

Michael A. Fournier  
James E. Hines

# Breeding ecology of the Horned Grebe *Podiceps auritus* in subarctic wetlands

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Number 99  
Canadian Wildlife Service



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## Abstract

The breeding ecology of the Horned Grebe *Podiceps auritus* was investigated on a 38-km<sup>2</sup> study area near Yellowknife, Northwest Territories (62°27'N, 114°22'W). Population size and productivity were monitored during 1986–1996. Other aspects of breeding biology were studied in 1986, 1989, 1991, and 1992.

## Résumé

Près de Yellowknife dans les Territoires du Nord-Ouest (62°27' de latitude N., 114°22' de longitude O.), sur une superficie de 38 km<sup>2</sup>, on a étudié l'écologie de la reproduction du Grèbe esclavon (*Podiceps auritus*). De 1986 à 1996, on a surveillé la taille de la population de même que la productivité de l'espèce. D'autres aspects de la biologie de la reproduction ont été étudiés en 1986, en 1989, en 1991 et en 1992.

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# 1. Introduction

The Horned Grebe *Podiceps auritus* has a wide temperate and boreal distribution. Two subspecies are recognized: *P. a. auritus*, which occurs in Iceland, Sweden, Finland, Norway, eastern Siberia, and the Baltic states, and *P. a. cornutus*, which breeds throughout western North America (del Hoyo et al. 1992). In Canada, the Horned Grebe nests as far north as the Mackenzie Delta in the Northwest Territories and Old Crow Flats in the Yukon (Godfrey 1986).

Studies of the breeding ecology of the Horned Grebe have been conducted in parkland habitats in Manitoba (Ferguson 1977; Ferguson and Sealy 1983), Saskatchewan (Sugden 1977), and Alberta (Riske 1976) and in boreal environments in Norway, Iceland, and Finland (Clase et al. 1960; Fjeldsa 1973a,b,c; Uusitalo 1976; Ulfvens 1988), but there have been no studies in the Canadian boreal forest.

During 1986–1996, we monitored the population size and productivity of Horned Grebes near Yellowknife, Northwest Territories, as part of a long-term study of subarctic waterfowl. In 1986, 1989, 1991, and 1992, we investigated various aspects of their breeding ecology in greater detail. Our objectives were to document the breeding biology of this species in a region where it had not been studied previously and to determine factors that may influence the productivity of grebe populations (and, by extension, that of other waterfowl) in the subarctic boreal forest.

# 2. Study area

## 2.1 Location and size

The primary study area was a 38-km<sup>2</sup> roadside transect that began approximately 16 km west of Yellowknife, Northwest Territories (62°27'N, 114°22'W), and continued approximately 48 km west, extending 0.4 km on each side of the road. To increase sample sizes, we also gathered data for Horned Grebes breeding on roadside ponds located along the highway between Yellowknife and the primary study area.

## 2.2 Climate

The study area occurs within the Subhumid High Boreal Ecoclimatic Region (Ecoregions Working Group 1989). The climate of the Yellowknife area is subarctic-continental, with long cold winters, short cool summers, and moderate snowfall, but with low annual precipitation. Average weather conditions during the breeding season for the Horned Grebe (May–August) are presented in Table 1. Annual precipitation averages 267.3 mm, consisting of 143.9 cm of snow and 154.0 mm of rainfall (Atmospheric Environment Service 1993). The frost-free period averages 111 days (range 86–147), extending from approximately 27 May to 16 September (Atmospheric Environment Service 1982).

High seasonal variation in day length occurs in the region, and long hours of daylight occur during the grebe breeding season. For example, on 21 June (summer solstice), the sun is above the horizon for about 20 hours, and twilight prevails during the remaining four hours.

**Table 1**  
Average weather conditions at Yellowknife, Northwest Territories during May–August, 1961–1990<sup>a</sup>

	Month			
	May	June	July	August
Mean temperature (°C)	5.0	13.1	16.5	14.1
Mean precipitation (mm)	16.6	23.3	35.2	41.7
Degree days above 5°C	71.2	244.6	355.2	280.9
Mean wind speed (km/h)	16	16	15	15
Prevailing wind direction	NE	S	S	S

<sup>a</sup> Adapted from Atmospheric Environment Service (1993).



## 2.3 Geology and physiography

Yellowknife lies within the Bear-Slave Upland division of the Kazan physiographic region (Bostock 1970). The study area is included in the Slave Geological Province and occurs on the edge of the Precambrian Shield (Stockwell et al. 1970). The topography is dominated by outcrops of bedrock that cover 25–30% of the land surface and consist largely of granite-gneiss, granodiorite, and granite. The terrain is flat to slightly rolling between outcrops. The region was inundated by a large glacial lake about 10 000 years ago, resulting in the deposition of clay, silt, sand, and gravel at the base of the outcrops (Aspler 1987).

## 2.4 Upland vegetation

The study area occurs in a zone of open subarctic woodland. Unfavourable climatic conditions, thin unproductive soils, and frequent fires limit the distribution, abundance, and size of trees in the region (Rowe 1972). The dominant species on rock outcrops and dry sites is jack pine *Pinus Banksiana*. Mesic areas support stands of white birch *Betula papyrifera*, trembling aspen *Populus tremuloides*, and occasionally white spruce *Picea glauca*, as well as tall shrubs such as American green alder *Alnus crispa*. Low, wet sites support stands of black spruce *Picea mariana*, willow (*Salix* spp.) thickets, and muskeg vegetation. The latter consists of sparse black spruce interspersed with tamarack *Larix laricina* and a shrub layer dominated by Labrador tea *Ledum groenlandicum* (Murdy 1963).

## 2.5 Wetlands

### 2.5.1 Wetland characteristics

There are 575 ponds on the study area; 262 are natural in origin, and 313 are “borrow pits” created during construction of the highway circa 1960. The median pond size is 0.2 ha for natural ponds (range <0.1–18.2 ha), <0.1 ha for borrow pits (range <0.1–1.1 ha), and 0.1 ha overall. Borrow pit ponds provide approximately 38 ha of wetland habitat. They are generally shallow and semipermanent in nature. Natural ponds encompass approximately 292 ha. These ponds are deeper and permanent, although some small bog ponds appear to have diminished in size over time as a result of succession.

Roadside ditches and borrow pits, often with exposed mud on their margins, generally provide the first open water for waterfowl arriving in early May. Most ponds are free of ice by mid-May, but larger natural ponds may contain ice until near the end of that month. The open-water season extends approximately 120–130 days, and most ponds are frozen by late September.

Data from recent analyses of the limnological characteristics of water bodies on the primary study area are summarized in Table 2.

### 2.5.2 Wetland vegetation

Some natural ponds have abrupt shorelines of rock outcrop or shrubs such as leatherleaf *Chamaedaphne calyculata* or sweet gale *Myrica gale*, but most are bordered by floating sedge mats (*Carex* spp.) of varying width.

**Table 2**  
Limnological characteristics of wetlands on the Yellowknife study area

Limnological parameter	Borrow pits (n = 70)	Natural ponds (n = 84)	Kruskal- Wallis test
	Mean ± S.E.	Mean ± S.E.	P
Conductivity (µS/cm)	336 ± 18	230 ± 10	<0.01
Turbidity (NTU)	3.4 ± 0.3	2.5 ± 0.2	0.02
Suspended solids (ppm)	4.9 ± 0.7	6.0 ± 0.8	0.72
Dissolved solids (ppm)	251 ± 11	204 ± 8	<0.01
Calcium (ppm)	29.7 ± 1.4	19.9 ± 1.0	<0.01
Colour	69 ± 4	106 ± 6	<0.01
Magnesium (ppm)	21.0 ± 1.1	14.4 ± 0.6	<0.01
Hardness (ppm)	161.1 ± 7.6	107.9 ± 4.9	<0.01
Ammonia (ppm)	0.021 ± 0.003	0.023 ± 0.002	0.16
Alkalinity (ppm)	152.8 ± 8.1	104.2 ± 6.1	<0.01
NO <sub>3</sub> /NO <sub>2</sub> (ppm)	0.01 ± 0.001	0.01 ± 0.001	0.98
Phosphorus (ppm)	0.014 ± 0.002	0.015 ± 0.002	0.86
pH	7.7 ± 0.1	7.3 ± 0.1	<0.01

Abundant species that contribute to the formation of these mats include marsh cinquefoil *Potentilla palustris*, buckbean *Menyanthes trifoliata*, and water arum *Calla palustris*. Other emergent plants include scouring rush *Equisetum fluviatile*, cattail *Typha latifolia*, and spike rush *Eleocharis palustris*.

The bottom substrate of natural ponds consists of organic muck. Common submergent plants include yellow pond-lily *Nuphar variegatum*, water milfoil *Myriophyllum exalbescens*, mare’s tail *Hippuris vulgaris*, bladderworts (*Utricularia* spp.), and pondweeds (*Potamogeton* spp.).

Most borrow pits have been extensively colonized by both emergent and submergent vegetation, although many still have patches of exposed clay along their margins. Cattail is most often the dominant emergent plant, but sedges and rushes are also common. Marsh cinquefoil, buckbean, and water arum are largely absent.

Bottom substrates of borrow pits consist mostly of clay. Submergent plant communities appear to be composed of the same species found in natural ponds, although yellow pond-lily is almost entirely absent.

### 3. Methods

#### 3.1 Roadside surveys

Roadside surveys were conducted during May and June to determine the chronology of spring migration and the breeding season of waterfowl, including grebes. Surveys were conducted early in the morning of every third day, from a vehicle driven at speeds below 30 km/h. At least two observers were present. Each observer scanned the ponds on his or her side of the road, and the number of waterfowl observed was recorded on 1:7500-scale maps of the study area. The portion of the pond considered to be visible from the road was delineated on the maps to minimize differences between observers. This “visibility strip” averaged 39 m (range 4–320 m) in width.

#### 3.2 Population surveys

We conducted ground surveys of the primary study area monthly, May through August during 1986–1996, following methods described by Murdy (1965). The surveys in May and June were conducted to determine the number of breeding pairs of waterfowl present, whereas the surveys in July and August provided estimates of the number of broods and young. Each survey was conducted between 06:00 and 10:30 over a three- to four-day period. Thirteen of the largest natural ponds were surveyed by canoe, whereas all other ponds were covered on foot. All waterfowl observed were recorded on 1:7500-scale maps of the study area.

Migrant grebes were probably present on the study area during the May survey in some years. Conversely, not all local breeders had arrived by the May survey date in other years (see Appendix 1). By the time the June surveys were conducted, most grebes were incubating and had become more secretive and less visible, and a few failed breeders (those with apparent low propensity for re-nesting) may have already departed the study area. As a result of these factors, we felt an estimate of average population size based solely on the May counts would be slightly high, whereas one based solely on the June counts would be low. Thus, we used the average counts from the two surveys to estimate the number of breeding pairs present in each year. Single grebes observed during the surveys were considered indicative of a breeding pair, as often both birds were not visible, particularly during incubation.

#### 3.3 Habitat description

Probable grebe nesting ponds were identified from the survey data. Grebe nests were then located by intensively searching the emergent vegetation of these ponds. At each nest, we recorded the plants used in nest construction and those providing cover and support. Water depth was calculated to the nearest centimetre as the mean of four measurements taken at cardinal points around the nest. Distances of the nest from shore and from open water were measured to the nearest 0.1 m.

All ponds on which grebes were recorded during the June breeding pair survey were classified as breeding ponds and were included in the analysis of pond type (natural versus man-made) and size (area). Pond size was determined from 1:7500-scale aerial photographs using a dot-grid overlay.

