THE UNIVERSITY OF MANITOBA

Adaptations of the Horned Grebe
for Breeding in Prairie Pothole Marshes

by

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ABSTRACT

Field studies of the Horned Grebe (Podiceps auritus) were conducted during the breeding seasons of 1974 and 1975 near Minnedosa, Manitoba. This paper documents the reproductive biology of Horned Grebes and describes their adaptations for nesting in unstable marsh habitats.

Nesting pairs defended Type A territories which ranged in size from 0.05 to 2.70 hectares. Occupation of a pothole by two or more nesting pairs occurred only on potholes larger than one hectare. Differential selection of permanent potholes for nesting reflected the grebes' dependence on open-water feeding areas. Interspecific territoriality by Horned Grebes was related to defense of their pairing and nesting platforms. Three factors were important in nest-site selection: (1) accessibility of the site from open water; (2) protection of the nest from wave action; and (3) concealment of the nest from predators. All nesting platforms were anchored to emergent vegetation.

Annual variation in initiation of first clutches was correlated with differences in air temperature during spring. Initiation of replacement clutches was influenced by the stage of the nesting cycle at which the previous nests were destroyed. Use of the same territory following failure of an incomplete clutch facilitated rapid clutch replacement. A seasonal decline in clutch size was observed and was possibly due to depleted energy reserves of females late in the nesting season and to an allocation of energy to the prebasic molt.

Incubation was shared by the sexes, but females assumed a reduced role in incubation during the period of egg-laying. Hatching was asynchronous. Successful nests were located farther from shore and in deeper water than nests destroyed by predators. Raccoons (Procyon lotor) were responsible for most of the egg loss. Egg loss to wave action was of secondary importance. Chick development and parental behaviour are described and compared to that of the Great-crested Grebe (Podiceps cristatus). An elaborate system of parental feeding by Horned Grebes reduced competitive disparities within broods that resulted from age differences among chicks.

The reproductive strategy of Horned Grebes is examined in relation to environmental stability, and possible selection pressures influencing this strategy are discussed.

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INTRODUCTION

Marsh habitats associated with shallow lake basins of glacial origin are characterized by their instability. The 'pothole marsh' community is described by Weller and Fredrickson (1973:288) as "an unstable ecosystem with extreme, short-term fluctuation from the near-terrestrial to near-aquatic system". Seasonal and annual fluctuations in habitat quality and quantity are largely due to variations in precipitation and subsequent changes in water levels. Wetland vegetation is highly sensitive to changing water levels, and undergoes rapid and extensive changes in species composition, distribution and abundance (Millar 1969). Plant succession in pothole marshes is continually being reversed (Millar _op. cit._).

Marsh-dwelling animals are therefore subjected to rapidly changing environmental conditions. Weller and Spatcher (1965) and Weller and Fredrickson (1973) investigated the impact of fluctuating habitat conditions on the distribution and abundance of several marsh bird species in Iowa. The availability of nesting cover in the form of emergent vegetation was of prime importance, and bird abundance and diversity were greatest when a well-interspersed cover-to-water ratio of approximately 50:50 prevailed.

In general, marsh birds are adapted to changing habitat conditions by their pioneering ability and mobility (Weller and Spatcher 1965). By shifting from marsh to marsh and by rapid colonization of newly-flooded habitats, overall population levels are maintained despite sub-optimal conditions in localized areas. However, adaptability of individual species is related to their degree of specialization. Relatively non-specialized species are more tolerant of changing conditions and are able to exploit a wide range of nesting habitats. For example, Red-winged Blackbirds (*Agelaius phoeniceus*) frequently nest in upland habitats when emergent cover is scarce (Weller and Spatcher *op. cit.*), or when they are excluded from their optimal niche space by Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Robertson 1972). Great adaptability is also evident in ducks of the genus *Anas*, which show remarkable flexibility in nest-site selection (Weller and Spatcher 1965).

In contrast, the grebes (Podicipedidae) form a highly specialized group of approximately 20 species. (The taxonomic status of a few forms is uncertain (see Simmons 1962; Storer 1963a).) As a result of their morphological specialization to an entirely aquatic existence, grebes are limited in both habitat and nest-site selection. Studies of the following species have demonstrated their dependence on open-water feeding areas and emergent nesting cover: Rolland's (*Rollandia rolland*) and Silver Grebes (*Podiceps occipitales*) (Burger 1974a); Horned Grebe (*P. auritus*) (Fjeldsa 1973a); Great-crested (*P. cristatus*), Red-necked (*P. grisegena*), Eared (*P. nigricollis*), and Little Grebes (*P. ruficollis*) (Gotzman 1965); and Western Grebe (*Aechmophorus occidentalis*) (Nuechterlein 1975). The use of dry-land nesting sites by Western Grebes, as reported by Nero (1958), is an exceptional occurrence.

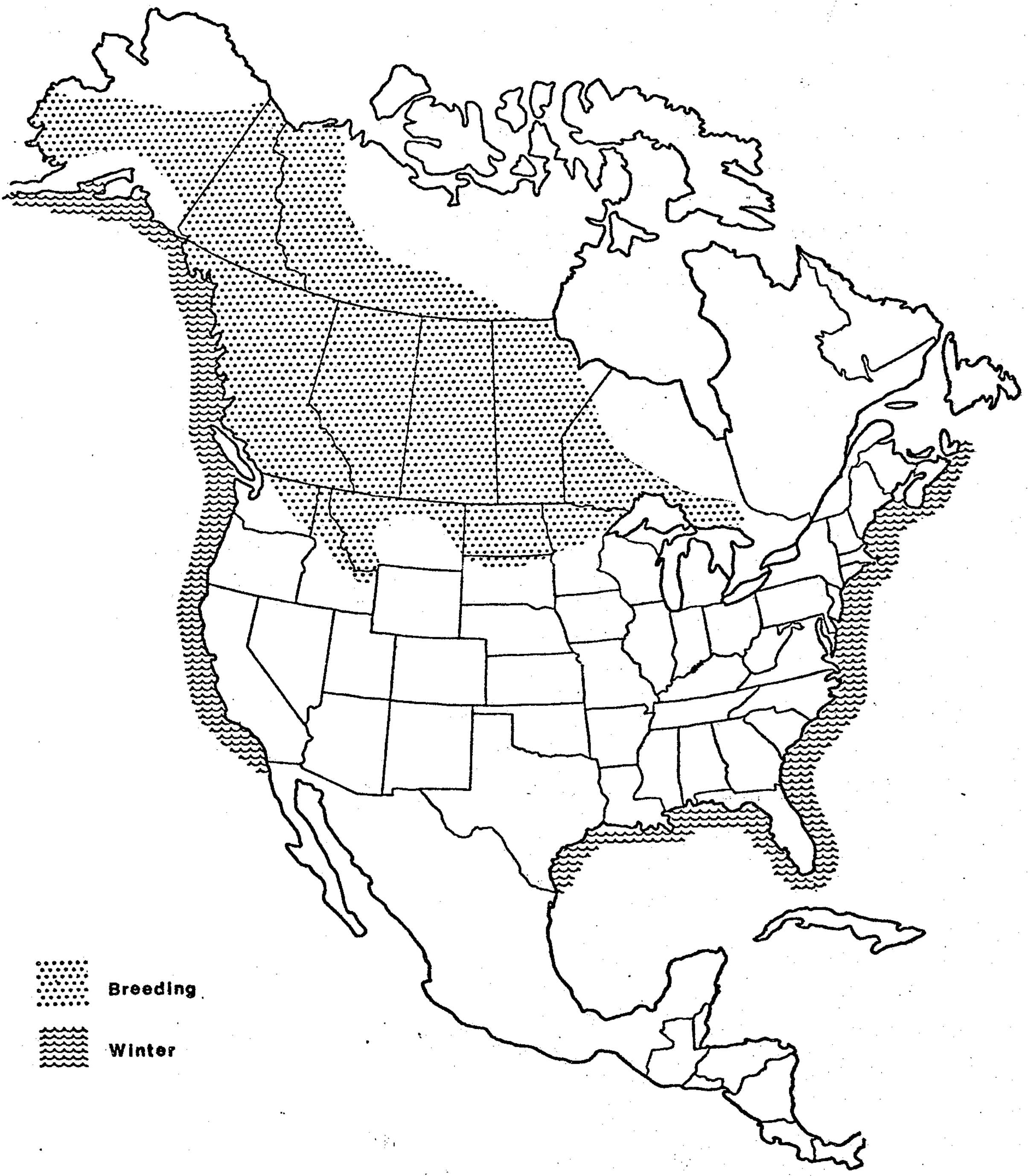
Thus, in unstable marsh habitats, the problems encountered by grebes and other specialized groups are apparent. However, considering the prominence of grebes in these habitats, it seems reasonable to expect that they have developed other breeding adaptations that compensate for their limited adaptability in habitat and nest-site selection.

Simmons (1970, 1974) suggested that many of the reproductive traits in the life history of the Great-crested Grebe are adaptations to an unpredictable food supply. Investigations of adaptive aspects of other grebes are lacking. The present study examines the reproductive biology of Horned Grebes in order to determine adaptations for nesting in prairie pothole marshes. This paper discusses adaptive aspects of territoriality, nest-site selection, egg-laying, incubation, hatching and parental behaviour.

The Horned Grebe, once considered to be a taxonomic uniform holarctic species (Parkes 1952), breeds throughout much of northern Asia, northern Europe, and northwestern North America. However, Fjeldsa (1973b) demonstrated geographical variation in this species and recognized three subspecies. *Podiceps auritus auritus* (Linnaeus 1758) breeds in Sweden, Finland, and the Baltic States, eastward to the Obj lowlands in the Union of Soviet Socialist Republics. *P. a. arcticus* (Boje 1822) breeds in Iceland, Scotland, northern Norway and, occasionally, in the Faeroe Islands. *P. a. cornutus* (Gmelin 1788) breeds throughout northwestern North America (and probably eastern Siberia).

The breeding and wintering ranges of *P. a. cornutus* (hereafter referred to as the Horned Grebe) in North America are depicted in Figure 1. Despite its widespread occurrence in western North America, no detailed accounts of its reproductive biology have been published. The reports of Bent (1919), DuBois (1919), Munro (1941), and Palmer (1962) are based on casual observations of a few breeding pairs from widely scattered localities, and are generally incomplete. More thorough ecological investigations have been conducted in Europe

Figure 1. North American distribution of the Horned Grebe. Drawn after Godfrey (1966) and Palmer (1962).


Breeding
Winter

(see Clase et al. 1960; Fjeldsa 1973a,c; Hogstrom 1970; Onno 1960). Agonistic and courtship behaviour of the Horned Grebe has been described and analysed in detail by Fjeldsa (1973d) and Storer (1969).

