K	76.8	4.3
1994	K	24.0	2.9
1994	K	24.0	4.8
1994	K	19.0	7.0
1994	K	19.0	4.5
1994	K	38.4	0.5
1994	K	8.0	9.5

Appendix 5. Aggregation index values (Clark and Evans 1954) and significant values for nearest neighbour distances for eleven nest sections at Whitefish Lake, Ontario, 1993 and 1994.

Section	Nearest nest	n	Aggregation index	Significance (z scores) (p=.05)
A1	19.7	10	0.06	-5.68
A2	4.2	3	0.02	-3.24
A3	30.2	19	0.05	-7.92
A4	52.9	27	0.04	-9.51
B	32.1	14	0.09	-6.47
C	25.3	10	0.13	-5.26
G	19.1	14	0.16	-6.00
H	9.1	3	0.19	-2.68
I	14.5	9	0.12	-5.02
J	22.3	13	0.17	-5.69
K	15.8	24	0.01	-9.25

Calculated using Clark and Evans (1954) model for an aggregation index.

Appendix 6. Characteristics of 16 northwestern Ontario lakes surveyed for Red-necked Grebes in 1994.

Lake	Surface area (ha)	TDS	Mean depth (m)	MEI
Chisamore*	276.5	74.8	1.2	62.4
Clovenhoof*	325.9	34.7	1.2	28.3
Hawk*	373.6	22.7	0.8	28.4
Muskeg*	3473.6	42.3	4.7	8.9
Ricestalk*	274.6	41.3	0.6	68.8
Batwing	624.2	26.0	6.6	4.0
Boulevard	54.4	29.9	1.7	25.2
Cloud	420.9	50.7	9.0	5.6
Dog	14804.3	45.1	29.6	1.5
Hazelwood	278.1	24.8	3.3	7.5
Oliver	199.1	44.2	22.7	1.9
Surprise	72.2	28.3	3.8	8.0
Swallow	361.0	23.3	1.6	14.6
Pelican**	2341.0	28.1	10.4	2.7
Abram**	2395.0	29.0	12.1	2.4
Eagle**(central)	16425.0	19.4	3.5	5.5

*Known wild rice lakes with no evidence of Red-necked Grebes.
** Lakes containing nesting Red-necked Grebes (1994 survey).