#### 3.4 Clutch initiation, clutch size, and egg size

Date of clutch initiation was estimated by backdating at a rate of one egg laid every two days (Dubois 1919; Ferguson 1977). Clutches that were known or suspected to have lost eggs prior to our discovery of the nest were excluded from the calculation of clutch initiation date and mean clutch size. Clutches were considered to be complete when the number of eggs remained constant during consecutive visits at least three days apart.

The maximum length ( $L$ ) and width ( $W$ ) of each egg were measured with calipers to the nearest 0.1 mm, and eggs were numbered with a soft lead pencil. If, when revisiting a nest, we found that marked eggs were missing, the area surrounding the nest was inspected to determine if eggs had been knocked off the nest platform, and nearby upland areas were searched for shells of eggs destroyed by predators. Egg volume ( $V$ , in  $\text{cm}^3$ ) was estimated using the equation:  $V = 0.000\ 507 (LW^2)$  (Hoyt 1979).

#### 3.5 Hatch date and nest success

Hatch date was defined as the date of hatch of the first egg in a clutch (hatch of eggs in a Horned Grebe clutch is asynchronous). Nest success, defined as the percentage of nests in which at least one egg hatched, was estimated by both the apparent method and a modified form of the Mayfield (1975) method (Bart and Robson 1982), which

assumed an eight-day laying period and a 23-day incubation period (Ferguson 1977). Ferguson (1977) reported laying periods of 7–8 days for clutches of five eggs and 8–9 days for clutches of six eggs. As average clutch size in our study was 5.3 eggs, we used the midpoint of this range for our estimate of laying period.

Estimates of nest success based on the apparent method are typically biased high. However, we believe our results may also be biased in the opposite direction because of loss of young during hatching or their first few days of life. It was not possible to follow all nests closely enough to observe the actual hatch, and nests were checked in a three- to seven-day rotation. Therefore, success was sometimes inferred from the presence of juvenile grebes on the nesting pond; conversely, failure was assumed for those ponds where no young were observed.

### 3.6 Adult departure and brood abandonment

The number of adult grebes present was recorded during each visit to the nesting pond. The dates of adult departure refer to the timing of abandonment of the brood. Pairs that did not hatch any eggs successfully and pairs that lost the entire brood in early stages of development were not included in the analysis of adult departure dates.

### 3.7 Production estimates

A minimum estimate of the number of broods and young produced on a given pond was derived from the highest count from either the July or August surveys. This approach was necessary owing to the protracted period of hatching, a result of asynchronous hatch and persistent re-nesting. Estimated totals of broods and young based on this information were considered to be low, because of the secretive and cryptic nature of young grebes and the prevalence of thick emergent and peripheral vegetation at most ponds. Therefore, results from the brood surveys were adjusted for visibility bias (Pollock and Kendall 1987) to estimate the number of broods and young grebes.

For 1989, 1991, and 1992, we developed visibility correction factors (VCFs) using counts of grebes from 20–25 intensively studied ponds. The numbers of broods and total young known to be present on these ponds from the intensive studies were compared with the results of our regular surveys to compute the VCFs:

$$\text{VCF} = \frac{B_{\text{intensive}}}{B_{\text{standard}}}$$

where  $B_{\text{intensive}}$  is the number of broods or young known to be present on the sample of ponds, and  $B_{\text{standard}}$  is the maximum number of broods or young counted on these same ponds during the regular July and August surveys.

Because of the relatively small sample sizes each year and the similarity of the annual VCFs, we combined the data from the three years to derive average VCFs (Appendix 2). These average values were applied to the data for all years.

### 3.8 Data analysis

Statistical procedures were conducted with the SAS software package for personal computers (SAS Institute 1985). One-way analysis of variance followed by Duncan's multiple range test (if the overall F-value was significant) was used to determine variation in clutch initiation date and nest site characteristics. Comparisons between the distributions of two samples were made using the Kruskal-Wallis test. The relationship between annual productivity and local weather conditions was examined using multiple regression procedures (Proc Reg, SAS Institute 1985). For this analysis, we considered the weather data for four broad periods based on the breeding chronology of the grebes: (1) arrival/territory establishment (1–19 May); (2) egg laying/early incubation (20 May – 10 June); (3) late incubation/hatching (11 June – 1 July); and (4) brood rearing (2–30 July).

## 4. Results

### 4.1 Spring arrival

The first open water on the study area typically occurred in roadside ditches and borrow pits during the last few days of April or the first few days of May. Roadside surveys indicated that the earliest Horned Grebes arrived about a week later. The median date on which the first grebes arrived on the study area during 1985–1996 was 10 May (range 5–13 May). Peak numbers were observed approximately 10 days later (median 20 May, range 8–30 May). The grebes appeared to arrive both singly and as pairs, mostly the latter.

### 4.2 Habitat use

#### 4.2.1 Pond use

Use of ponds by Horned Grebes was influenced by both pond size and type (Fig. 1). Horned Grebes largely avoided ponds less than 0.1 ha in size, despite the abundance of such ponds on the study area. The median size of ponds used by grebes was 0.4 ha (range <0.1–18.2 ha,  $n = 741$ ). There was a large difference in the size of man-made versus natural ponds used for nesting, with median values equalling 0.3 ha (range <0.1–1.1 ha,  $n = 326$ ) and 1.0 ha (range <0.1–18.2 ha,  $n = 415$ ) for the two pond types. The most heavily used ponds (i.e., highest percentage of available ponds occupied) were those in the 0.3- to 2.0-ha size range. Large natural ponds (>2.0 ha) showed consistent, moderate use. Densities of breeding pairs were greatest on small (0.1–1.0 ha) ponds (Fig. 2). Among ponds 0.1–2.0 ha in size, grebes nearly always made greater use of man-made than of natural ponds, both by percentage and by density (Figs. 1 and 2).

On three occasions, we observed several pairs of grebes nesting on single, relatively small ponds. In 1991, four nests were observed on a 0.6-ha pond, and in 1992, five nests were found on a 2.8-ha pond. The most unusual situation we encountered was that of eight nests on a 3.8-ha pond in 1991. Although we did not measure distances between these nests, all were judged to be within 30 m, and several were within 10 m, of their nearest neighbour. None of these nests had physical obstructions (e.g., dry land or very dense vegetation) separating them, and most had little or no visual isolation.

#### 4.2.2 Nest site characteristics

Grebes nested prior to significant development of new emergent growth in the ponds and thus were largely dependent upon the availability of residual stands of cattails and the more permanent cover provided by living or dead willows. All nests examined ( $n = 237$ ) were anchored to emergent plants, which provided both cover and support. This involved a single plant type at 76% and two types at 24% of the nests. Eight genera of plants comprised all covering and supporting materials (Table 3). Most Horned Grebes nested in cattails or willows, which occurred at 54% and 48% of all nests, respectively.

The mean water depth at nest locations was  $61 \pm 2$  cm (SE) (range 17–147 cm,  $n = 208$ , Fig. 3). There were significant differences among years (Table 4).

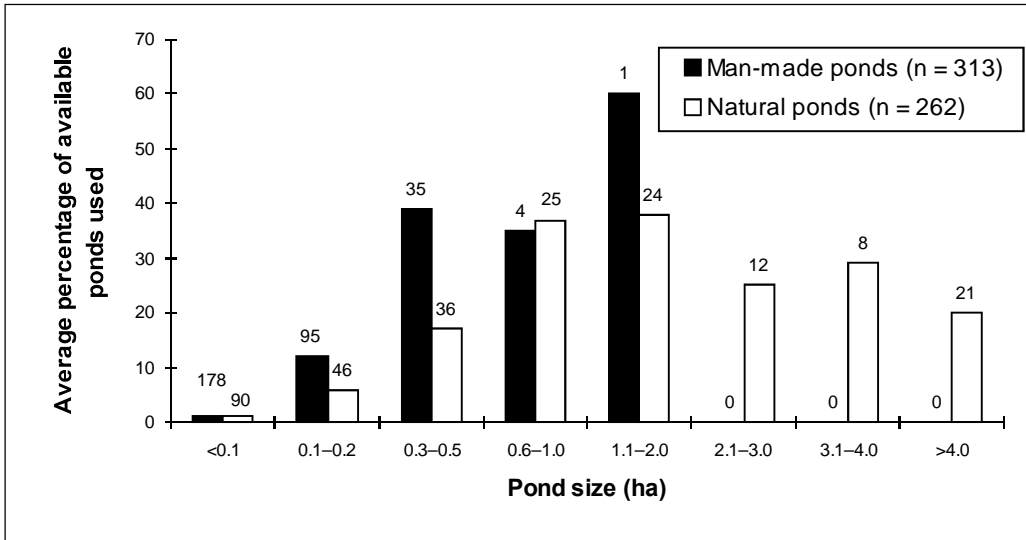
The mean distances of nests from shore and from nests to open water were  $8.3 \pm 0.3$  m (range 0.7–27.8 m,  $n = 206$ ) and  $2.3 \pm 0.2$  m (range 0–16.9 m,  $n = 204$ ), respectively. There were no significant differences among years for either of these parameters (Duncan's multiple range test,  $P > 0.05$ ).

### 4.3 Nest materials

Fifteen plant genera were used as nest material (Table 5). These included eight submergent plants, five emergent plants, and two riparian trees or shrubs, the leaves of which were apparently retrieved from the bottom of the pond. Sedge and cattail were present in 83% and 75% of all nests, respectively. Although more types of submergent plants were used, emergent species generally comprised the largest portion of the nest. The only exception to this was sphagnum (*Sphagnum* spp., apparently retrieved from the pond bottom), which made up a significant portion of some nests.

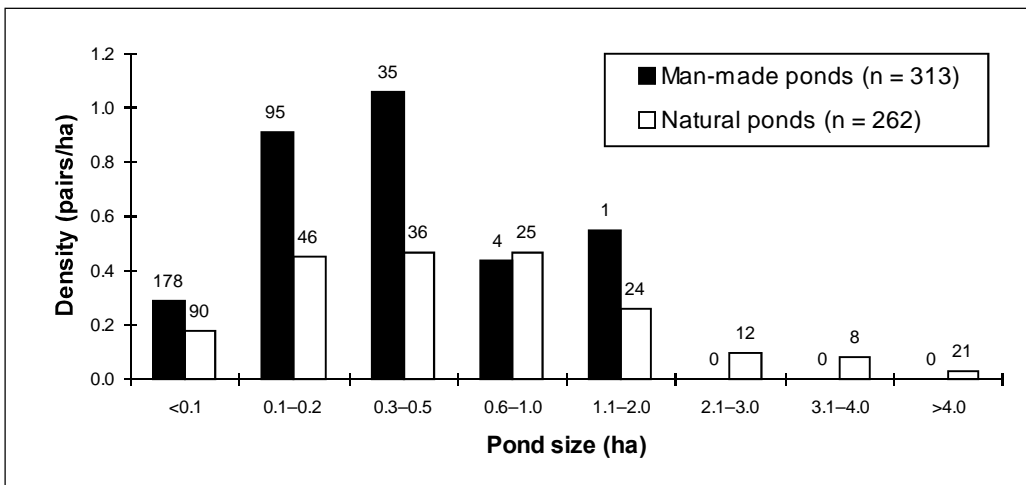
**Figure 1**

Average percentage of available ponds used by breeding Horned Grebes on the Yellowknife study area, 1986–1996