STUDY AREA

Field work was conducted on prairie pothole marshes within the region of southwestern Manitoba frequently termed the 'Minnedosa pothole district'. Encompassing an area of over 10,000 km^2, the Minnedosa district lies within the aspen parkland, the transition zone between the grasslands on the south and the coniferous forests on the north (Bird 1930). The extent of the Minnedosa pothole district and location of the study area are shown in Figure 2. Most observations were made in an area of 75 km^2 located south of Minnedosa (50°15'N; 99°50'W) in the Rural Municipality of Odanah (Figure 3). I concentrated efforts in locating nesting pairs of Horned Grebes to a region 400 m wide (200 m on each side of the road allowance) along a 73 km transect of unpaved road, giving an area of 29.2 km^2. In addition, all wetlands within a study block of 5.2 km^2 (two adjacent sections of land) were surveyed at weekly intervals. Each year (1974 and 1975) over 450 potholes were surveyed for nesting grebes.

The glacial history of the Minnedosa region is evident from its undulating to steeply sloping topography. Drainage is poor, and runoff water accumulates in enclosed glacial basins, locally called potholes or sloughs, which in some areas occupy more than 35 percent of the total land acreage (Ehrlich _et al_. 1957). The rolling terrain results in a relatively small runoff area so that water levels vary directly with the amount of precipitation. Kiel _et al_. (1972:37) noted that "deviations of 20 percent or more from normal precipitation noticeably change pothole habitat, and the changes are accentuated by two or more successive years of above or below normal precipitation".

Figure 2. Map of southern Manitoba showing location of study area within the Minnedosa pothole district.

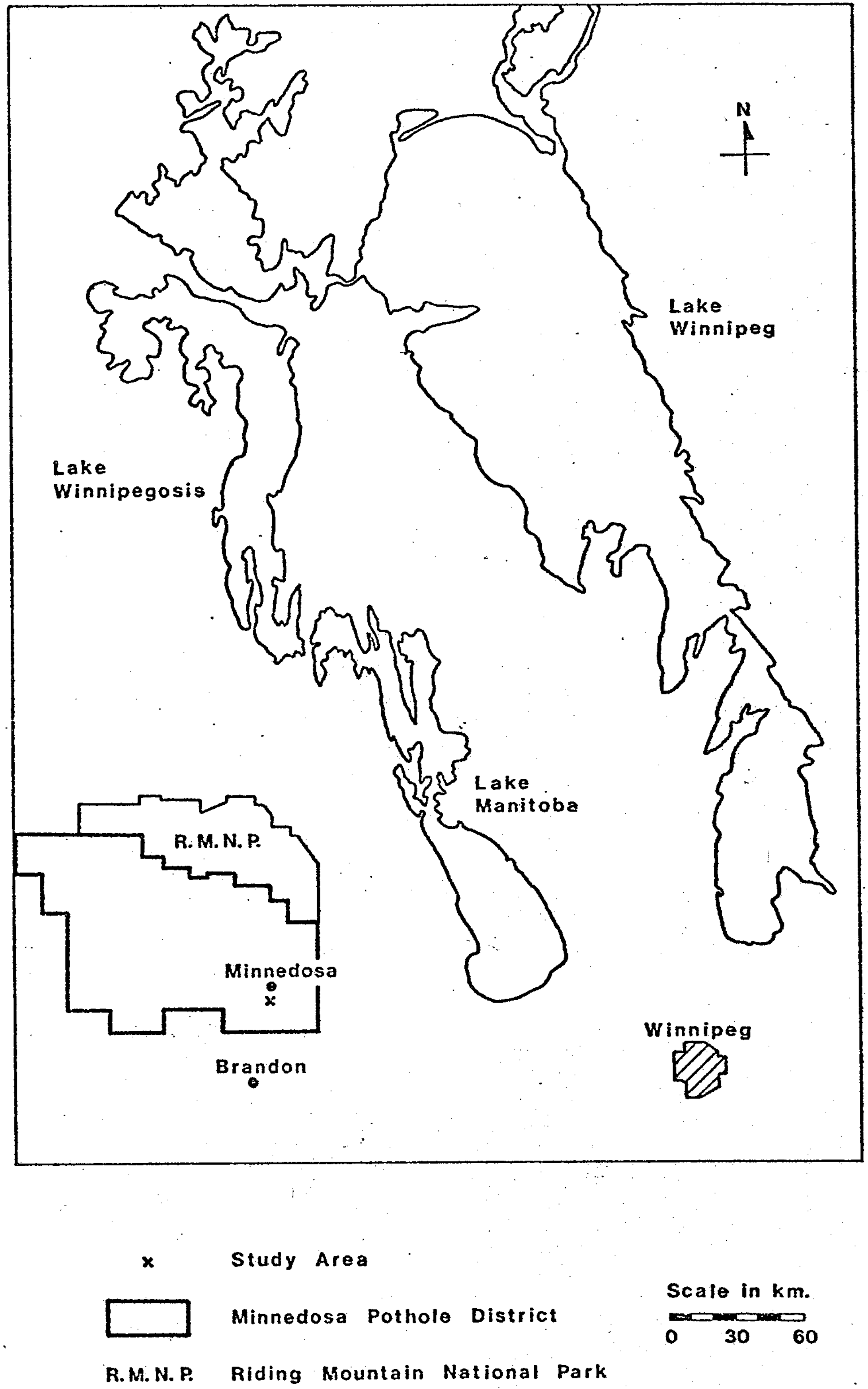
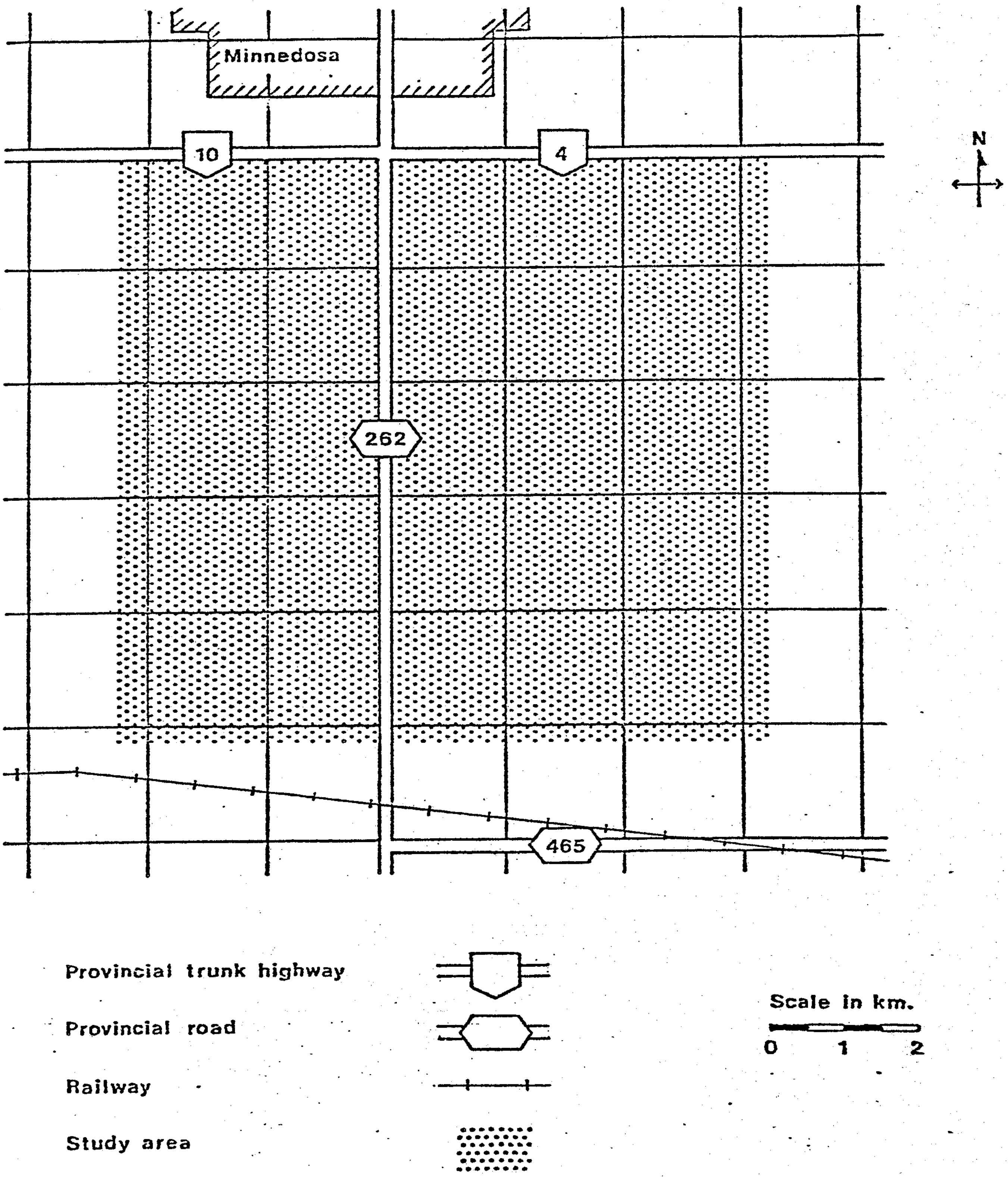

N
Lake Winnipeg
Lake Winnipegosis
Lake Manitoba
R. M. N. P.
Minnedosa
Brandon
Winnipeg
x Study Area
Minnedosa Pothole District
R. M. N. P. Riding Mountain National Park
Scale in km.
0 30 60

Figure 3. Location of study area, Rural Municipality of Odanah, Manitoba.


Minnedosa
10
4
N
262
465
Provincial trunk highway
Provincial road
Railway
Study area
Scale in km.
0
1
2

The fertile, agricultural lands of the study area are interspersed with numerous pothole marshes (Figure 4). The number of potholes varied from eight to 21 per km^2, with a mean of 15 per km^2. Pothole size varied considerably, from 0.04 to 47.5 ha, although most were within the range 0.4 to 4.0 ha. Mixed woodlands of Manitoba maple (*Acer negundo* L.), balsam poplar (*Populus balsamifera* L.), trembling aspen (*P. tremuloides* Michx.) and bur oak (*Quercus macrocarpa* Michx.) occur as small, isolated 'bluffs' on many elevated sites.

The climate of the Minnedosa pothole district is described by Ehrlich *et al*. (1957). Mean annual temperature at Minnedosa is 1.1 degrees Celsius (n = 64 years). The frost-free period (the length of time between dates of the last frost in spring and the first frost in autumn) varies from 85 to 100 days. Mean annual precipitation at Minnedosa is 43.7 cm (n = 65 years), with approximately 75 percent of the total annual precipitation falling as rain during April to October. The remaining 25 percent falls as snow during November to March.

The topography, hydrology, soils and vegetation of the Minnedosa district are described by Bird (1961), Ehrlich *et al*. (1957) and Kiel *et al*. (1972).

PRODUCTIVITY OF POTHOLES

Potholes within the glaciated prairie region are highly productive. Although they are regarded as naturally eutrophic lakes, Barica (1974) points out that the eutrophication process has been accelerated in the Minnedosa district by land management practices. Extensive land clearing and the widespread use of soil fertilizers have increased the mineral and nutrient levels in many wetland systems.

Figure 4. Aerial photograph of a portion of the Minnedosa study area, July, 1974. (Roads delimit an area of 2.59 km^2.)

Consequently, phytoplankton production is exceptionally high (Lawler _et al_. 1974).

Detailed studies of invertebrate populations and productivity are lacking. However, the remarkable growth rates of Rainbow Trout (_Salmo gairdneri_) cultured in potholes within the Minnedosa district indicate a generally high limnic productivity. Trout of marketable size have been produced in one summer (6-month growing period) without supplementary feeding (Lawler _et al_. 1974). This rapid growth is attributed to the abundance of invertebrate foods and to the absence of competitive fish species (Johnson _et al_. 1970). Few potholes contain native fish due to the regular occurrence of winterkill, but Fathead Minnows (_Pimephales promelas_) and Brook Sticklebacks (_Culaea inconstans_) are permanent residents of some of the larger, deeper potholes (Lawler _et al_. 1974).

The Minnedosa pothole district is considered to be one of the most important breeding habitats for waterfowl in North America (Smith _et al_. 1964). Statistics on the density and species composition of the waterfowl population are presented by Kiel _et al_. (1972).

CLASSIFICATION OF POTHOLES

Several classification systems have been applied to wetlands in the glaciated prairie region (reviewed by Stewart and Kantrud 1969). Millar (1969) recognized four major zones of wetland vegetation: wet-meadow zone; shallow-marsh zone; deep-marsh zone; and open-water zone. I classified the Minnedosa potholes into four types according to the distribution of these vegetative zones. Such a classification also gives an indication of water permanency since the zones can often be correlated with water depth and duration of submergence. The wetland types are described as follows:

Type I. Temporary potholes dominated by the wet-meadow zone. Pothole basins are very shallow and are submerged for only a short period in spring following snow melt. The wet-meadow zone is characterized by short, fine-textured grasses such as wild barley (*Hordeum jubatum* L.), and by many terrestrial plant species that germinate on the exposed wet soil in late spring.

Type II. Seasonal potholes dominated by the shallow-marsh zone. Central areas of these potholes normally retain water until July or August, and are characterized by grasses or grasslike plants of intermediate heights. They often include sedge (*Carex* spp.), spikerush (*Eleocharis* spp.), water parsnip (*Sium suave* Walt.), and whitetop (*Scolochloa festucacea* (Willd.) Link.).

Type III. Semi-permanent and permanent potholes dominated by the deep-marsh zone. Central areas of pothole basins retain water throughout the summer and frequently into fall and winter. Tall, coarse emergents such as bulrush (*Scirpus* spp.) and cattail (*Typha* spp.) are dominant. If present, the open-water zone occupies less than 50 percent of pond basin. A well-developed shallow-marsh zone is often present in peripheral areas.

Type IV. Permanent potholes dominated by the open-water zone. The open-water zone occupies more than 50 percent of pond basin and is characterized by submergent plants, including common bladderwort (*Utricularia vulgaris* L.), pondweed (*Potamogeton* spp.), water crowfoot (*Ranunculus* spp.), and water milfoil (*Myriophyllum* spp.). In many potholes the central portion of the basin is too deep to support submergent vegetation. A permanent pothole typically has elements of all four vegetative zones. The wet-meadow, shallow-marsh, and deep-marsh zones often occur as concentric, marginal bands, their distributions determined mainly by water depth and duration of submergence.

This classification has only short-term application since unstable water conditions are characteristic of most potholes. Climatic variability and subsequent changes in water levels necessitate an annual classification of many wetlands during periods of irregular precipitation. In the above descriptions only the more common plant species of each major zone are given. An extensive list of wetland plant species and their relative abundances under varying conditions of salinity are presented by Stewart and Kantrud (1969).

METHODS

Field work at Minnedosa was conducted from 27 April through 27 August, 1974, and from 17 April through 30 September, 1975. Preliminary observations were made in May, 1973.

Many behavioural traits of Horned Grebes facilitate investigations of their nesting habits. They are conspicuous birds of open-water areas and, like all grebe species, rely on diving (rather than flying) as the principal means of escape. Thus, they are more sedentary than most marsh-nesting birds. All nesting and brood-rearing activities were conducted within well-defined territories and, in most cases, the territory of each pair encompassed an entire pothole. Such a distribution facilitated observations of individual pairs throughout all stages of the breeding cycle.

During incubation, adult Horned Grebes were captured by flushing them off the nest into a two-inch mesh gill-net set in the water between the nest site and the open water. Fifty grebes (43 adults and 7 juveniles) were captured, sexed (adults only), measured, and banded with United States Fish and Wildlife Service aluminum bands (Size 6). Females were banded on the right leg and males on the left leg. This permitted me to distinguish the sexes in the field late in the breeding season when sexual differences in plumage and behaviour were no longer reliable criteria for determining a bird's sex. In May and June adults were sexed on the basis of differences in behaviour, in the onset of the prebasic molt, in the length of the nuptial plumes, and in the colouration of the neck and flanks (see Fjeldsa 1973b,d; Storer 1969). Sexual dimorphism in the Horned Grebe was quantified by measuring three morphological characters. Tarsus length was measured with calipers (to nearest 0.1 mm) from the back of the joint between the tibia and metatarsus to the joint at the base of the middle toe. Culmen length was measured (to nearest 0.1 mm) from the tip of the upper mandible to the base of the feathers on the forehead. The flattened wing was measured to the nearest 0.5 mm from the anterior end of the carpal joint to the tip of the longest primary.

In 1975, 22 adults were individually marked with red and/or blue feather dyes applied to the yellow 'horns' and/or white secondary remiges. This marking lasted until the nuptial head plumes were shed during the prebasic molt, usually in early July, and permitted positive identification of individual birds.

Nesting pairs were checked every one-to-three days from territorial establishment until the end of hatching. All nests were located in shallow water and were readily accessible from the shore. Nest abandonment due to human disturbance was rare. To determine habitat requirements of the Horned Grebe for nesting, I measured the following nest-site parameters at the time of clutch initiation: water depth; distance to nearest open water; distance to nearest shoreline; and dominant species of emergent cover. Eggs were measured (width and length to nearest 0.1 mm) with calipers and numbered with a waterproof marker in the order of laying. When a nest was destroyed, I attempted to determine the cause of its destruction. Nests destroyed by predators were easily recognized by the presence of broken eggs and shell fragments on the nest platform and in the water around the nest. Nests washed out by wind and wave action were identified by the damaged appearance of the nest, and by the presence of intact eggs in the water. Loss of these nests were also correlated with periods of high winds.

Behavioural aspects of territoriality, incubation, parental care, and chick development were studied from a blind located near the territory, or from a parked car. Remote observations were made with 7 x 35 binoculars and a 20 to 45 power spotting scope. More detailed procedures are described in the appropriate sections.

Unless stated otherwise, statistical tests follow Sokal and Rohlf (1969). Means are expressed as ± two standard errors. Nomenclature of North American birds follows the A.O.U. check-lists (1957, 1973). Scientific names of fish and mammals follow Scott and Crossman (1973) and Banfield (1974), respectively. Nomenclature of plants follows Gleason and Cronquist (1963). The terminology of postures and displays of the Horned Grebe are from Storer (1969).

RESULTS AND DISCUSSION

SEXUAL STAGE OF THE BREEDING CYCLE

Spring Arrival

Horned Grebes were first observed on the study area on 29 April, 1974 and 30 April, 1975. The peak influx occurred during the first week of May. During this time most grebes were assembled in flocks on large potholes (ranging in size from 3.0 to 47.5 ha) and on other permanent water areas. The largest concentration observed was 119 individuals on Minnedosa Lake (100 ha) on 1 May, 1974. Flock size varied considerably, from five to 47 individuals.

Observations of courtship behaviour in early May indicated that many grebes returned to the breeding grounds unpaired. Within the flocks, 'Advertising' was the most common courtship activity. It functions to bring together potential mates, or members of a pair that have been temporarily separated (Storer 1969). Grebes responding to the advertising bird approach it and a 'Discovery Ceremony' may follow. Storer (op. cit.) considers 'Advertising' followed by a 'Discovery Ceremony' to be a prime factor in forming and strengthening the pair-bond. Fjeldsa (1973d:185) believes that pair formation occurs only when the birds become "sufficiently aroused to perform further displays immediately afterwards". In the courting flocks, the 'Discovery Ceremony' rarely led to further courtship.

While the courting flocks were under observation in early May, I encountered many isolated pairs on smaller potholes. The behaviour of these birds differed greatly from that of the birds in flocks. Courtship activities performed by the isolated pairs were more closely associated with platform-building and mating than with pair formation, and were indicative of birds with well-established pair-bonds. Pairs often engaged in platform-building and soliciting, and 'Weed Rush', 'Head Shaking', and 'Triumph Ceremonies' were frequently observed.

Fjeldsa (1973d) reported that up to 75 percent of the Horned Grebes return paired to the breeding lakes in Iceland and Norway. Although I do not have quantitative data which show actual proportions, behavioural evidence suggests that both paired and unpaired birds return to the Minnedosa area. A numerical evaluation is complicated by the movement of transients through the study area during spring migration.

Establishment of Territories

Horned Grebes displaying territorial behaviour (see Fjeldsa 1973d) were observed as early as 7 May in 1974 and 1975. Since pair formation precedes possession of a territory, the earliest pairs to occupy territories were probably those that returned paired. Territories were secured 10.9 ± 1.6 days before clutch commencement (n = 29 pairs). During this time the birds rarely left their territories. In fact, once a territory is established, it is unusual for either adult to leave it during the course of the entire breeding cycle. In over 650 visits to nests, only twice had a territory temporarily been vacated by one or both members of the resident pair. Successful pairs remained on their territories until their young were independent of parental care.

The Territory

On the Minnedosa area Horned Grebe territories are basically Type A (Nice 1943), although early in the spring I observed some pairs copulating before their territories were established. In 91 percent of pairs studied, the territory encompassed an entire pothole. Territory size varied from 0.05 to 2.70 ha with an average of 0.78 ha (Table 1). Co-existence of two or more nesting pairs occurred only on potholes larger than one hectare. Of 85 potholes that supported nesting pairs, only three supported simultaneously more than one pair. Two potholes of 1.09 and 1.12 ha each supported two pairs, and a third pothole of 2.58 ha supported four nesting pairs.