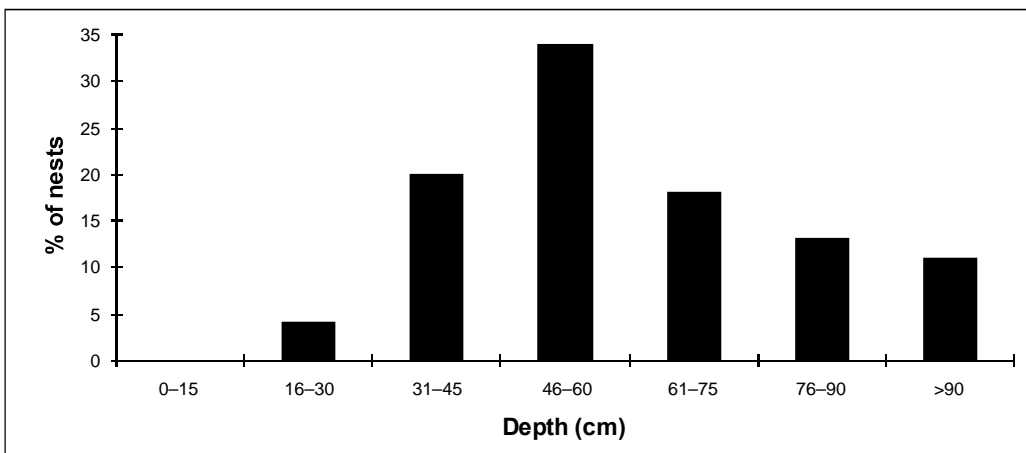
**Figure 2**

Average densities of Horned Grebes breeding on man-made and natural ponds on the Yellowknife study area, 1986–1996



**Figure 3**

Frequency distribution of water depth at nest sites for Horned Grebes breeding on the Yellowknife study area



**Table 3**

Plants used as cover or support at Horned Grebe nests on the Yellowknife study area (n = 238)

Genus and/or species	No. of nests	%
<i>Typha latifolia</i>	93	39
<i>Salix</i> spp. (alive or dead)	79	33
<i>Alnus</i> spp.	4	2
<i>Carex</i> spp.	4	2
<i>Picea</i> spp. (dead)	1	<1
<i>Typha latifolia</i> + <i>Salix</i> spp.	19	8
<i>Carex</i> spp. + <i>Salix</i> spp.	17	7
<i>Typha latifolia</i> + <i>Carex</i> spp.	11	5
<i>Typha latifolia</i> + <i>Equisetum</i> spp.	4	2
<i>Carex</i> spp. + <i>Potentilla palustris</i>	2	1
<i>Carex</i> spp. + <i>Equisetum</i> spp.	2	1
<i>Betula</i> spp. + <i>Typha latifolia</i>	1	<1
<i>Alnus</i> spp. + <i>Carex</i> spp.	1	<1

**Table 4**

Yearly variation in depth (cm) of water at Horned Grebe nest sites on the Yellowknife study area

Year	Mean $\pm$ SE	n	Duncan's multiple range test <sup>a</sup>	
1986	40 $\pm$ 3	16		C
1989	56 $\pm$ 3	42	B	
1991	64 $\pm$ 2	88	A	B
1992	67 $\pm$ 3	62	A	
Combined	61 $\pm$ 2	208	–	–

<sup>a</sup> Similar Duncan groupings indicate no significant difference between means ( $P > 0.05$ ).

**Table 5**

Nest materials used by Horned Grebes on the Yellowknife study area (n = 236)

Genus and/or species	No. of nests	%
<i>Carex</i> spp.	197	83
<i>Typha latifolia</i>	178	75
<i>Sphagnum</i> spp.	97	41
<i>Equisetum fluviatile</i>	50	21
<i>Salix</i> leaves	50	21
<i>Eleocharis palustris</i>	18	8
<i>Calla palustris</i>	13	6
<i>Utricularia</i> spp.	10	4
<i>Ceratophyllum demersum</i>	8	3
Miscellaneous leaves	7	3
<i>Hippuris vulgaris</i>	8	3
Miscellaneous twigs	6	3
<i>Myriophyllum exalbescens</i>	6	3
<i>Nuphar variegatum</i>	3	1
<i>Potamogeton</i> spp.	3	1
<i>Populus</i> (leaves)	1	<1
<i>Ranunculus gmelinii</i>	1	<1

#### 4.4 Clutch initiation

First clutches were initiated from 20 May to 11 June, with a mean date of 29 May  $\pm$  0.4 day (n = 100) (Fig. 4). Dates of clutch initiation were significantly later in 1992 than in 1989 or 1991 (Table 6).

Second (replacement) clutches were initiated between 27 May and 20 June, with a mean date of 9 June  $\pm$  1 day (n =

21). Although sample sizes were too small to allow us to test for differences between most years (Table 6), there was no significant difference (Kruskal-Wallis test, 1 df,  $P = 0.43$ ) between 1991 and 1992 in initiation date of replacement clutches.

#### 4.5 Clutch size and egg size

The mean size of first clutches was  $5.30 \pm 0.08$  eggs (n = 114) (Table 7). Mean clutch size in 1986 was significantly lower than the mean for 1989 (Kruskal-Wallis test, 1 df,  $P = 0.05$ ) but was not significantly different from the means for 1991 (Kruskal-Wallis test, 1 df,  $P = 0.12$ ) and 1992 (Kruskal-Wallis test, 1 df,  $P = 0.06$ ). There were no other differences among years.

Mean size of replacement clutches was  $5.11 \pm 0.27$  (n = 18). There were no significant differences between first clutches and replacement clutches in 1991 (Kruskal-Wallis test, 1 df,  $P = 0.98$ ,  $n_1 = 37$ ,  $n_2 = 11$ ) or 1992 (Kruskal-Wallis test, 1 df,  $P = 0.20$ ,  $n_1 = 28$ ,  $n_2 = 4$ ). Sample sizes were too small for comparisons in 1986 and 1989. In the pooled samples for all four years, mean size of second clutches was 0.19 less than for first clutches; this difference was not significant (Kruskal-Wallis test, 1 df,  $P = 0.35$ ).

The mean length of 888 eggs was  $44.5 \pm 0.1$  mm, and the mean width was  $30.6 \pm 0.04$  mm. Mean length of eggs measured in 1989 ( $44.8 \pm 0.1$  mm, n = 194) was significantly larger than those measured in 1991 ( $44.5 \pm 0.1$  mm, n = 320) (Kruskal-Wallis test, 1 df,  $P = 0.04$ ) and 1992 ( $44.1 \pm 0.1$  mm, n = 273) (Kruskal-Wallis test, 1 df,  $P < 0.01$ ). Mean length in 1991 was also significantly larger than in 1992 (Kruskal-Wallis test, 1 df,  $P = 0.03$ ). Mean length of eggs measured in 1986 ( $44.5 \pm 0.2$  mm, n = 101) was not significantly different from the means for any of the other three years (Kruskal-Wallis tests, 1 df,  $P \geq 0.08$ ). Mean width of eggs measured in 1989 ( $30.9 \pm 0.1$  mm, n = 194) was significantly larger than those measured in 1986 ( $30.5 \pm 0.1$  mm, n = 101) (Kruskal-Wallis test, 1 df,  $P = 0.04$ ), 1991 ( $30.6 \pm 0.1$  mm, n = 320) (Kruskal-Wallis test, 1 df,  $P = 0.03$ ), and 1992 ( $30.4 \pm 0.1$  mm, n = 273) (Kruskal-Wallis test, 1 df,  $P < 0.01$ ). Mean width in 1991 was also significantly larger than in 1992 (Kruskal-Wallis test, 1 df,  $P < 0.01$ ).

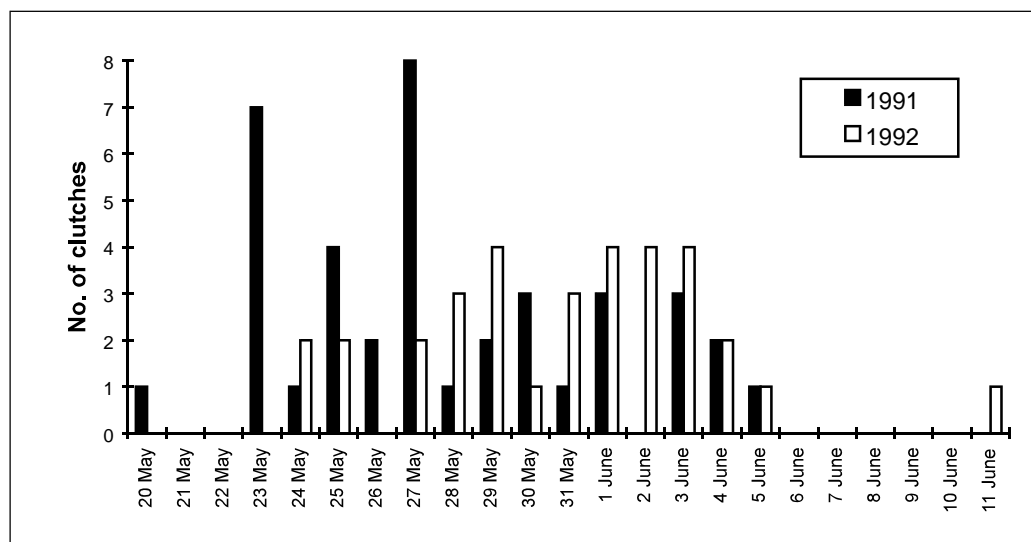
Lengths of eggs from initial and replacement clutches were similar (Kruskal-Wallis test, 1 df,  $P = 0.66$ ), with means of 44.5 mm and 44.4 mm, respectively. Width of eggs from initial clutches was significantly larger than that of replacement clutches, with means of 30.6 mm and 30.3 mm, respectively (Kruskal-Wallis test, 1 df,  $P = 0.01$ ).

Estimated mean egg volume was  $21.2 \pm 0.1$  cm<sup>3</sup>. There were significant differences in egg volume between all pairs of years (1986, 21.0 cm<sup>3</sup>; 1989, 21.7 cm<sup>3</sup>; 1991, 21.2 cm<sup>3</sup>; 1992, 20.7 cm<sup>3</sup>) (Kruskal-Wallis tests, 1 df,  $P \leq 0.05$ ) except 1986 and 1991 (Kruskal-Wallis test, 1 df,  $P = 0.99$ ). Estimated volumes of eggs from initial clutches were significantly larger (Kruskal-Wallis test, 1 df,  $P = 0.05$ ) than those of replacement clutches, with means of 21.2 cm<sup>3</sup> and 20.7 cm<sup>3</sup>, respectively.

There were no significant differences (Kruskal-Wallis tests, 1 df,  $P \geq 0.60$ ) in length, width, or volume between first-laid eggs in a clutch (n = 34) and subsequent eggs (n = 95) from those same clutches.

**Figure 4**

Frequency distribution of estimated clutch initiation dates for initial Horned Grebe nesting attempts on the Yellowknife study area in 1991 and 1992

**Table 6**

Yearly variation in dates of Horned Grebe clutch initiation (first clutches) on the Yellowknife study area

Year	Mean $\pm$ SE	n	Duncan's multiple range test <sup>a</sup>	
1986	30 May $\pm$ 1	9	A	B
1989	28 May $\pm$ 1	19		B
1991	28 May $\pm$ 1	39		B
1992	31 May $\pm$ 1	33	A	
Combined	29 May $\pm$ 0.4	100	-	-

<sup>a</sup> Similar Duncan groupings indicate no significant difference between means ( $P > 0.05$ ).