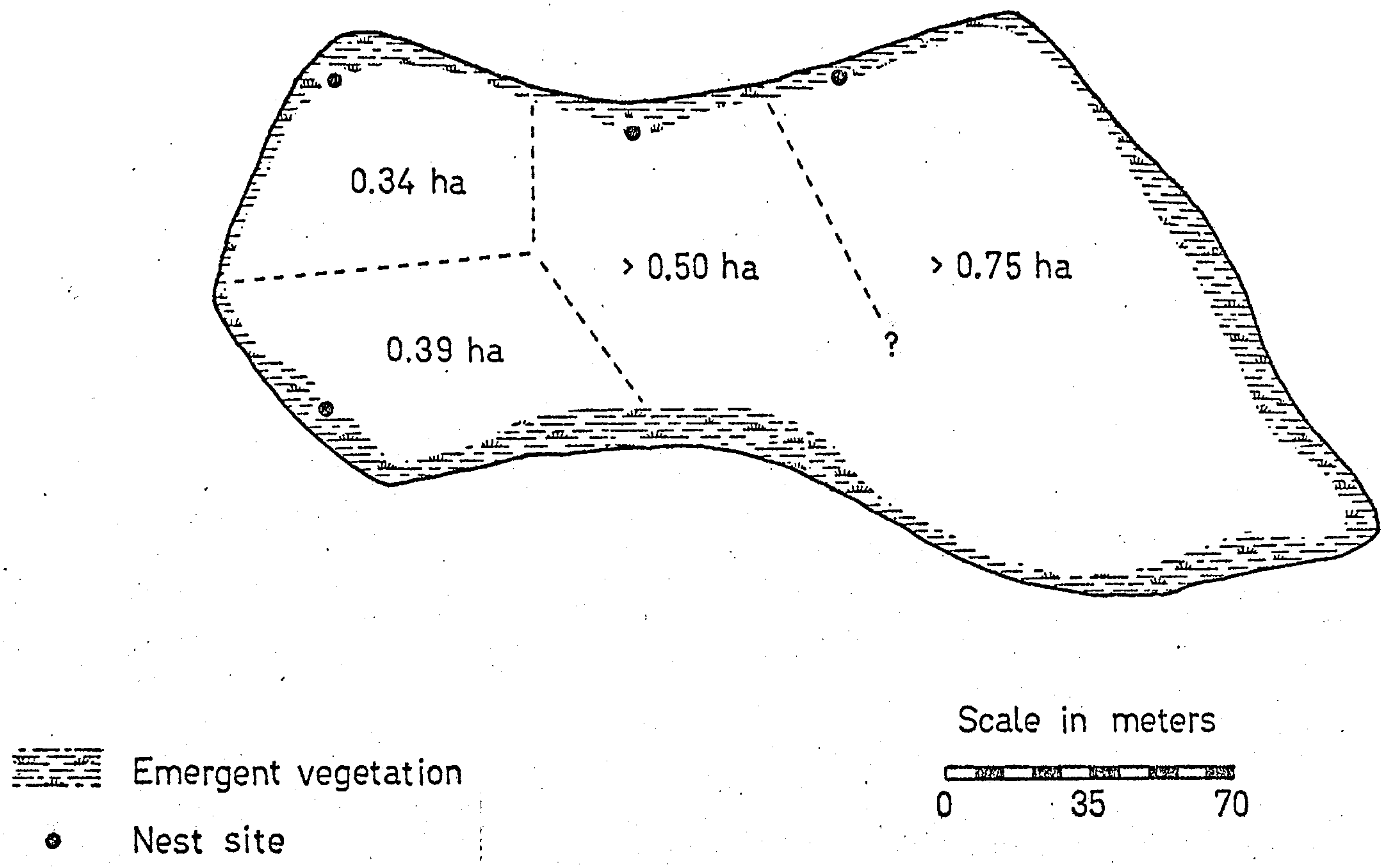
Where a pothole supports two or more pairs, each pair defends an area of open water and associated shoreline (Figure 5). Territorial boundaries were determined by observations of spatial distributions of pairs, and pair interactions between adjacent territories.

Some of the variation in territory size probably reflects the methods used in its determination. (Territory (pothole) size was determined by planimetry from aerial photographs supplied by the National Air Photo Library, Department of Energy, Mines, and Resources, Ottawa.) In calculating territory size of pairs that were distributed one pair per pothole, I was unable to determine the exact size of the defended area because conspecifics and territorial disputes were rarely observed on these potholes. Thus, the territory was assumed to include the entire pothole since, in the absence of other pairs, the resident birds were able to use all areas for feeding and brood-rearing. Calculations based on this assumption tend to overestimate territory size if, in fact, the resident pairs actively defended only part of the pothole.

Table 1. Territory size of Horned Grebes at Minnedosa.

Size (ha)	Number
0.00 - 0.25	2 (3%)
0.26 - 0.50	27 (36%)
0.51 - 0.75	17 (22%)
0.76 - 1.00	8 (11%)
1.01 - 1.25	8 (11%)
1.26 - 1.50	9 (12%)
1.51 - 1.75	1 (1%)
> 1.75	3 (4%)
Total	75

Figure 5. Configuration of territories on a pothole which supported four nesting pairs of Horned Grebes in 1974.


0.34 ha
> 0.50 ha
> 0.75 ha
0.39 ha
?
Emergent vegetation
Nest site
Scale in meters
0
35
70

On the other hand, this variability in territory size may reflect the quality of each pothole for breeding. As all nesting, feeding, and brood-rearing activities are confined to the territory, the availability of resources is likely an important determinant of its size. Fjeldsa (1973c) found that food supply and availability of nest sites were prime factors in determining territory size of Horned Grebes in Iceland and Norway. Pairs breeding on oligotrophic ponds required a minimum area of 0.21 ha, compared to a minimum of only 0.03 ha for pairs breeding on eutrophic ponds. Similarly, minimum areas for co-existence of nesting pairs on oligotrophic and eutrophic ponds were five and 1.2 ha, respectively. In nesting habitats where emergent cover was restricted to small, localized areas, Fjeldsa (op. cit.) reported 'loose colonies' of Horned Grebes which defended Type B territories no larger than 0.001 to 0.005 ha. He explained such breeding distributions as a response to a general deficiency of nest sites in nearby areas.

On the Minnedosa study area it is unlikely that availability of nest sites was an important determinant of territory size in either 1974 or 1975. Stands of emergent vegetation several meters in width occupied the peripheral areas of permanent potholes, and dominated the basins of semi-permanent potholes. Bulrush, cattail, and whitetop were particularly abundant and provided adequate nesting cover for grebes and other over-water nesting birds.

Food supply, however, was likely a decisive factor in determining territory size. Defense of an area that provides sufficient food resources for adults and young (in birds with Type A territories) is crucial for successful breeding (see Hinde 1956). For Horned

Grebes, Fjeldsa (1973c) obtained a significant correlation between tendency to attack (territorial defense) and abundance of food. He found that large territories in areas of poor food resources reflected high aggressive levels of pairs that nested in these habitats. Although potholes of the Canadian prairies are generally considered to be eutrophic, differences in limnic productivity from pothole to pothole undoubtedly exist. The magnitude of these differences and their effects on habitat selection by grebes and other marsh birds are poorly understood. Bartonek and Hickey (1969) and Perret (1962) demonstrated the importance of aquatic invertebrates as preferred waterfowl foods during the breeding season in southwestern Manitoba. The lack of information concerning the abundance of potential invertebrate foods in different pothole marshes, however, warrants a closer examination of invertebrate productivity.

The hypothesis that Horned Grebes show no habitat preference and that they select pothole types in relation to their availability was tested. Relative abundance of pothole types was determined by classifying all wetlands within an area of 8.4 km^2. (Temporary wetlands (Type I) were excluded from the analysis because of their ephemeral water supply and unsuitability as nesting habitat.) Horned Grebes at Minnedosa showed a distinct preference for permanent potholes dominated by the open-water zone (Table 2). Differential selection of Type IV potholes reflects the grebes' dependence on permanent, open-water feeding areas. In terms of water permanency, only Type III and Type IV wetlands retain water long enough to permit rearing a grebe brood to fledging. Basins of seasonal potholes (Type II) usually dry up by July or early August. In 1974 one pair established a territory

Table 2. Differential habitat selection by Horned Grebes.

Pothole Type	Relative Abundance[a]		Number of Territories[a]	
II	29	(17.3%)	1	(1%)
III	39	(23.2%)	9	(11%)
IV	100	(59.5%)	75	(88%)
Totals	168		85	

[a] $x^2 = 30.4$; 2 df; $P < 0.005$

on a Type II pothole. However, the nest (containing three eggs) was deserted when the water level receded and the basin became overgrown with a dense growth of sedge. Emergent vegetation undoubtedly restricts the movements and foraging abilities of Horned Grebes, which acquire most of their food by diving. My observations indicate that most foraging is done in open-water areas where diving and capture of prey are unobstructed.

Defense of Territories

Although the male is generally more aggressive than the female, territories are defended by both sexes, either alone or together. Agonistic behaviour is characterized by ritualized forms of threat and appeasement which are described in detail by Fjeldsa (1973d) and Storer (1969). Horned Grebes display both intraspecific and interspecific territoriality.

On potholes supporting only one pair of nesting Horned Grebes, any intruding conspecifics are quickly expelled from the territory. The 'Threat Display' followed by chasing is the most common form of agonistic behaviour. Chasing consists of pursuit by swimming, by diving, by pattering along the water surface, and by flying. Breast-to-breast fighting is rare, as the intruding birds display appeasement and retreat from the resident birds.

On localities where neighbouring pairs defended adjacent territories, attack and chasing were replaced by mutual threat displays along territory boundaries. The 'Threat Posture' often gave way to the 'Hunched Posture', and these were interspersed with the 'Head Shaking Ceremony' and the 'Triumph Ceremony'. Prior to egg-laying, both members of a pair were usually involved in boundary disputes.

Interspecific territoriality develops shortly after the territory is established, peaks during egg-laying and incubation, and quickly diminishes after hatching. Unlike intraspecific aggression which occurs throughout the territory, interspecific territoriality is most pronounced in the vicinity of pairing platforms and nests. In 110 observed interactions, Horned Grebes successfully defended this area against 14 bird species and one species of mammal (Table 3). Most attacks originate from below the water surface. When an intruder on the water nears the pairing platform or nest, the defending grebe usually dives, approaches the intruder underwater, and then surfaces directly underneath it. It appears that, at least in some cases, the grebes use their bills to stab or pinch the feet and legs of other birds on the water.

Interspecific aggression by Horned Grebes has been reported previously by Fjeldsa (1973d), but he did not discuss its adaptive significance. The prime function of interspecific territoriality seems to be defense of the pairing platforms and nest platforms. Their location in the water near the open-water zone makes them ideal loafing sites for other birds, particularly ducks which prefer loafing sites in the water that provide unrestricted visibility of the surrounding area (see Sowls 1955). Loafing sites with these characteristics are limited on pothole marshes. The following species were observed using abandoned grebe platforms as loafing or preening sites: Mallard, Shoveler (<u>Anas clypeata</u>), American Coot, Lesser Yellowlegs (<u>Tringa flavipes</u>), Black Tern, and Muskrat. Kevan (1970) reported

Table 3. Interspecific territoriality of Horned Grebes as revealed by aggressive encounters with other species.

Species	Number of Encounters
Eared Grebe (*Podiceps nigricollis*)	1
Pied-billed Grebe (*Podilymbus podiceps*)	6
Mallard (*Anas platyrhynchos*)	4
Pintail (*A. acuta*)	2
Green-winged Teal (*A. crecca*)	2
Blue-winged Teal (*A. discors*)	15
Redhead (*Aythya americana*)	4
Ring-necked Duck (*A. collaris*)	1
Canvasback (*A. valisineria*)	5
Lesser Scaup (*A. affinis*)	6
Ruddy Duck (*Oxyura jamaicensis*)	12
American Coot (*Fulica americana*)	46
Black Tern (*Chlidonias niger*)	1
Red-winged Blackbird (*Agelaius phoeniceus*)	4
Muskrat (*Ondatra zibethicus*)	1
Total	110

that ducks on Astotin Lake, Alberta favoured the nests of Red-necked Grebes as loafing sites.

Defense of platforms may also be related to competition for nest sites by other over-water nesting birds, especially American Coots which are abundant on the study area. My observations indicate that Horned Grebes are especially intolerant of them. Over 41 percent of observed interspecific encounters involved coots (see Table 3). This high incidence of grebe-coot interactions also reflects the aggressive nature of coots (see Fredrickson 1970; Ryder 1959), and their abundance on the Minnedosa study area. On most potholes, including those occupied by nesting Horned Grebes, there was at least one pair of nesting coots in 1974 and 1975. In northwestern Minnesota, Burger (1973) reported intense competition for nest sites between Franklin's Gulls (*Larus pipixcan*) and American Coots. The gulls selectively defended their nest sites against coots.

A third possible function of interspecific territoriality is to reduce egg predation by opportunistic bird species. Reports of American Coots eating eggs are summarized by Burger (1973), and include observations of egg predation on nests of Pied-billed Grebe, Franklin's Gull, and Red-winged Blackbird. In 1974 G. Stewart and I observed a coot peck and partially eat two Red-necked Grebe eggs on the nest platform. Gould (1974) reported predation on Western Grebe eggs in California by Black Terns and Yellow-headed Blackbirds. Both species are common summer residents of the Minnedosa study area.

Platform Behaviour

The term 'platform behaviour' applies to those behaviours that are directly associated with mating. Unlike waterfowl, grebes lack an intromittent organ. Consequently, copulation cannot occur in the water. Mating usually takes place on a platform built by the pair, although I have observed Horned Grebes attempt to copulate on rocks and logs projecting above the water surface.

Construction of a platform is similar to that described for other grebe species. Both sexes gather a variety of plant materials, mostly decaying vegetation recovered from the pothole bottom. These are placed in a protected area, usually within standing emergent vegetation. As the material accumulates, one bird often mounts the platform and arranges the material while the other continues to add new material. A platform capable of supporting the weight of both grebes can be built in a few hours.

Pairing platforms are not necessarily built within the territory. Early in the spring I have observed pairs engaged in platform building several days before territories were established. These platforms are likely built by grebes which returned to the breeding grounds already paired and in an advanced breeding condition.

In Iceland, Fjeldsa (1973c) found that the number of platforms built by Horned Grebes was related to the age of the members of a breeding pair. His data show that 'first-year' birds tend to build more pairing platforms than do birds with past breeding experience. I was unable to age most breeding pairs on the Minnedosa area. The majority of pairs built at least one pairing platform within the territory, and some pairs built as many as four.

The precopulatory and copulatory behaviour of Horned Grebes is described by Fjeldsa (1973d) and Storer (1969). Fjeldsa's description of the behaviour of the passive bird during copulation differs from that given by Storer who states (p. 200) that "before and during copulation the passive bird remains in the Inviting Posture". Fjeldsa (1973d) indicates that the head of the passive bird is often raised, may be turned from side to side, and may even touch the breast of the active partner. These components of copulatory behaviour were believed to occur only in the Podilymbini and not in the Podicipedini, of which the Horned Grebe is a member (Storer 1963a). At Minnedosa, I observed nine complete copulations in 1974 and 21 in 1975. My observations verify those made by Storer (1969) in that the passive bird remained in the Inviting Posture during mating. Uusitalo (*in* Fjeldsa 1973d) did not observe motions of the head in Horned Grebes in Finland. Thus, there appears to be geographical variation in this component of the copulatory behaviour. Head-motions by the passive bird have been observed in *P. a. arcticus*, but they appear to be absent in *auritus* and *cornutus*.

Although its function is poorly understood, reverse mounting has been observed in many grebe species: Eared, Red-necked, Pied-billed, and Western Grebes (Storer 1969); Great Grebe, *Podiceps major* (Storer 1963b); New Zealand Dabchick, *P. rufopectus* (Storer 1971); Great-crested Grebe (Simmons 1974); and Horned Grebe (Fjeldsa 1973d; Storer 1969). Storer (1963a) reported that reverse mounting likely occurs early in the breeding season in all grebe species. I observed reverse mounting by Horned Grebes three times.

Nest-building

Selection of the nest site and nest construction represent the final phases in the sexual stage of the breeding cycle. Individual pairs examine many potential sites in the emergent vegetation before selecting the nest site. These inspections are characterized by a specific behaviour, the most important component of which appears to be 'Head-bobbing'. Both Fjeldsa (1973d) and Storer (1969) observed 'Head-bobbing' by Horned Grebes under circumstances where the birds were disturbed by human interference. 'Head-bobbing' has not been mentioned previously in association with nest-site selection. Storer (op. cit.) accurately described (p. 187) this behaviour by comparing it to 'Head-bobbing' by American Coots. The grebes "bob their heads forward and back as a coot does, but with a slower, smoother motion."

The following observations are typical of the 'searching behaviour'. On 21 May, 1975, both members of pair 12 were observed inspecting a group of cattails along the southeast shore. The female initiated the search and the male followed closely behind. Both birds continually 'Head-bobbed' and often picked at the vegetation with their bills. The searching behaviour proceeded until each clump of emergent vegetation along the periphery of the pothole had been visited. When the last clump had been examined, both birds swam to the open-water zone and began feeding. On 24 May, a nest containing one egg was found within one of the clumps of cattail.

Nests are more elaborately constructed than are pairing platforms. Once the nest platform has been built, finer materials are added and shaped by the birds to form a depression which later receives the eggs. These materials, including a variety of floating and submerged aquatic plants, are added to the nest throughout the egg-laying and incubation periods.

All nests located on the study area were anchored to emergent vegetation (Table 4). Over 84 percent were located in either whitetop, bulrush, or cattail, the three most abundant emergents of semi-permanent and permanent potholes on the study area. Nests built before 25 May were usually anchored to residual vegetation from the previous growing season. Unless flattened in winter by snow, residual emergents (particularly rigid forms such as bulrush and cattail) provide sufficient nesting cover early in the season. Additional support is provided by the new growth when it appears above the water surface, usually in late May.

Water depth, measured at 119 nests, averaged 39.2 ± 2.2 cm. No nests were located in water less than 16 cm deep (Table 5), and only two (1.7 percent) were located in water less than 20 cm deep. A minimum water depth of 20 cm seems necessary to allow the grebes easy underwater access to and from the nest site. Also, nests located in shallow water may become stranded on dry land. Water levels of many potholes occupied by nesting Horned Grebes receded as much as 15 to 20 cm in one month, especially during hot, dry weather.

Accessibility of a nest site is influenced by its proximity to open water. Over 76 percent of 122 nests were located within two meters of open water (Table 5). Unbroken stands of emergent vegetation between a nest and open water likely impede the grebes' movements to and from the nest site. On the other hand, nests must be located far enough into the vegetation to receive protection from wave action. Wave action decreases in amplitude with increasing nest-to-open water distance, the rate of wave dissipation being related to the density of emergent vegetation (Nuechterlein 1975).

Table 4. Distribution of Horned Grebe nests according to the dominant species of emergent cover.

Species	Number of Nests
Whitetop (*Scolochloa festucacea* (Willd.) Link.)	41 (31.8%)
Bulrush (*Scirpus* spp.)	39 (30.2%)
Cattail (*Typha* spp.)	29 (22.5%)
Water parsnip (*Sium suave* Walt).	8 (6.2%)
Goosefoot (*Chenopodium* spp.)	3 (2.3%)
Willow (*Salix* spp.)	2 (1.6%)
Sedge (*Carex* spp.)	1 (0.8%)
Water crowfoot (*Ranunculus* spp.)	1 (0.8%)
Unidentified residual forms	5 (3.8%)
Total	129

Table 5. Location of Horned Grebe nests at Minnedosa, 1974 and 1975.

Water Depth[a] (cm)	Number of Nests	Distance to Open Water[b] (m)	Number of Nests	Distance to Shore[c] (m)	Number of Nests
0 - 15	0 (0.0%)	0 - 1.0	55 (45.1%)	0 - 3.0	14 (12.2%)
16 - 30	29 (24.4%)	1.1 - 2.0	38 (31.2%)	3.1 - 6.0	43 (37.4%)
31 - 45	59 (49.6%)	2.1 - 3.0	17 (13.9%)	6.1 - 9.0	31 (27.0%)
46 - 60	24 (20.2%)	3.1 - 4.0	8 (6.6%)	9.1 - 12.0	15 (13.0%)
61 - 75	6 (5.0%)	4.1 - 5.0	2 (1.6%)	12.1 - 15.0	4 (3.5%)
76 - 90	1 (0.8%)	5.1 - 6.0	2 (1.6%)	15.1 - 18.0	8 (6.9%)
Totals	119		122		115

[a] $\bar{x} = 39.2 \pm 2.2$ cm

[b] $\bar{x} = 1.5 \pm 0.2$ m

[c] $\bar{x} = 6.8 \pm 0.7$ m

Nest-site selection by many grebe species involves a response to the interrelated variables of water depth, proximity to open water, vegetation density, and wave action (see LaBastille 1974; Burger 1974a; Chabreck 1963; Gotzman 1965; and Nuechterlein 1975). The model of nest-site selection proposed by Nuechterlein (*op. cit.*) for Western Grebes nesting in shoreline habitats is applicable to Horned Grebes nesting in prairie pothole marshes. However, a fifth environmental parameter, proximity to shore (and its relationship to mammalian predation), was found to be an important determinant of nesting success of Horned Grebes at Minnedosa. This likely relates to the recent invasion of the Raccoon (*Procyon lotor*) in southwestern Manitoba (see Cowan 1973). Today, the Raccoon is considered to be the main predator on over-water nests in the Minnedosa pothole district (Kiel *et al.* 1972). Details of the relationship between egg loss to predators and proximity of nests to shore are discussed later (see p. 68).

Nest-site selection by Horned Grebes at Minnedosa is therefore influenced by two opposing forces. Predation pressures tend to maximize nest-to-shoreline distance, while exposure to wave action tends to increase nest-to-open water distance. The site selected must also meet the minimum depth requirement (20 cm) and permit access to and from the nest.