**Table 7**

Horned Grebe clutch sizes (first clutches) on the Yellowknife study area

Year	Clutch size					Mean $\pm$ SE	n
	3	4	5	6	7		
1986	1	7	5	5	1	4.90 $\pm$ 0.24	19
1989	1	1	14	12	2	5.43 $\pm$ 0.15	30
1991	1	5	14	16	1	5.30 $\pm$ 0.14	37
1992	0	2	14	10	2	5.43 $\pm$ 0.14	28
All years	3	15	47	43	6	5.30 $\pm$ 0.08	114

#### 4.6 Hatch date

In 1991 and 1992, 69% of successful first nesting attempts hatched between 21 June and 27 June (Fig. 5). There was a significant difference (Wilcoxon two-sample test,  $P < 0.01$ ) in hatching dates of first nests between these years. In 1991, the median date of hatch for first nesting attempts ( $n = 36$ ) was 22 June (range 16 June – 10 July), and in 1992 it was 25 June (range 17 June – 6 July,  $n = 28$ ). There was no significant difference (Wilcoxon two-sample test,  $P > 0.50$ ) between these years in hatching dates of renests. The overall median date of hatch for renests ( $n = 8$ ) was 5 July (range 26 June – 19 July).

#### 4.7 Nest success

Apparent nest success was 59% for first nesting attempts ( $n = 148$ ) and 61% for renests ( $n = 33$ ) (Table 8). The Mayfield estimate of daily survival rate of nests was  $0.982 \pm 0.005$  in both 1991 and 1992, an average nest success of approximately  $56 \pm 4\%$ . A comparison of these estimates of nesting success indicated no significant differences ( $\chi^2 = 0.2201$ , 2 df,  $P = 0.90$ ).

The fate of nests in 1991 and 1992 is indicated in Table 9. Predation was the major cause of nest destruction accounting for 96% of all destroyed nests ( $n = 52$ ), whereas inclement weather caused only minor damage, with 4% of destroyed nests lost to flooding.

Successful nests were located in deeper water than unsuccessful nests ( $63 \pm 2$  cm vs.  $57 \pm 3$  cm) (Kruskal-Wallis test, 1 df,  $P = 0.05$ ). There were no significant differences between successful and unsuccessful nests in distance from shore or distance to open water (Kruskal-Wallis tests, 1 df,  $P = 0.93$  and  $P = 0.21$ , respectively).

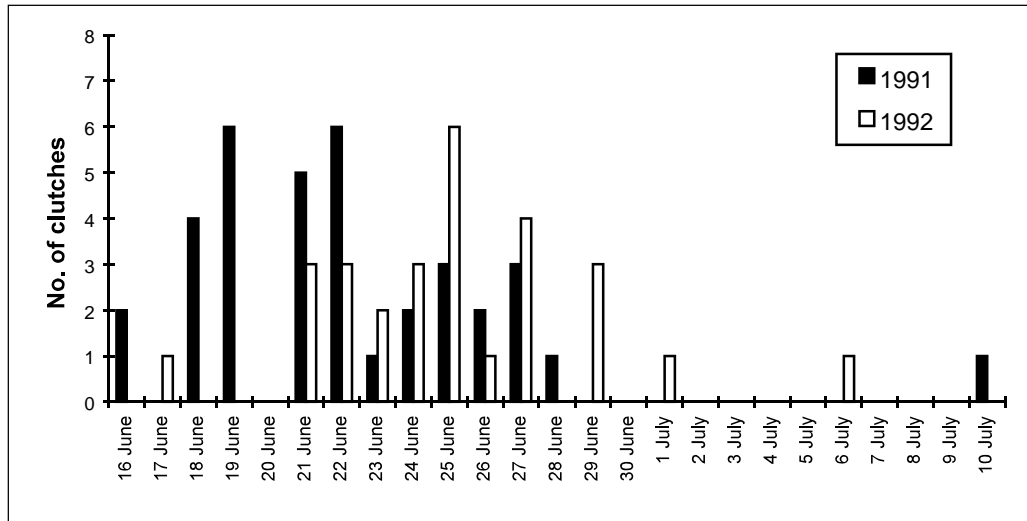
##### 4.7.1 Nest predation

In four years of study, we documented predation of 141 eggs in 52 clutches. We were unable to determine whether predation involved total or partial destruction of a clutch in six cases where both destroyed eggs and active nests were found during our first visit to a pond. Eighty-three percent (38) of the remaining 46 cases involved the loss of all eggs (1–6) from a nest, whereas 17% (8) involved partial losses (1–4 eggs) from clutches of 2–6 eggs.

Six of 52 clutches (12%) were suspected to have been destroyed by Common Ravens *Corvus corax* based on the appearance and location (at the base of trees or shrubs) of the destroyed eggs and/or the presence of ravens in the vicinity of the nesting pond. The destruction of nine clutches (17%) was attributed to mink *Mustela vison*, based in some cases on the presence of feces in the nest bowl. In six of these nine cases, an adult grebe, presumably the incubating bird, was killed and a bare sternum and attached wings were found at

**Figure 5**

Frequency distribution of estimated hatch dates of Horned Grebe clutches (first clutches only) on the Yellowknife study area in 1991 and 1992

**Table 8**

Apparent success of Horned Grebe nests on the Yellowknife study area

	No. of nests	No. of successful nests	% successful nests
First nests	148	88	59
Renests	33	20	61
All nests	181	108	60

**Table 9**

Fate of nests on intensively studied ponds on the Yellowknife study area, 1991 and 1992

Fate	No. of nests	% of nests
Hatched	87	55
Destroyed by predator	50	32
Flooded	2	1
Abandoned	6	4
Unknown	13	8
Total	158	100

or near the nest. Some of these birds may have been killed by Great Horned Owls *Bubo virginianus* and the eggs subsequently scavenged. American Coots *Fulica americana* were rare on the study area, and no egg destruction by this species was observed or suspected.

For 14 of the 52 destroyed clutches (27%), we could not determine whether the predator was avian or mammalian. The remaining 23 clutches (44%) were apparently destroyed by an unidentified avian predator(s). In all of these clutches, egg destruction was characterized by a largely intact shell with a moderate-sized hole in one side, and eggs were found in unvegetated or sparsely vegetated upland areas near the breeding ponds. The loss of these eggs was most likely attributable to ravens but perhaps also to California Gulls *Larus californicus* or Herring Gulls *Larus argentatus*.

#### 4.8 Brood loss and brood size

Total loss of broods in early developmental stages was observed for eight of 72 breeding pairs (11%) in 1991, which involved the loss of at least 14 chicks, and four of 58 breeding pairs (7%) in 1992, which involved the loss of at least four chicks.

Size of broods at or beyond the one-quarter grown stage (>12 days of age) ranged from one to six, with an overall mean of  $2.3 \pm 0.1$  ( $n = 90$ ) (Table 10). Comparison of data among years (1989, 1991, and 1992) for first nesting attempts indicated a significantly lower mean brood size in 1991 than in 1992 (Kruskal-Wallis test, 1 df,  $P = 0.03$ ). Our sample of broods produced from renests was small and did not allow comparison among years. However, samples were adequate to compare brood sizes between first nests and renests in 1991; there was no significant difference between the means (Kruskal-Wallis test, 1 df,  $P = 0.09$ ). Comparison of brood sizes between first nests and renests for all years combined (pooled data: first nests,  $n = 72$ ; renests,  $n = 18$ ) also indicated no significant difference (Kruskal-Wallis test, 1 df,  $P = 0.98$ ).

Most young were one-half to three-quarters grown (approximately 23–38 days of age) when the brood surveys were conducted. Assuming minimal mortality beyond this stage, 2.3 likely represents a good (perhaps slightly high) estimate of brood size at fledging. Using this value (2.3) for brood size at fledging and previously reported estimates of survival rate to fledging for Horned Grebe young of 64% (Ferguson 1977) and 60% (Ulffvens 1988), we estimated that approximately 3.6–3.8 young were hatched per successful pair.

#### 4.9 Departure of adults and young

Unsuccessful pairs disappeared from the study area at various times depending on the timing of clutch loss and their propensity for renesting. Some appeared to leave very early in the breeding season. In 1991 and 1992, 17 of 146 pairs (12%) observed early in the breeding season on apparent nesting ponds (ponds on which they had been



**Table 10**  
Brood sizes (>12 days of age) on intensively studied ponds on the Yellowknife study area

Year	Brood size						Mean $\pm$ SE	n
	1	2	3	4	5	6		
<b>First nests</b>								
1989	10	5	5	5	1	1	2.4 $\pm$ 0.3	27
1991	10	8	3	2	0	0	1.9 $\pm$ 0.2	23
1992	5	4	10	2	1	0	2.6 $\pm$ 0.2	22
Combined	25	17	18	9	2	1	2.3 $\pm$ 0.2	72
<b>Renests</b>								
1989	1	2	1	1	0	0	2.4 $\pm$ 0.5	5
1991	1	6	3	1	0	0	2.4 $\pm$ 0.2	11
1992	2	0	0	0	0	0	1.0	2
Combined	4	8	4	2	0	0	2.2 $\pm$ 0.2	18
<b>All nests</b>								
1989	11	7	6	6	1	1	2.4 $\pm$ 0.3	32
1991	11	14	6	3	0	0	2.0 $\pm$ 0.2	34
1992	7	4	10	2	1	0	2.4 $\pm$ 0.2	24
Combined	29	25	22	11	2	1	2.3 $\pm$ 0.1	90

present for at least several days, platforms had been built, and/or clutches initiated) departed prior to 7 June. Some of these grebes may subsequently have attempted to nest elsewhere. However, most appeared to be inexperienced breeders and may not have made further attempts at nesting. Initial nesting efforts of these grebes were characterized by unusually exposed nest locations, laying of eggs at more than one location, failure to incubate eggs, and leaving eggs highly exposed to potential predators.

Pairs that lost their entire brood in early stages of development invariably abandoned the breeding pond shortly after the loss of the last chick. Both members of failed breeding pairs appeared to depart from the breeding pond at about the same time.

Successful breeding pairs abandoned their broods once the young were able to feed themselves and generally well before the young had fledged (Fig. 6). However, unlike failed breeders, both members of a successful pair generally did not depart at the same time. There were no significant differences in the median dates of departure of the first adults (Wilcoxon two-sample test,  $P > 0.42$ ) or the second adults (Wilcoxon two-sample test,  $P > 0.13$ ) from the breeding ponds between the years 1991 and 1992. The date of departure of the first adult from intensively studied ponds ranged from approximately 17 June to 31 July, with a median date of 13 July ( $n = 46$ ). Departure of the second adult ranged from 11 July to 14 August, with a median date of 28 July ( $n = 46$ ). Thus, the adults departed approximately 15 days apart. We were unable to determine whether there was any pattern as to which sex departed first or second. Although the sexes are often distinguishable (by size and subtle differences in plumage) early in the breeding season when the nuptial plumage is fresh and bright, by the beginning of the brood-rearing period the plumage has faded considerably and the sexes are generally more difficult to identify, particularly if both adults are not observed simultaneously.

Most young grebes left the study area during August (Fig. 6). In 1991, 63 young grebes were present on 8 August and occurred at 28 (72%) of the ponds surveyed ( $n = 39$ ); on 13 August, 48 young were present, occurring at 19 (49%) of

the ponds; and on 3–4 September, five young were present on four (10%) of the ponds. In 1992, 56 young grebes were present on 4–6 August, occurring at 25 (89%) of the ponds surveyed ( $n = 28$ ); and on 26 August, seven young were present at five (18%) of these ponds.