PARENTAL STAGE OF THE BREEDING CYCLE

Egg-laying

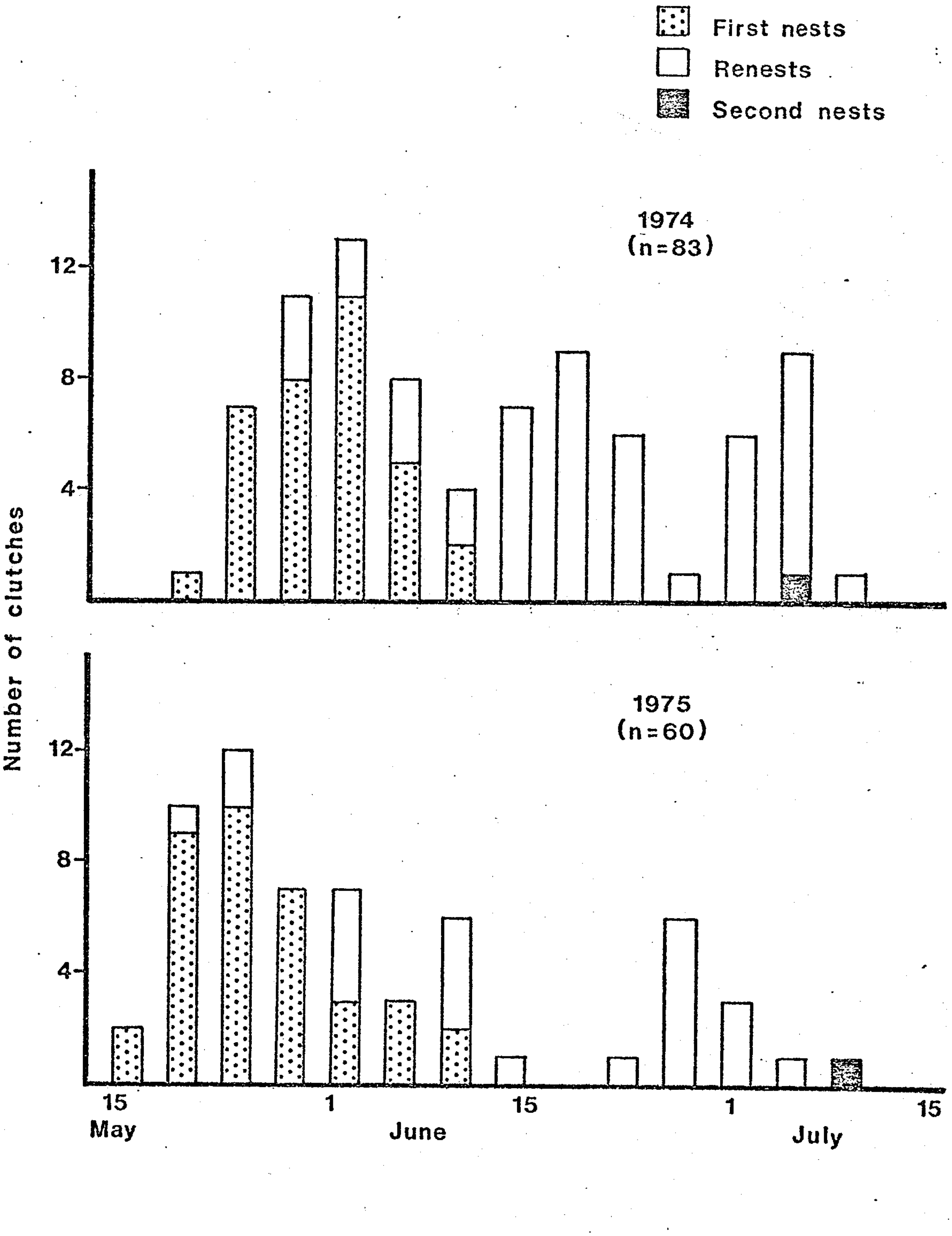
Eggs were laid over a period of 53 days in 1974 (22 May to 13 July) and 57 days in 1975 (17 May to 12 July). Laying dates were recorded by direct observation in 135 nests, and were calculated (using known incubation periods) from hatching dates in eight other nests. Regular visits to each territory at one-to-three day intervals enabled me to divide nests into three categories: first nests; renests; and second nests.

First Nests

A first nest is the initial nesting attempt of a pair in any breeding season. Initiation of egg-laying of first clutches ranged from 22 May to 11 June in 1974 (n = 34), and from 17 May to 10 June in 1975 (n = 36). Initiation of egg-laying in 1975 was significantly earlier than in 1974 ($x^2 = 28.59$; 3 df; $P < 0.005$) (Figure 6). In 1974, 50 percent of first nesting attempts had been initiated by 1 June. In 1975, however, egg-laying in 50 percent of first nests had been initiated by 25 May, seven days earlier than in the previous year.

It is generally accepted that breeding in birds is timed to that period of the year which enhances the probability for survival of both young and adults, and that the availability of food for the young is the main ultimate factor in the evolution of breeding seasons (see Immelmann 1971; Perrins 1970). In any given year, however, individuals respond to proximate stimuli that permit physiological and behavioural adjustments to the immediate environmental conditions. Annual variations

Figure 6. Seasonal pattern of egg-laying as revealed by dates of laying of the first egg in each clutch. (Each bar represents a 4-day interval.)


First nests
Renests
Second nests
1974
(n=83)
1975
(n=60)
Number of clutches
12
8
4
12
8
4
15
May
1
June
15
1
July
15

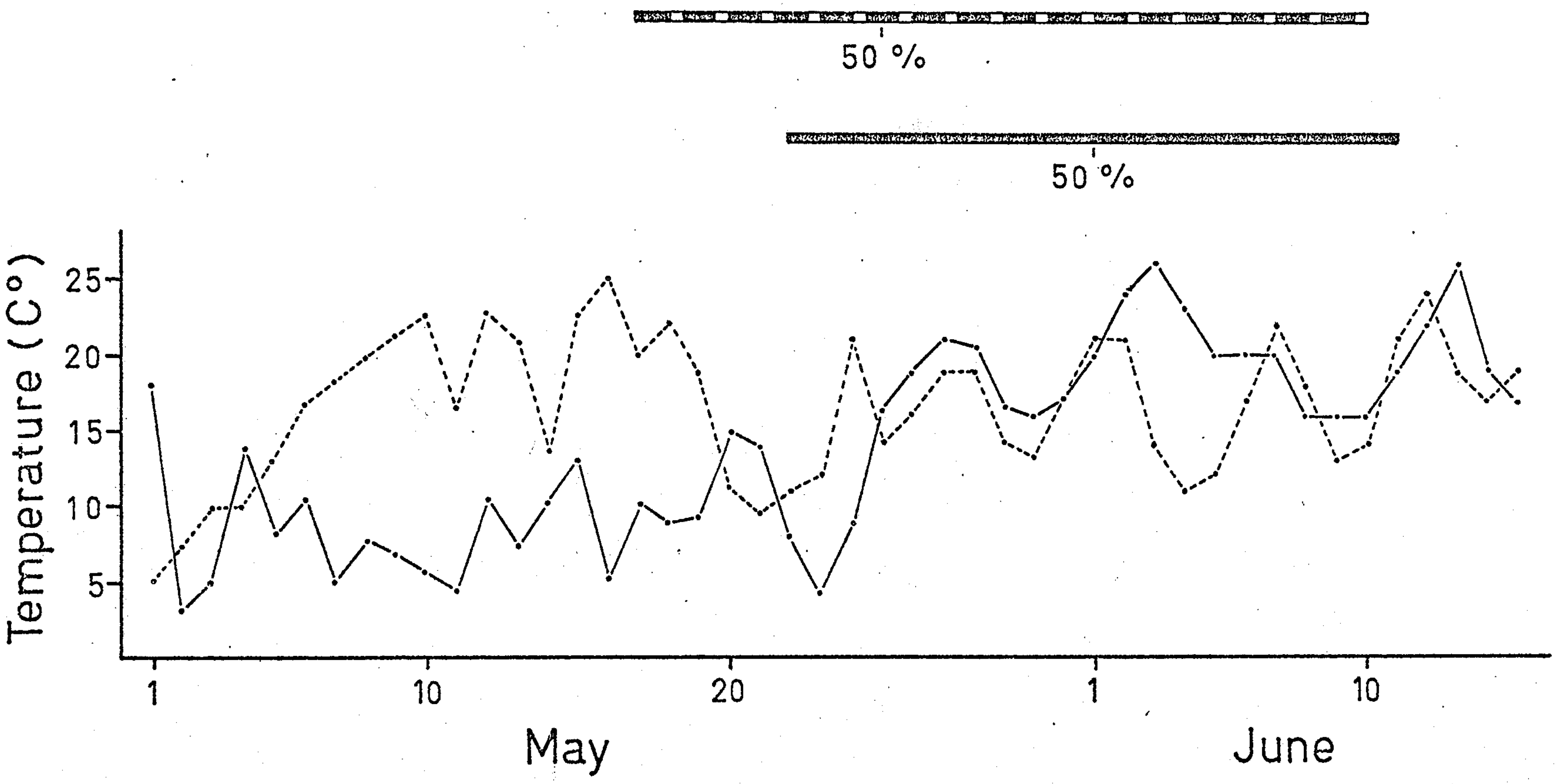
in the onset of breeding activity are widespread among temperate bird species.

Weather conditions prior to egg-laying are among the many environmental factors believed to function in the proximate control of breeding. Kluyver (1952) showed that annual variations in the onset of laying in the Great Tit (Parus major) were due largely to differences in air temperature in the spring. It is well-documented that ovulation in birds is inhibited by cold spring temperatures (Marshall 1959), and that most species breed later in a cold, late spring than in a warmer, earlier one (Immelmann 1971).

At Minnedosa, annual variations in egg-laying by Horned Grebes are correlated with differences in spring temperature (Figure 7). Mean maximum daily temperatures in May were 10.9 degrees Celsius and 16.3 degrees Celsius in 1974 and 1975, respectively. The advanced breeding in 1975 may be due to direct effects of temperature on the birds' reproductive condition, or the effects may be more indirect. Annual variations in spring temperature undoubtedly affect the biological productivity of potholes at all trophic levels. It is likely that some components of the pothole ecosystem influenced by climatic variability are themselves important stimuli for the proximate control of breeding.

In Iceland, Fjeldsa (1973c) found that, apart from climatic and other abiotic factors, many social and behavioural factors were involved in the proximate timing of laying. They included interactions during mating, success in territory establishment, proximity of neighbouring pairs and past breeding experience.

Figure 7. Annual variation in egg-laying in relation to maximum daily temperature in 1974 (solid lines) and 1975 (broken lines). Bars represent clutch initiation periods of first nests.