#### 4.10 Population size and productivity

The estimated number of breeding pairs on the study area during 1986–1996 averaged 81 (range 64–106), a mean population density of 2.2 pairs/km<sup>2</sup> (range 1.7–2.8 pairs/km<sup>2</sup>). Population size increased from an average of 74 pairs in 1986–1989 to 95 pairs in 1990–1993 and then declined to 73 pairs in 1994–1996 (Table 11).

A visibility correction factor was developed to account for bias in data from brood surveys. The average of the individual correction factors calculated in three years of intensive study was applied to survey data from all years (1986–1996). Thus, the numbers of broods and young observed during surveys were adjusted by factors of 1.16 and 1.35, respectively. Actual numbers of grebes counted during surveys are presented in Appendix 1, and data used to calculate the correction factors are contained in Appendix 2.

The estimated number of young produced on the study area each year was quite variable, ranging from 46 to 175 and averaging 111 overall. On average, an estimated 60% of the pairs produced broods (range 33–87%), for a mean of 2.2 young per successful pair (range 1.6–2.6) or 1.4 per breeding pair (range 0.6–2.0) (Table 11).

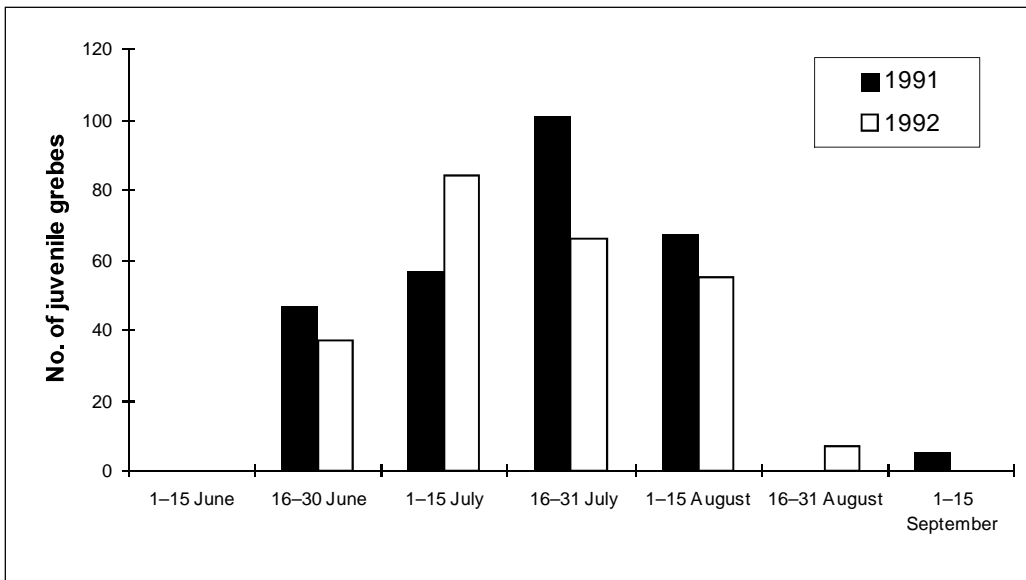
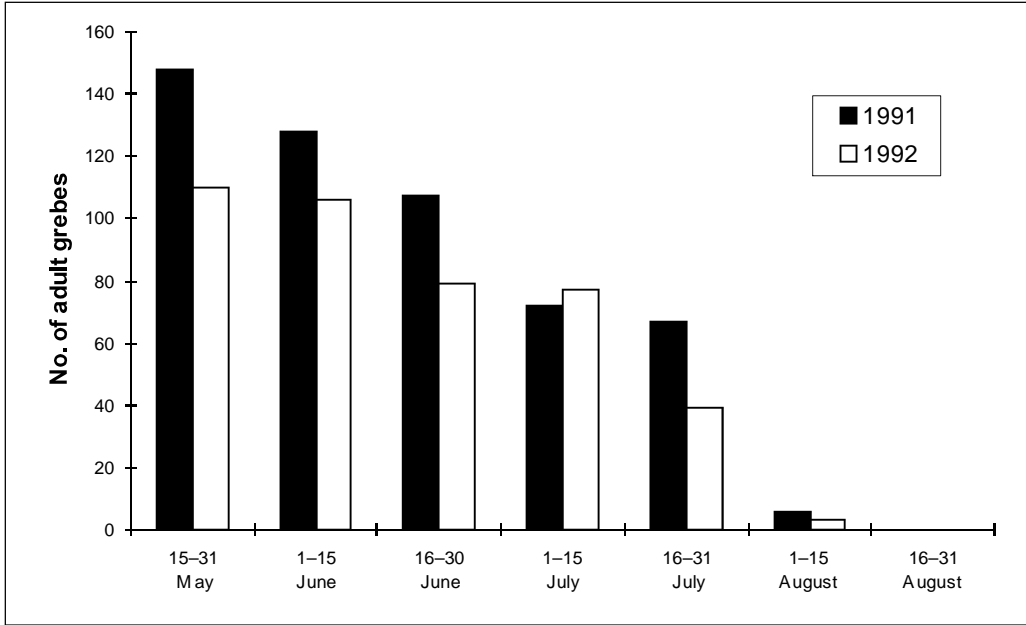
The productivity of Horned Grebes appeared to be related to weather conditions during the spring and summer, most noticeably in years of extreme weather conditions. The year of lowest reproductive output, 1988, was the coldest and latest spring recorded in 1986–1996. Snowmelt was delayed, and many ponds became ice-free much later than usual. The summer of 1988 was also the wettest recorded during the 11 years of study. In contrast, 1991, the year when the greatest numbers of broods and young were produced on the study area, was exceptionally warm during early May and dry during the summer (Table 12).

The number of young per successful breeding pair was correlated with several weather variables (Table 13). The regression equation for the number of young per successful breeding pair showed good fit to the data ( $R^2 = 0.93$ , Table 14) and suggested that high productivity was correlated with high mean daily temperature during the prenesting period and low precipitation later in the summer. Other indices of grebe productivity were less well correlated with the weather data (Table 13), and the next best-fitting regression equation accounted for only 54% of the variation in reproductive success (Table 14). Mean daily temperature during the prenesting period was the variable that appeared most consistently in the regression equations.

The average per capita reproductive output of the study population was a product of brood success (the percentage of pairs that produce broods) and average brood size (young produced per successful pair). Of these two demographic parameters, brood success was by far the more variable annually and therefore more apt to cause changes in annual productivity (Table 11). With the exception of 1988, the average number of young produced per successful pair was relatively constant from year to year.

**Figure 6**

Chronology of departure of adult and young Horned Grebes from the Yellowknife study area in 1991 and 1992



Productivity of the Horned Grebe population during one year apparently influenced the number of breeding pairs present on the study area in subsequent years. Years of relatively high reproductive success were followed, in most instances, by increases in the breeding population (Fig. 7). An exception to this trend occurred in the spring of 1992, when freezing conditions predominated in mid-May and forced grebes and ducks to concentrate in the remaining areas of open water. We suspect that the breeding pair estimates for 1992 may have been low, possibly because some potential breeding pairs did not return to the study area after the ponds once again became ice-free. Some Horned Grebes had already begun to lay when these subzero temperatures occurred. All nests observed during that period contained only one egg, and, as incubation either had not yet begun or was discontinuous, a number of eggs were frozen.

**Table 11**  
Estimated population size and productivity of Horned Grebes on the Yellowknife study area, 1986–1996<sup>a</sup>

Year	No. of breeding pairs	Density (no. of pairs/km <sup>2</sup> )	No. of broods (% success)	Total no. of young	No. of young per successful pair	No. of young per breeding pair
1986	69	1.8	23 (33%)	49	2.13	0.71
1987	67	1.8	49 (73%)	118	2.41	1.76
1988	80	2.1	28 (35%)	46	1.64	0.58
1989	78	2.1	68 (87%)	159	2.34	2.04
1990	104	2.7	49 (47%)	102	2.08	0.98
1991	106	2.8	81 (76%)	175	2.16	1.65
1992	76	2.0	63 (83%)	143	2.27	1.88
1993	95	2.5	56 (59%)	137	2.45	1.44
1994	84	2.2	42 (50%)	107	2.55	1.27
1995	71	1.9	31 (44%)	71	2.29	1.00
1996	64	1.7	52 (81%)	114	2.19	1.78
Average	81	2.2	49 (60%)	111	2.23	1.37

<sup>a</sup> Numbers of broods and young have been corrected for visibility bias.

**Table 12**  
Spring and summer weather conditions at Yellowknife during the breeding season of the Horned Grebe, 1986–1996

Year	Arrival (1–19 May)			Laying (20 May – 10 June)			Late incubation/hatching (11 June – 1 July)			Brood rearing (2–30 July)		
	Mean temp. (°C)	Total precip. (cm)	Precip. days	Mean temp. (°C)	Total precip. (cm)	Precip. days	Mean temp. (°C)	Total precip. (cm)	Precip. days	Mean temp. (°C)	Total precip. (cm)	Precip. days
1986	3.1	0.3	7	9.9	1.4	11	12.1	1.3	8	16.6	0.7	7
1987	3.0	0.3	2	11.1	0.0	1	14.3	2.3	10	16.6	0.3	7
1988	-1.6	0.1	1	8.1	1.7	11	13.6	2.7	8	15.8	3.5	13
1989	4.0	1.1	7	8.3	0.1	3	14.3	1.2	8	17.6	1.5	8
1990	1.2	0.1	2	9.4	0.2	5	15.4	0.2	4	17.0	2.3	8
1991	7.9	0.4	2	7.8	3.5	14	15.3	0.6	7	17.4	0.6	10
1992	1.9	0.6	4	7.9	0.6	5	13.8	1.1	1	15.4	0.9	6
1993	4.3	2.1	4	7.6	0.1	1	13.2	0.0	0	15.4	2.2	13
1994	5.1	0.4	4	14.0	0.6	3	13.0	0.7	5	19.4	0.9	5
1995	2.7	0.0	1	12.3	0.2	1	14.8	0.6	6	14.5	0.9	7
1996	-1.1	0.2	5	11.6	0.2	3	15.6	1.5	3	18.0	0.5	4
Avg.	2.8	0.5	4	9.8	0.8	5	14.1	1.1	5	16.7	1.3	8

**Table 13**  
Correlation between grebe productivity and spring and summer weather conditions, 1986–1996<sup>a</sup>

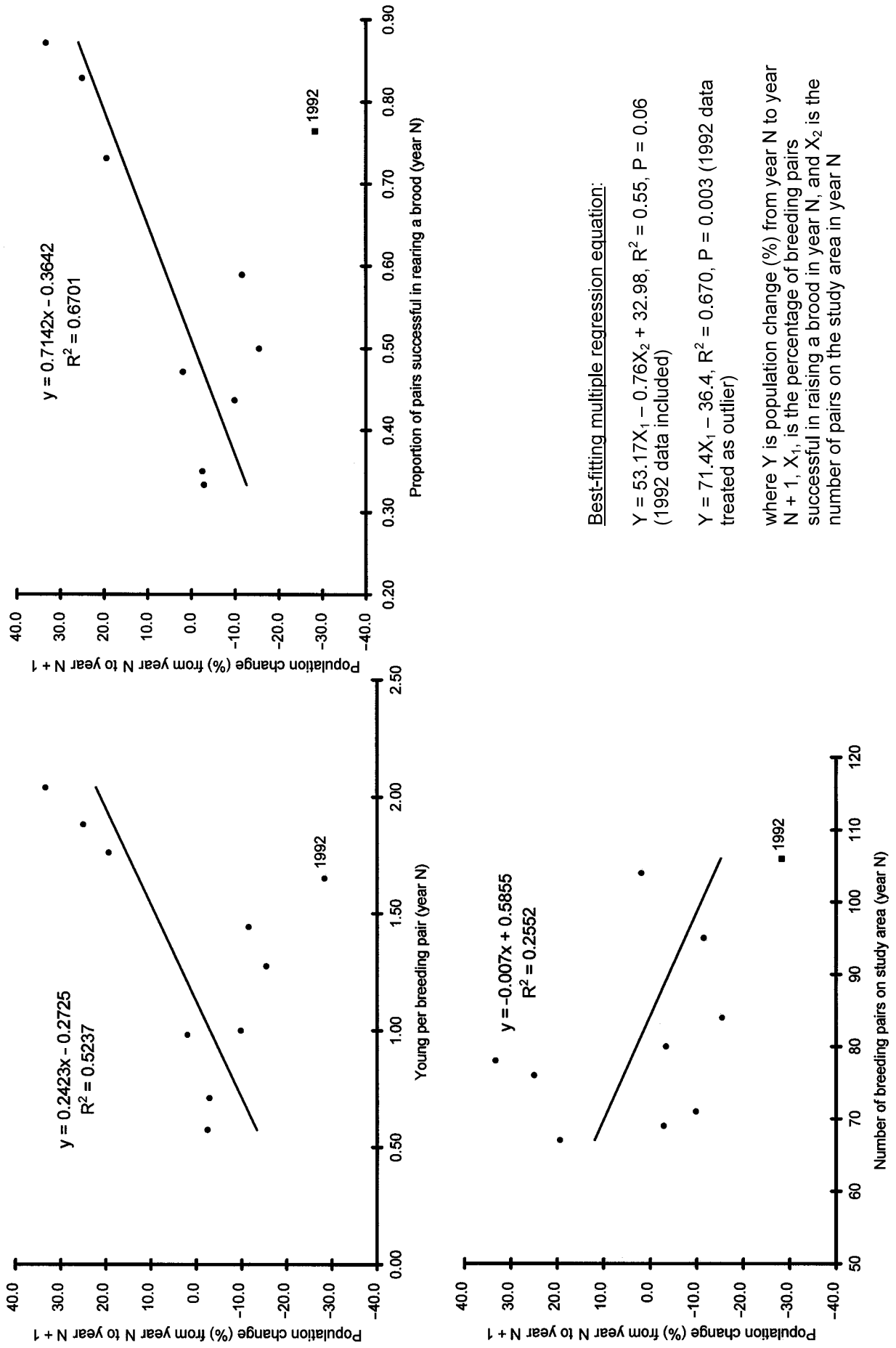
Grebe productivity	Arrival (1–19 May)			Laying (20 May – 10 June)			Late incubation/hatching (11 June – 1 July)			Brood rearing (2–30 July)		
	Mean temp. (°C)	Total precip. (cm)	Precip. day	Mean temp. (°C)	Total precip. (cm)	Precip. day	Mean temp. (°C)	Total precip. (cm)	Precip. day	Mean temp. (°C)	Total precip. (cm)	Precip. day
Number of broods	<b>0.51*</b>	0.37	0.10	-0.45	0.22	0.02	<b>0.47*</b>	-0.32	-0.24	0.22	-0.37	-0.15
% brood success	0.21	0.27	0.27	-0.23	-0.09	-0.24	0.45	-0.00	-0.17	0.17	-0.40	-0.35
Number of young	<b>0.58</b>	<b>0.47*</b>	0.17	-0.35	0.10	-0.13	0.38	-0.38	-0.27	0.20	<b>! 0.46</b>	-0.21
Young/successful pair	<b>0.58</b>	0.46	0.32	0.40	-0.45	<b>-0.66</b>	0.11	<b>-0.49*</b>	-0.25	0.06	<b>-0.72</b>	-0.43
Young/breeding pair	0.30	0.36	0.31	-0.13	-0.19	-0.37	0.36	-0.08	-0.19	0.15	<b>-0.48*</b>	-0.37

<sup>a</sup> Bold type with \* indicates P < 0.15; underlined bold type indicates P < 0.10.

**Table 14**  
Stepwise multiple regression of grebe productivity and spring and summer weather conditions, 1986–1996

Productivity variable	Regression model	R <sup>2</sup>	F	P
Number of broods	y = -84.8 + 3.75x <sub>1</sub> + 8.76x <sub>2</sub> x <sub>1</sub> = arrival mean temp. x <sub>2</sub> = late incubation/hatching mean temp.	0.54	4.77	0.04
Number of young	y = 86.0 + 9.06x <sub>1</sub> x <sub>1</sub> = arrival mean temp.	0.33	4.48	0.06
Young/successful pair	y = 2.41 + 0.04x <sub>1</sub> - 0.03x <sub>2</sub> - 0.09x <sub>3</sub> x <sub>1</sub> = arrival mean temp. x <sub>2</sub> = laying precip. days x <sub>3</sub> = brood rearing total precip.	0.93	31.69	0.0002
Young/breeding pair	y = 1.78 - 0.31x <sub>1</sub> x <sub>1</sub> = brood rearing total precip.	0.23	2.72	0.13

**Figure 7**  
The effects of productivity and number of breeding pairs in year N on population growth in year N + 1



Best-fitting multiple regression equation:

$$Y = 53.17X_1 - 0.76X_2 + 32.98, R^2 = 0.55, P = 0.06$$

(1992 data included)

$$Y = 71.4X_1 - 36.4, R^2 = 0.670, P = 0.003$$

(1992 data treated as outlier)

where Y is population change (%) from year N to year N + 1, X<sub>1</sub> is the percentage of breeding pairs successful in raising a brood in year N, and X<sub>2</sub> is the number of pairs on the study area in year N

## 5. Discussion

### 5.1 Chronology

#### 5.1.1 Spring arrival

The earliest date of arrival of Horned Grebes at Yellowknife (5 May) was approximately 7–10 days later, and peak influx was about two weeks later, than was reported by Ferguson (1977) for the Minnedosa, Manitoba, region and by Riske (1976) for central Alberta. Thus, grebes breeding on our study area may spend as much as two weeks longer on wintering areas or in migration than grebes breeding farther south.

#### 5.1.2 Clutch initiation

In contrast to the later dates of arrival and peak influx, the temporal distribution of nest initiation on our study area is very similar to that observed by Ferguson (1977) (Appendix 3). This suggests that the prenesting period may be shorter on our study area. If that is true, there are at least two plausible explanations: (1) a higher proportion of grebes may return to our study area paired, possibly because of a longer wintering/migration period (Ferguson [1977] noted that many grebes returned to his study area unpaired); and (2) grebes on our study area may spend a shorter time in establishing territories, possibly owing to advanced reproductive status at arrival (Ferguson [1977] reported that territories were secured 9–13 days before clutch commencement).

#### 5.1.3 Hatch date

Hatching of Horned Grebe clutches near Yellowknife occurred over a protracted period owing to variation in nest initiation dates among breeding pairs, asynchronous hatch within a clutch, and high rates of re-nesting. Horned Grebe pairs at all stages of the reproductive cycle, egg laying to brood rearing, were present during the first part of the hatching period in mid- to late June. Ferguson (1977) observed a similar situation and reported a hatching period of 54 days. Although our data do not allow such an exact measurement, the hatch period appeared to be shorter on our study area. In Ferguson's (1977) study, there were two instances in which a pair of grebes laid and hatched a second clutch after successful production of their first brood. None did so on our study area.

#### 5.1.4 Departure of adults and young

Departure of adults from nesting and brood-rearing areas has not been well documented in the literature. Fjeldsa (1973a) observed that family groups generally remained together for about six weeks, but in late seasons this period might be as short as three weeks. He also noted that adults do not necessarily leave simultaneously. Ferguson (1977) reported that departure of adults was influenced by brood size — one adult departing shortly after the “carrying period” in small broods, but both adults remaining until all chicks were independent in large, divided broods.

Comparison of median dates of hatch with median dates of adult departure in our study indicates that the first adults to depart the breeding ponds did so about 20 days into the brood-rearing period. The second adults departed about 33 days into the brood-rearing period. Fledging of Horned Grebe young occurs from 45–50 (Ferguson 1977) to 55–60 (Fjeldsa 1973a) days of age. Thus, most broods on our study area were abandoned by at least one adult when the chicks were less than half grown, and both adults generally departed well before the young fledged. Abandonment of broods does not appear to have a significant negative impact on survival of young, however, as most mortality occurs in early developmental stages (Fjeldsa 1973a; Ferguson 1977). For example, Ferguson (1977) reported that 78% of all mortality of young occurred within the first 10 days of life.

Early departure of adults may confer nutritional advantages to young and/or adults. The nutritional requirements of adults may be at a high point in the annual cycle following egg laying, incubation, and early brood rearing (which includes both carrying and active feeding of young). If the availability of food is limited on breeding ponds (which, on our study area, averaged only 0.4 ha in size), the survival of young may be enhanced if adult departure reduces competition for this resource.

Although large concentrations were never seen, we observed small groups (approximately 3–7) of adult Horned Grebes on the nearby North Arm of Great Slave Lake in late July and early August (but not in June; MAF, pers. obs.). The timing of these observations coincides with the departure of adult grebes from the study area and suggests that birds from the surrounding region may spend a period of time on Great Slave Lake (or other large lakes in the area) prior to their departure to wintering areas. Riske (1976) observed that as the number of Horned Grebes present on breeding areas in

central Alberta decreased, there was a concomitant increase in numbers on large bodies of water in the region. Munro (1941) observed small groups (6–12), which he presumed to be failed breeders, on lakes in the Cariboo region in July.

## 5.2 Habitat selection

### 5.2.1 Pond use

The sizes of ponds used for nesting by Horned Grebes in the Yellowknife region corresponded closely to values reported in other studies (Appendix 3) and confirmed a preference for small ponds. On our study area, 69% of breeding ponds were less than 1 ha in size, a result very similar to that observed by Faaborg (1976, 60% <1 ha in size) and Riske (1976, 70% <1.2 ha). However, Horned Grebes in our study and others used large bodies of water as well.

Horned Grebes on our study area exhibited a preference for man-made over natural wetlands. This may be related to differences in physical or chemical properties between the two pond types. For example, Heglund et al. (1994) found that Horned Grebes were most likely to occur on wetlands with longer shoreline length, higher pH, and increased levels of chlorophyll *a*. Murdy (1963, 1965) described man-made ponds along the Yellowknife highway as more fertile and alkaline than most of the natural water areas. We also noted differences in water chemistry between the two pond types (Table 2), including higher values for conductivity, turbidity, dissolved solids, calcium, magnesium, hardness, alkalinity, and pH on average for man-made ponds.

Some species of grebes may be adept at taking advantage of new wetlands created by human activities (e.g., reservoirs, quarries, and borrow pits) (for a review, see Riske 1976). Although there are no data to indicate how many Horned Grebes were present on our study area prior to the construction of the highway (and thus the man-made ponds), it seems logical to conclude that the local population has increased. Man-made ponds represent 54% of all ponds available on the study area, including 56% of all ponds in the preferred 0.1- to 1.0-ha size range. Thus, these ponds provide much of the available habitat and appear to be preferred over natural wetlands. The density of grebes per hectare of available wetland habitat on our study area was about six times higher on man-made ponds (0.81 pairs/ha) than on natural wetlands (0.14 pairs/ha). Further, the density of Horned Grebes on our study area is much higher than in the surrounding region where man-made wetlands do not occur (see Section 5.4.3 below). Density of Horned Grebes seems to be related to the density of small ponds on an area, and anything that increases the number of ponds of the preferred size is apt to increase densities.