50 %
50 %
Temperature (C°)
25
20
15
10
5
1
10
20
1
10
May
June

Renests

A renest is the replacement of a destroyed clutch in the same nesting season. In the event of nesting failure, most Horned Grebe pairs attempted at least one renest. Of 40 pairs whose first nesting attempts failed, 68 percent renested on the same territory. The actual proportion of pairs that renested is likely underestimated because pairs that deserted their original territories (potholes) following nesting failure were not relocated. It is likely that these pairs laid replacement clutches on new territories, especially if the previous nests were destroyed early in the breeding season. Six pairs were known to renest at least twice and another six pairs renested three times, all on their original territories.

The pattern of renesting in 1975 differed from that in 1974 (Figure 6). Egg-laying in 1975 had a bimodal distribution, with the first peak corresponding to the laying of first clutches in May and early June, and the second, smaller peak corresponding to the laying of replacement clutches in late June and July. Egg-laying in 1974 was more uniformly distributed throughout the nesting season. In 1974 high failure of first nests (71 percent) contributed to the uniform nesting activity. Fifty-nine percent of all nests studied in 1974 were renest attempts. In 1975 loss of first nests was lower (56 percent). In response to the increased nesting success, the grebes attempted fewer renests which accounted for only 40 percent of all 1975 nests. The peak of renesting activity in late June, 1975 is due to the replacement of clutches destroyed by high winds during the period 19 to 26 June. Over 29 percent of all nests active during this period were washed out by wave action.

It was not always possible to determine the exact date that a particular nest was destroyed, especially if it was destroyed by predators. However, by inspecting nests every one-to-three days, I was able to obtain a good estimate of the time required by a pair to initiate a replacement clutch following nesting failure. (A more accurate estimate could be made for nests washed out by wave action by correlating their destruction with periods of high winds.) The following analysis includes only those pairs that renested on the same territory. If all data are lumped, the time required to initiate a replacement clutch varied from less than two to nine days (n = 36 nests). When nesting failure occurred during laying (n = 28), the first egg of the replacement clutch was often laid within two days of the nest loss (43 percent). The majority of replacement clutches (79 percent) were initiated within four days of the nesting failure. In contrast, unsuccessful nests that contained complete clutches (n = 8) were rarely replaced within four days (13 percent). Egg-laying in the remaining 87 percent began five to nine days following nesting failure.

Thus, for pairs that renest without a change in territory, the time required to initiate a replacement clutch is related to the stage of the nesting cycle at which the first nest is destroyed. Selection of a nest site and construction of a new nest do not retard clutch replacement. Both are often accomplished in less than two days. Furthermore, laying often begins before construction of the nest is complete. Unsuccessful sites are rarely reused; only 6 percent of all renests (n = 73) were located on previously unsuccessful sites. The rapid replacement of clutches, regardless of when they were destroyed, suggests that food availability is not a critical factor limiting the females' abilities to produce eggs. The frequency with which renesting occurs also lends support to this hypothesis.

Fjeldsa (1973c) reported differences in initiation of replacement clutches depending on the age of the members of a breeding pair. On the average, egg-laying was started 13 days and 20 days after nesting failure in 'old' and 'first-year' birds, respectively. However, he treated these values with caution because his pairs were not marked.

Following nesting failure, the probability that a pair will renest on the same territory is influenced by the stage of the nesting cycle at which the previous nest is destroyed (Table 6). Only first nests are included in this analysis which is based on the assumption that all pairs laid a replacement clutch following the loss of their first clutches. Clutches containing fewer than five eggs were considered to be incomplete. Of all first nests in 1974 and 1975 in which laying had been completed (n = 44), 98 percent contained five or more eggs. When a nest containing an incomplete clutch was destroyed, the probability that the pair would renest on the original territory was 89 percent. When a completed clutch was destroyed, however, the probability declined to 50 percent (Table 6).

Fjeldsa (1973c) found that the rate of territory reuse in P. a. arcticus was influenced by the cause of nesting failure. The probability of a change in territory was 41 percent if nests were destroyed by wave action or other abiotic factors. If nesting failure was due to predation (including egg-robbing by boys), the probability increased to 74 percent. Although data for the Minnedosa population are

Table 6. Occupation of territories by Horned Grebes following failure of first nesting attempt.

First Nest	Number of Pairs Used Original Territory	 Did Not Use Original Territory	Totals
Clutch Incomplete	17	2	19
Clutch Complete	9	9	18
Totals	26	11	37

x^2 (adjusted) = 5.13; 1df; $P < 0.025$.

inconclusive due to small samples, a similar trend was obtained. Regardless of when they were destroyed, all first nests lost to wave action (n = 7) were replaced on the original territory. For nests destroyed by predators the data reflect the trend established earlier. New territories were established more often if the clutch was complete when destroyed (69 percent of 13 nests) than if it was incomplete (zero percent of ten nests).

The ability to renest is of considerable importance to species breeding in areas (or habitats) where nest losses are high. Within wide limits, any increase in the number of nesting attempts by a pair augments its chances of producing offspring. Because restricted breeding seasons of temperate zones impose limits to the nesting potential, pairs that minimize the time between nesting attempts will be at a selective advantage. Following failure of an incomplete clutch, Horned Grebes rarely move to a new location. Use of the same territory facilitates the rapid initiation of a replacement clutch. However, loss of a complete clutch to predators may deter the grebes from renesting on the same territory.

Finally, three additional observations concerning renests are noteworthy. Replacement of eggs in partially destroyed clutches was observed twice. In the first case, four of seven eggs disappeared from a nest three to five days after completion of the clutch. The female replaced all four eggs; the first egg was laid seven to ten days after the egg loss. In a second nest, four of five eggs were washed out two to three days after completion of the clutch. Replacement of these eggs began five days after their destruction. The nest was destroyed before a conclusive examination was made, but three replacement eggs had been laid.

One renesting attempt following loss of a brood was observed in 1974. Two of seven eggs in the first nest hatched; the remaining five were taken by a predator. Both chicks died within five days of hatching. The pair built a new nest within the original territory, and the female laid the first of five eggs seven to ten days after the chicks disappeared.

Second Nests

Laying of a second clutch after successful nesting was observed in only two cases. In 1974 a pair initiated a second clutch on 3 July, ten days after hatching of the last egg of the previous clutch. The same nest platform was used for the second clutch. Identification of this pair was based on the presence of its first brood. Some chicks from this brood were still being fed by their parents at the time of initiation of the second clutch. In the second case, laying of the second clutch began on 9 July, 1975, 16 days after the previous clutch hatched. This pair, in which the female was individually marked, built a new nest on a site 3.5 m from the first nest. In both cases where a second nest was attempted, the first nesting attempt had been successful. Of a total of three chicks that hatched from second clutches, none fledged.

Second nests have been reported for most grebe species, but are infrequent in temperate species and are considered rare in the Horned Grebe (Fjeldsa 1973c). In four of the nine second nests observed by Fjeldsa (op. cit.), young from the first nests assisted the parents in feeding their younger siblings. At Minnedosa, however, once the young from first broods were independent, they were no longer tolerated by the adults (see p. 78). Young from first broods were often threatened or attacked by their parents when second-brood chicks were being fed.

As a result of their infrequent occurrence and low chick survival, second nests likely contribute little to the total production of young in any season.

The Eggs

Mean dimensions of 591 eggs were 30.2 x 44.3 mm with extremes of 27.8 and 33.0 x 39.0 and 48.4 mm. Eggs from the Minnedosa population are smaller than those from Iceland and Norway, but slightly larger than those from Baltic regions (Table 7). Fjeldsa (1973b:79) suggested that large egg dimensions in *P. a. arcticus* "may be an adaptation to climate as large eggs imply large energy reserves and larger size of the newly-hatched young, and thus perhaps a better cold-resistance."

Within a clutch the interval between laying of consecutive eggs is variable. One and two day intervals are common and occasionally the laying interval is three days. Total egg-laying periods for the three most frequent clutches are as follows: seven to eight days for a clutch of five eggs; eight to nine days for a clutch of six; and nine to 11 days for a clutch of seven.

Clutch Size

The size of 79 complete clutches varied from three to eight eggs, with a mean of 5.9 eggs. Clutches of five, six and seven eggs were most common, comprising 81 percent of nests examined (Table 8). No annual differences in clutch size were observed. Mean clutch size in 1974 (n = 43 nests) was 5.9 eggs, the same as in 1975 (n = 36 nests). Despite earlier nesting in 1975, clutch size of first nests did not differ significantly between years. Clutch size of first nests averaged 6.5 eggs and 6.4 eggs in 1974 (n = 21) and 1975 (n = 22), respectively (t = 0.38; 41 df; NS).

Table 7. Variation in egg size of the Horned Grebe.

	Width (mm)	Length (mm)		
Locality	$\bar{x}$	$\bar{x}$	n	Source
Baltic regions	29.7	44.2	697	Fjeldsa (1973b)
Minnedosa, Manitoba	30.2	44.3	591	Present study
Norway	30.8	45.5	499	Fjeldsa (1973c)
Iceland	30.9	45.8	1637	Fjeldsa (1973c)

Table 8. Clutch size of Horned Grebes at Minnedosa, 1974 and 1975.

Nests	Clutch Size						Total
	3	4	5	6	7	8	
Number	2	8	19	25	20	5	79
Percent	3	10	24	32	25	6	