Our observation in 1991 of eight nests on a 3.8-ha pond, a density of 2.1 breeding pairs per hectare, appears to be unusual, particularly for the North American subspecies. The Horned Grebe is generally a highly territorial, solitary-nesting species, although Clase et al. (1960) reported a colony of at least 36 birds at Myvatn, Iceland, and Fjeldsa (1973a) noted occasional “semicolonial” behaviour. Other exceptions to the solitary nesting habit have been reported, particularly on large water bodies and/or water bodies with high levels of vegetation interspersed, where visual isolation is high (Fjeldsa 1973a,c; Faaborg 1976; Ferguson 1977;

Sugden 1977; Ferguson and Sealy 1983). However, these situations usually involved only two or three pairs of grebes. Clase et al. (1960) attributed such associations to the “size and suitability of the sedge beds as a nesting site rather than any colonial habit.” Fjeldsa (1973a) noted that coexistence of two or more pairs of Horned Grebes occurred on “productive” ponds and postulated a direct relationship between food supply and breeding density. On his study area, grouped nests occurred on large water bodies with an abundant food supply and (presumably) a scarcity of nest sites. The year in which we observed this concentration of nests (1991) was also the year of highest population density (2.8 pairs/km<sup>2</sup>) in the 11 years of our study. This may have resulted in a shortage of suitable nest sites on the study area in that year. As noted above, visual isolation was low or nonexistent among most of the eight nests we observed, indicating that high visual isolation is not necessary for aggregated nesting to occur.

### 5.2.2 Nest site characteristics

The presence of sufficient residual emergent vegetation to provide nesting cover early in spring (i.e., before production of new growth) appears to be an important factor in the selection of wetlands for nesting by Horned Grebes. The high use of residual cattail and willow as cover or support for nests observed near Yellowknife is consistent with the observations of other investigators (Fjeldsa 1973b,c; Ferguson 1977). Protection or enhancement of residual emergent cover may be a useful management tool in some situations.

Horned Grebes often approach and depart from the nest underwater, and a minimum depth of approximately 20 cm appears necessary to allow easy underwater access to and from the nest (Ferguson 1977). We observed only two nests in shallower water (18 cm and 17 cm). Mean depth in all years on our study area, as in other studies, exceeded this value considerably. The differences we observed in depth at nest sites between years undoubtedly reflected annual differences in water levels on the study area rather than differences in site selection by the grebes. However, the difference we observed in mean depth between successful and unsuccessful nests suggests this factor may influence reproductive success. Ferguson (1977) also noted that successful nests were located in deeper water than unsuccessful nests.

Two main factors likely influence the positioning of Horned Grebe nests within the emergent vegetation zone. Risk of predation forces grebes to build their nests well away from the shoreline, whereas exposure to wind forces them to nest within emergent vegetation, where wave action is reduced (Ferguson 1977). Distance of nests from shore and distance from nests to open water on our study area were similar to those observed in other studies (Appendix 3), suggesting a broadly similar response to these potentially destructive factors. We did not observe differences in these parameters between successful and unsuccessful nests. Few nests were lost to wave action (flooding) on our study area (Table 9), probably because of the generally small size of ponds used for nesting, and predation by strictly land-based predators such as foxes was not observed. In contrast to our results, Ferguson (1977) reported an average 12% of nests destroyed by wave action and found that successful nests were located significantly farther from shore than unsuccessful nests. This latter difference is likely attributable to the

presence of raccoons *Procyon lotor* on Ferguson's (1977) study area (see Section 5.4.2 below).

### 5.2.3 Nest materials

Although we did not measure availability of the various nest materials used by Horned Grebes, it was obvious that the most common nest materials, sedge and cattail, were also the dominant types of emergent vegetation on the study area. Ulfvens (1988) suggested that choice of nest materials by Horned Grebes was related not to preference but simply to availability. Uusitalo (1976) also found a significant correlation between plant availability and use in the nest.

## 5.3 Geographic variation in reproductive parameters

### 5.3.1 Clutch size and egg size

Horned Grebes nesting near Yellowknife lay fewer, slightly larger eggs than those nesting in Manitoba (Ferguson 1977; Arnold 1989) but produce more eggs than those in central Alberta (Riske 1976). In general, clutch sizes in North American populations are higher than those of the European subspecies (Appendix 3). Clutch size ranges from a low of 3.4 eggs reported for Finland (Ulfvens 1988) to a high of 5.9 eggs in Manitoba (Ferguson and Sealy 1983), with that observed on our study area (5.3) approaching the upper limit of this range. Such broad variation may be the result of a number of factors, including differences in weather conditions, population density, food availability, body condition of laying females, and the evolutionary history of the subspecies (Fjeldsa 1973a; Johnsgard 1987).

Variation in clutch size among years at a single study site, as we observed, has been reported previously. Fjeldsa (1973a) observed yearly variation and noted a general tendency for reduced clutch size if it was wet and cool during the laying period. Our results appear to support Fjeldsa's (1973a) observation, as clutch size was smallest in the relatively late spring of 1986.

Ulfvens (1988) observed that initial clutches were significantly larger than replacement clutches. Ferguson (1977) also reported that mean clutch size of renests overall was significantly lower than that of first nests, although renests initiated early in the season did not differ from first nests. The lack of a significant difference in our results may be related to small sample size or to differences in timing of nest losses, rates of predation and types of predators, or other unknown factors.

In some species of waterfowl, larger eggs may confer nutritional or physiological advantages to hatchlings (e.g., Lesser Snow Geese *Chen caerulescens*, Ankney 1980; American Coots, Alisauskas 1986). However, Arnold (1989) suggested that this was unlikely to be the case in Horned Grebes, as fresh egg mass was poorly correlated with lipid and energy content and only moderately correlated with protein content. Thus, the larger linear dimensions and volumes of eggs we observed in comparison to those of Ferguson (1977) and Arnold (1989) (Appendix 3) probably do not imply such advantages, nor necessarily represent adaptation to harsh subarctic climatic conditions.

### 5.3.2 Renesting

Horned Grebes on our study area were persistent in renesting. Several pairs were successful in their third nesting attempt in 1991, and one pair was successful in its fourth nesting attempt in 1992. Ferguson (1977) also found that Horned Grebes in Manitoba renested persistently, laying eggs up to the middle of July. Fjeldsa (1973a) reported that the probability that a breeding failure would be followed by a renesting effort was 88% on his study area. High rates of renesting result in a very protracted nesting period. However, renesting efforts probably make a very significant contribution to the overall productivity of Horned Grebes.

### 5.3.3 Brood loss and brood size

The average rate of complete brood loss for Horned Grebes nesting on our study area was 9%. We could find no previous reference to this phenomenon among grebes to provide comparative data. However, this rate is similar to that reported for Canvasbacks *Aythya valisineria* (average 12% under normal conditions) by Leonard et al. (1996), although it is much lower than the rates reported for Ring-necked Ducks *Aythya collaris* (19%) by McAuley and Longcore (1988), for Mallards *Anas platyrhynchos* (37%) by Orthmeyer and Ball (1990), and for Canvasbacks (35%) by Korschgen et al. (1996).

The size of broods recorded near Yellowknife is similar to that reported by other investigators in North America (Riske 1976; Ferguson 1977) (Appendix 3). Ferguson (1977) reported an average brood size of 4.3 chicks at hatching and 2.7 at fledging (giving a 63% rate of survival to fledging) for the prairie pothole region near Minnedosa, Manitoba. Our estimated brood size of 2.3 chicks at fledging is consistent with that of Ferguson (1977), especially in light of the slightly lower clutch size observed on our study area.

## 5.4 Productivity

### 5.4.1 Nest success

Apparent nest success near Yellowknife was high (60%) and consistent (range 56–69%) over the three years in which it was monitored. Our analysis using the Mayfield method provided similar results. Riske (1976) reported occasional very low nesting success in some parkland breeding areas as a result of low water levels and, possibly, high winds.

### 5.4.2 Nest predation

Predation was the major cause of nest loss on our study area and accounted for 86% of all known nest losses. Other birds appeared to be the most common predators of Horned Grebe eggs. At least 56% of all predation was by birds — 12% by ravens, and 44% by one or more unidentified avian predators. The rate of nest loss attributed to avian predators is undoubtedly an underestimate, given that 27% of all predation could not be classified as either avian or mammalian. In contrast, Ferguson (1977) found that loss of Horned Grebe eggs to avian predators was low compared with losses to mammals, primarily because grebes of both sexes were very aggressive (i.e., capable of defending the

nest against other birds) and rarely left the nest unattended. The avian predators present in the Yellowknife region (particularly ravens) appear to present a more formidable challenge to nesting Horned Grebes than those present on Ferguson's (1977) study area. Potential avian predators identified by Ferguson (1977) included American Crow *Corvus brachyrhynchos*, Black-billed Magpie *Pica pica*, American Coot, Black Tern *Chlidonias niger*, and Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. All of these species except the Yellow-headed Blackbird occur on our study area but are uncommon or rare.

Mammalian predation on our subarctic study area is lower than in Manitoba, where Ferguson (1977) reported that raccoons were responsible for most of the predation of Horned Grebe nests.

#### 5.4.3 Population size and productivity

Both size of the breeding population of Horned Grebes on the study area and production of young varied from year to year, with production being the more variable of the two parameters. In general, increases in the number of breeding pairs followed years of above-average reproductive success, and decreases in breeding pairs typically occurred after years of lower reproduction. However, the overall correlation between reproductive success and subsequent population growth was only moderate. This result seems likely to be affected by the difficulties inherent in trying to accurately measure either population size or productivity. Other factors not investigated in this study (e.g., mortality, immigration, emigration) would also have influenced population growth.

In a highly territorial species such as the Horned Grebe, some upper limit to the number of breeding pairs (and, by extension, reproductive output) on a local area may be set by social interactions. Whether such limiting breeding population densities were attained on our study area is not entirely clear, although the regression analyses suggested a negative relationship between population size and subsequent population growth (Fig. 7).

Observations of aquatic bird populations and habitat near Yellowknife and elsewhere in the subarctic indicate that the breeding pair densities attained by Horned Grebes on our study area are higher than elsewhere in the region. In 1989, surveys carried out on a 15-km<sup>2</sup> site located 50 km east of the primary study area indicated a population of approximately eight pairs of Horned Grebes or 0.5 pairs/km<sup>2</sup>. In comparison, the density on the primary study area averaged 2.2 pairs/km<sup>2</sup>. This higher density undoubtedly reflects the large number of small man-made and natural ponds on the study area and perhaps also the enriched nature of the man-made wetlands.

Average productivity on our study area was within the range of values reported in other studies (Appendix 3). There was, however, a great deal of annual variation in the number of young produced per breeding pair and most other measures of productivity. Only Fjeldsa (1973a) provided comparable production data (extending over a period of six years, only four of which were consecutive); he observed "considerable differences in production" between years. Fjeldsa (1973a) reported that much of the annual difference in Horned Grebe production could be attributed to spring weather, with correlations between low reproductive success and cool and wet conditions (especially snowfall) during the

breeding season and between mortality of chicks and inclement weather during hatch. Our data support these conclusions, in that warm temperatures early in the breeding season and dry conditions during the brood-rearing period appeared to enhance reproductive success. Favourable weather early in the breeding season could influence productivity by allowing earlier or more successful initial breeding efforts, by increasing invertebrate prey abundance, or by enhancing growth rates of emergent vegetation used as cover and support for nests. Excessive precipitation during the hatching and early brood-rearing period may have a direct negative impact upon juvenile survival.



## 6. Suggestions for future research

This study has begun to address a lack of information on the Horned Grebe in the northern portions of its range in Canada. However, many aspects of the ecology of these birds in the subarctic, and elsewhere, remain to be studied. Capture and marking of grebes would provide more detailed information on a variety of subjects, including mate and site fidelity; sex-specific timing of arrival and departure, and division of labour throughout the reproductive cycle; age-related variation in reproductive success and survival; and locations of staging and wintering areas.

Relationships between wetland productivity and grebe use and reproductive success should be investigated. Related studies on body condition and the acquisition and utilization of nutrients for breeding might provide some interesting insights, particularly in light of the high rates of reneating observed in this species. The contribution of reneating efforts to the overall productivity of local breeding populations should be quantified. Growth rates and plumage development of juveniles and age at fledging also require further study.

The relative dearth of studies of the Horned Grebe in North America provides a wealth of research opportunities. Information available in the comparatively large body of European literature regarding the species should lead prospective investigators to research topics beyond those suggested herein. We encourage others to undertake studies of this fascinating species.

## 7. Summary

The breeding ecology of the Horned Grebe *Podiceps auritus* was investigated on a 38-km<sup>2</sup> study area near Yellowknife, Northwest Territories (62° 27'N, 114° 22'W). Population size and productivity were monitored during 1986–1996. Other aspects of breeding biology were studied in 1986, 1989, 1991, and 1992. Our objectives were to document the breeding biology of this species in a region where it had not been studied previously and to determine factors that may influence the productivity of grebe populations in the subarctic boreal forest.

There were 575 ponds on the study area: 262 of natural origin, and 313 “borrow pits” created during construction of the highway circa 1960. Use of ponds by Horned Grebes was influenced by both pond size and type. Grebes largely avoided ponds less than 0.1 ha in size, made extensive use of those in the range 0.3–2.0 ha, and showed moderate but consistent use of ponds larger than 2.0 ha. Ponds used by grebes ranged in size from <0.1 to 1.1 ha (median 0.3 ha) for borrow pits and from <0.1 to 18.2 ha (median 1.0 ha) for natural ponds, with a median of 0.4 ha overall.

Emergent plants provided cover and support for nests. The most frequently used plants, cattail and willow, occurred at 54% and 49% of all nests, respectively. Depth of water at nests ranged from 17 to 147 cm, with a mean of  $61 \pm 2$  (SE) cm. The mean distance of nests from shore was  $8.3 \pm 0.3$  m (range 0.7–27.8 m), and the mean distance from nests to open water was  $2.3 \pm 0.2$  m (range 0–16.9 m).

Fifteen types of plants were used as nest-building materials. Most nests contained sedge (83%) or cattail (75%).

First clutches were initiated during the period 20 May to 11 June, with a mean date of  $29 \text{ May} \pm 0.4$  day. Replacement clutches were initiated between 27 May and 20 June, with a mean date of  $9 \text{ June} \pm 1$  day. Most pairs renested following destruction of a clutch. Several pairs renested twice, and one pair renested three times. Mean size of first clutches was  $5.30 \pm 0.08$  eggs. Mean size of replacement clutches was  $5.11 \pm 0.27$  eggs.

Sixty-nine percent of successful first nesting attempts hatched between 21 and 27 June. Median dates of hatch for first nesting attempts were 22 June in 1991 and 25 June in 1992. The median date of hatch for renests was 5 July.

Apparent nest success was 59% for first nesting attempts and 61% for renests; a modified Mayfield estimate was  $56 \pm 4\%$  overall.

Egg loss was predominantly attributed to unidentified avian predators (44%), mink (17%), and ravens (12%).

An estimated 3.6–3.8 young were hatched per successful pair. Twelve of 130 pairs (9%) observed during more intensive studies in 1991 and 1992 lost their entire broods. Size of broods at or beyond the one-quarter grown stage (>12 days of age) ranged from 1 to 6, with an overall mean of  $2.3 \pm 0.1$ . This likely represents a good estimate of brood size at fledging.

Departure of the first members of successful pairs from breeding ponds ranged from 17 June to 31 July, with a median of 13 July. Departure of the second adult ranged from 11 July to 14 August, with a median of 28 July. Most young grebes had left the study area by late August, but a few remained into early September.

The average number of breeding pairs on the study area during 1986–1996 was 81 (range 64–106), or 2.2 pairs/km<sup>2</sup> (range 1.7–2.8). The average number of young produced per year was 111 (range 46–175), or 1.4 per breeding pair (range 0.6–2.0). High productivity of Horned Grebes was correlated with warm temperatures during the prenesting period and low precipitation later.

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# Appendices

**Appendix 1**  
Summary of numbers<sup>a</sup> of Horned Grebes observed on the Yellowknife study area, 1986–1996

Year	May survey	June survey	July survey			August survey		
	Pairs	Pairs	Pairs	Broods	Juveniles	Pairs	Broods	Juveniles
1986	80	57	23	16	30	1	4	6
1987	82	51	66	40	83	2	13	30
1988	97	62	33	17	25	5	12	14
1989	86	69	72	37	71	11	36	63
1990	111	97	60	9	18	9	40	71
1991	127	84	47	61	114	2	29	44
1992	74	78	54	41	75	8	39	77
1993	107	83	58	30	63	5	28	53
1994	91	77	62	15	27	3	23	51
1995	67	74	69	12	17	11	18	39
1996	55	73	64	17	39	19	36	57

<sup>a</sup> Numbers of broods and juveniles are not corrected for visibility bias.

**Appendix 2**

Data used to calculate visibility correction factors for number of chicks and number of broods

1989 (n = 22)			1991 (n = 25)			1992 (n = 20)		
Pond number	Survey count	Intensive count	Pond number	Survey count	Intensive count	Pond number	Survey count	Intensive count
B32	4	1	B13	1	1	B1	3	4
B40	1	7	B15	1	1	B10B	0	1
B45A	2	4	B40	1	1	B13	1	2
B52A	3	4	B52A	2	2	B32	3	3
B53	4	4	B53	0	2	B40	2	2
B55	1	1	B58	2	2	B45A	2	3
B58A	0	1	B74A	1	3	B52A	4	4
B74A	3	4	B76A	1	2	B73I	3	4
B76	5	5	B81	7	14	B103A	2	2
B76A	4	0	B94B	1	2	B117B	3	3
B81	2	3	B96	2	2	B146A	3	3
B88	2	1	B101A	2	2	B154	2	3
B103A	2	4	B122A	1	1	B155A	2	3
B130	1	2	B130	1	1	22	1	1
B135	1	3	B135	3	3	35/36	0	3
B145A	0	1	B146A	0	2	86	1	1
B155A	2	2	B154	2	2	114	3	3
B167	4	6	B155A	3	3	145	3	3
2	0	2	17	1	1	152	1	1
17	1	1	22	2	2	221A	0	1
35/36	0	1	35/36	3	3			
114	2	2	86	2	4			
			114	0	1			
			152	10	13			
			221B	2	3			
Total chicks	44	59		51	73		39	50
Correction factor	59/44 = 1.34			73/51 = 1.43			50/39 = 1.28	
Average = 1.35								
Total broods	18	21		22	25		17	20
Correction factor	21/18 = 1.17			25/22 = 1.14			20/17 = 1.18	
Average = 1.16								

**Appendix 3**

## Comparison of Yellowknife study area results with studies of Horned Grebes in other geographic locations

	Location	Reference		
<b>Size of ponds used for nesting</b>				
0.2->500 ha	Finland, Norway, Iceland	Fjeldsa 1973c		
0.1-5.2 ha	North Dakota	Faaborg 1976		
0.1-8.4 ha	Manitoba	Ferguson 1977		
<1.2 ha (70%); 1.2-2.0 ha (30%)	Alberta	Riske 1976		
<0.1-18.2 ha	Yellowknife	Present study		
<b>Distance from nests to shore</b>				
10 m	Finland	Uusitalo 1976 <sup>a</sup>		
6.8 ± 0.7 m	Manitoba	Ferguson 1977		
8.3 ± 0.3 m	Yellowknife	Present study		
<b>Distance from nests to open water</b>				
1.7 m	Finland	Uusitalo 1976 <sup>a</sup>		
1.5 ± 0.2 m	Manitoba	Ferguson 1977		
2.3 ± 0.2 m	Yellowknife	Present study		
<b>Water depth at the nest</b>				
43 ± 19 cm	Norway	Fjeldsa 1973c		
45 ± 26 cm	Iceland	Fjeldsa 1973c		
37 cm	Finland	Uusitalo 1976 <sup>a</sup>		
30 cm	Finland	Ulfvens 1988		
39 ± 2 cm	Manitoba	Ferguson 1977		
86 cm	Saskatchewan	Sugden 1977		
61 ± 2 cm	Yellowknife	Present study		
<b>Clutch initiation dates for first nests</b>				
12 May – 20 July	Iceland, Norway	Fjeldsa 1973a		
17 May – 11 June	Manitoba	Ferguson 1977		
20 May – 11 June	Yellowknife	Present study		
<b>Clutch size (range, n)</b>				
4.28 ± 0.1	—	63	Estonia	Onno 1960 <sup>a</sup>
3.79	1-6	233	Norway	Fjeldsa 1973a
4.5	—	46	Finland	Von Haartman et al. 1963-1972 <sup>a</sup>
5.3 ± 0.3	—	12	Finland	Uusitalo 1969 <sup>a</sup>
4.5 ± 1.3	—	49	Finland	Uusitalo 1976 <sup>a</sup>
5.00 ± 1.2	—	68	Finland (archipelago)	Ulfvens 1988
3.42 ± 0.8	—	26	Finland (lakes)	Ulfvens 1988
3.75	1-7	537	Iceland	Fjeldsa 1973a
5.9	3-8	43	Manitoba	Ferguson and Sealy 1983
4.37 ± 0.2	3-7	—	Alberta	Riske 1976
5.30 ± 0.1	3-7	114	Yellowknife	Present study
<b>Egg size (length, width, n)</b>				
45.5 mm	30.8 mm	499	Norway	Fjeldsa 1973a
45.8 mm	30.9 mm	1637	Iceland	Fjeldsa 1973a
44.2 mm	29.7 mm	697	Baltic	Fjeldsa 1973a
44.3 mm	30.2 mm	591	Manitoba	Ferguson 1977
43.7 mm	30.1 mm	19	Manitoba	Arnold 1989
44.5 mm	30.6 mm	888	Yellowknife	Present study
<b>Egg volume (n)</b>				
29.0 cm <sup>3</sup>	499		Norway	Fjeldsa 1973a
29.4 cm <sup>3</sup>	1637		Iceland	Fjeldsa 1973a
20.1 cm <sup>3</sup>	19		Manitoba	Arnold 1989
21.2 cm <sup>3</sup>	888		Yellowknife	Present study
<b>Brood size (approximate fledging)</b>				
3.09 ± 1.20			Finland (archipelago)	Ulfvens 1988
1.52 ± 0.71			Finland (lake)	Ulfvens 1988
2.74			Manitoba	Ferguson 1977
2.26			Alberta	Riske 1976
2.3 ± 0.1			Yellowknife	Present study

*Continued*

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**Appendix 3 (cont'd)**Comparison of Yellowknife study area results with studies of Horned Grebes in other geographic locations

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	Location	Reference
<b>Productivity (young/breeding pair)</b>		
1.91	Finland	Ulfvens 1988
1.5–1.88	Finland, Norway, Iceland	Fjeldsa 1973a
1.59	Finland	Uusitalo 1976 <sup>a</sup>
1.27	Alberta	Riske 1976
1.4	Yellowknife	Present study

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<sup>a</sup> Original not seen, cited in Ulfvens (1988).



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