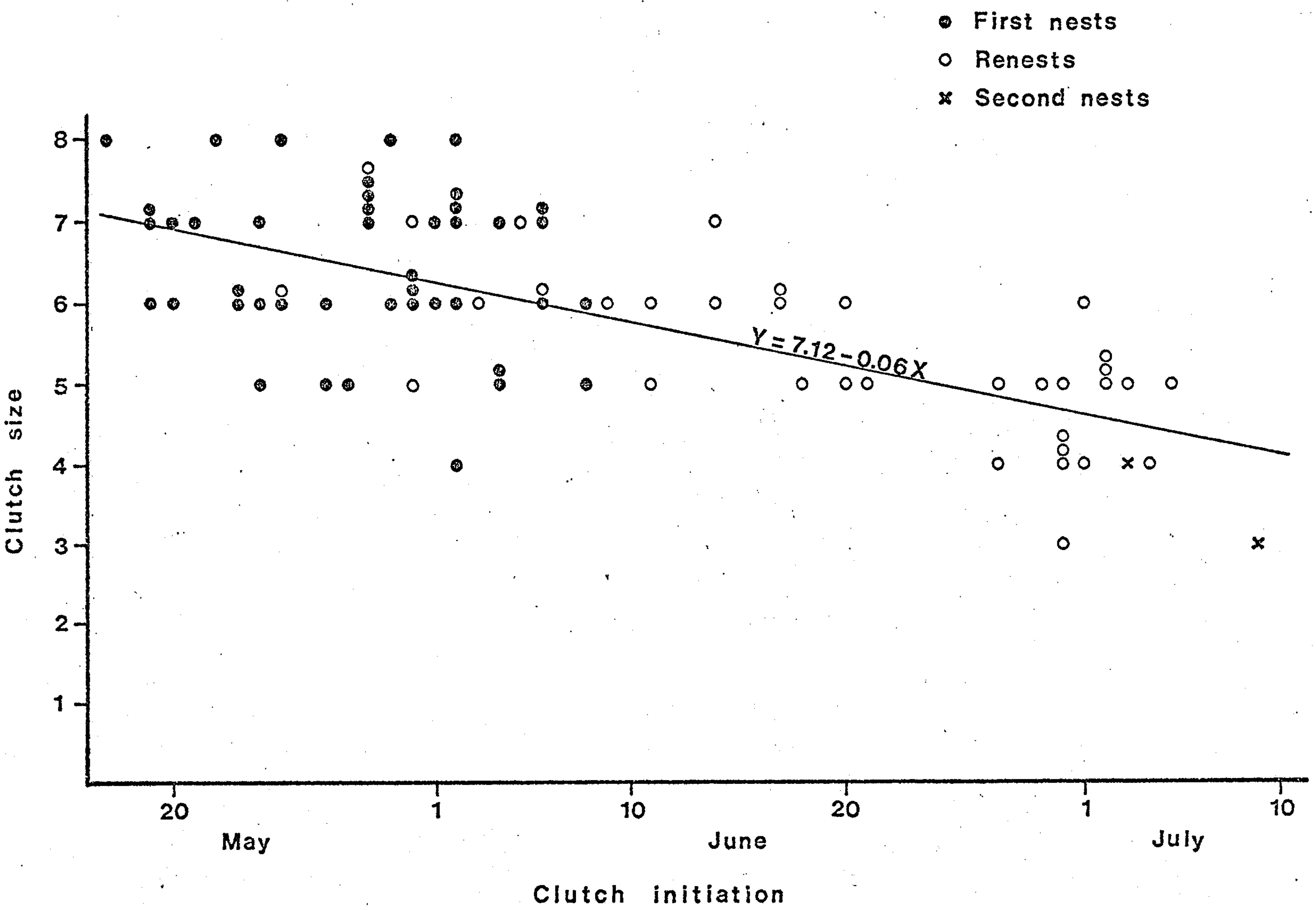
The present study indicates that clutch size is considerably higher than that reported by many workers. Most state that the clutch size of Horned Grebes in North America is four or five, sometimes three or six eggs (see Bent 1919; Palmer 1962). Bent (1919) reported nests containing as many as nine or ten eggs, but suggested that these large clutches were the product of more than one female. Considering the distribution of nesting pairs on the Minnedosa study area (one pair per pothole), it is unlikely that large clutches are due to two or more females laying in the same nest. Furthermore, nesting grebes are highly aggressive towards conspecifics, and territories are defended by both sexes.

Bent (1919:22) admits that "the eggs of the Horned Grebe are absolutely indistinguishable from those of either the Eared or the Pied-billed Grebes". It is possible that nests containing nine or ten eggs and reported to be nests of Horned Grebes were, in fact, nests of Pied-billed Grebes, which often lay clutches of nine and ten eggs (Chabreck 1963; Glover 1953; personal observations). These two species nest in similar habitats and, in the breeding season, are sympatric throughout much of northwestern North America.

Of course, the possibility of regional differences in clutch size of the Horned Grebe can not be disregarded. Unfortunately, most of the literature available does not specify the locality in which the nests were found. Detailed studies of other North American populations are needed in order to confirm that the differences in clutch size are as great as the present study suggests.

Variation in clutch size in relation to date of laying is shown in Figure 8. A comparison of the 1974 and 1975 regression lines

Figure 8. Variation in clutch size in relation to date of laying.


● First nests
○ Renests
× Second nests
Y = 7.12 − 0.06 X
Clutch size
8
7
6
5
4
3
2
1
20
1
10
20
1
10
May
June
July
Clutch initiation

by analysis of covariance (Snedecor and Cochran 1967) revealed no significant annual differences in regression coefficients (F = 0.14; 1,75 df; NS) nor in elevations (F = 2.20; 1,76 df; NS). Therefore, data from the two years were pooled. A significant correlation (r = -0.70) between clutch size and laying date was obtained (t = 8.60; 77 df; P < 0.001).

A seasonal decline in clutch size is characteristic of many bird species and is usually regarded as an adaptation to a decreased availability of food for the young or for the laying female late in the season. Many studies (see Klomp 1970) indicate that it is more difficult to raise offspring late than early in the breeding season and several authors have suggested that the seasonal decline in clutch size is an adaptation to these circumstances. There is, however, little evidence that the reduced clutch size is directly related to food supply (Klomp op. cit.).

It is unlikely that the seasonal decline in clutch size of Horned Grebes at Minnedosa is an adaptation to a deteriorating food supply for the young. I found no evidence to suggest that the adults encountered difficulty in finding food for their young late in the season. Horned Grebes feed their young until they are about 20 days of age (see p. 75). The adults obtain most of the food by diving, while the young remain on the water surface and wait to be fed. When feeding young, the adults surface each time that a prey is captured. Thus, by recording the length of time that an adult remains submerged in a foraging dive, it is possible to measure the degree of difficulty that an adult has in obtaining prey. Fjeldsa (1973a) found that the duration of foraging dives by Horned Grebes in Iceland was a good indicator of food abundance. In 1975 foraging dives of adults feeding young were timed with a stop-watch (to nearest 0.1 sec) for seven families (see Table 9). Differences in mean duration of foraging dives recorded early in the season (broods A, B, C, and D) as opposed to late in the season (broods E, F, and G) are slight. Pairs feeding young late in the season had no more difficulty in obtaining food than did pairs raising offspring early in the season. This is supported by observations of foraging success. In all feeding sessions observed, the adults rarely made an unsuccessful foraging dive.

Differences in fledging success between early-hatched broods (hatching before 25 June) and late-hatched broods (hatching after 25 June) are also small. Chick survival to fledging in early-hatched broods (57 fledged/81 hatched; 70 percent) did not differ significantly from late-hatched broods (45/74; 61 percent) ($x^2 = 0.54$; 1 df; NS).

It has been suggested for many species that the seasonal decline in clutch size is mainly due to age-related differences in clutch size and time of laying (Klomp 1970). In general, birds breeding for the first time begin laying later and tend to lay smaller clutches than older birds. In the Horned Grebe at Minnedosa, variation in clutch size of first nests contributed little to the seasonal decline in clutch size. The correlation ($r = -0.23$) between clutch size of first nests and laying date is not significant ($t = 1.51$; 41 df; NS).

In populations where renests and second nests occur regularly, the seasonal decline in clutch size is often explained as being due to the reduced clutch size of these nests. At the beginning of a breeding season, a female has only a certain amount of energy which can be devoted to reproductive activities (egg production, incubation, feeding

Table 9. Foraging efficiency of adult Horned Grebes feeding young at different times of the breeding season.

	Brood	Date	Mean Duration of Dives (sec)	n
Early-hatched Broods[a]	A	24 June	7.2 ± 1.4	52
	B	1 July	7.8 ± 1.3	55
	C	2 July	7.5 ± 1.4	22
	D	2 July	6.1 ± 1.0	48
Late-hatched Broods[b]	E	25 July	10.6 ± 2.5	31
	F	26 July	5.6 ± 0.7	62
	G	3 August	5.6 ± 0.7	71

[a] $\bar{x}$ = 7.2 ± 0.7 sec (n = 177)

[b] $\bar{x}$ = 6.5 ± 0.7 sec (n = 164)

young, and so on). If the first nest is destroyed, clutch size in subsequent nesting attempts will be smaller since part of the energy available for reproduction has already been expended (see Lack 1966; Klomp 1970). The present data are reasonably consistent with this hypothesis. Mean clutch size of all renests (5.3 ± 0.3 eggs) was significantly lower than that of first nests (6.4 ± 0.3 eggs) ($t = 5.02$; 75 df; $P < 0.001$). However, mean clutch size of renests initiated early in the season (before 15 June) (6.2 ± 0.4 eggs), presumably when females were still energetically strong, did not differ significantly from that of first nests ($t = 0.85$; 53 df; NS). Early in the season replacement clutches of six and seven eggs were common (Figure 8). Furthermore, there was a significant correlation ($r = -0.70$) between clutch size of renests and laying date ($t = 5.54$; 32 df; $P < 0.001$).

Fjeldsa (1973c) suggested that the seasonal decline in clutch size of Horned Grebes in Iceland and Norway was due to an allocation of energy to the body molt. In general, growth of the basic plumage in females of _P. a. arcticus_ begins in mid-July (Fjeldsa 1973b). Clutches laid after mid-July were always small (Fjeldsa 1973c). Although there is considerable individual variation, most females at Minnedosa begin the prebasic molt in mid-June. The ornamental head plumes are molted early and white feathers appear on the cheeks of some females as early as the last week in June. By mid-July most females are in an advanced state of body molt. Since egg-laying continues well into July, there is considerable overlap between breeding and molting.

For most bird species, reproduction and molting are considered to be mutually exclusive events since both are energetically demanding processes (Amadon 1966). It has been shown recently, however, that molt-breeding overlap is of regular occurrence in many tropical species (Foster 1975), and that it may have adaptive significance. If food resources permit, individuals may prolong their breeding period by extending it into the period of molt (Foster 1974). An extension of the breeding period would impart strong selective advantage to species breeding in areas where the probability of nesting success is low. Energetically, however, molt-breeding overlap may be favoured only when accompanied by a reduction in energy devoted to reproduction. One way of reducing reproductive costs is by lowering clutch size. Foster (1974:188) concluded that the combination of reduced clutch size, molt-breeding overlap, extended breeding periods, and more potential renestings "is one means by which birds may maximize their reproductive output in areas where nesting success is extremely low...".

If food resources permit molt-breeding overlap, it should impart the same benefits to species breeding in temperate regions. Detailed studies on the degree of overlap within individuals and its influence on clutch size are needed. The hypothesis that molt-breeding overlap contributes to the seasonal decline in clutch size of Horned Grebes remains to be tested.

Incubation

Continuous incubation begins after the first egg of a clutch is laid. The incubation period, recorded as the interval between the laying of an egg and the emergence of the chick from that egg, is normally 23 days. However, in two nests, hatching did not begin until the first eggs had been incubated for 28 and 34 days. This indicates that, in some pairs, incubation is only partly effective during the first few days that the nest is attended. Although the adults incubated throughout the laying period, the heat being applied to the eggs must have been less than that required for normal embryonic development. In species where incubation is shared by the parents, the principal means of regulating egg temperature is by adjusting the tightness of sit (White and Kinney 1974).

Incubation Rhythm

Role of the sexes in incubation was studied in 1975 by recording the duration of attentive periods (the amount of time an adult spends on the nest before being relieved by its mate). Observations were made on eight pairs of grebes, both during and after egg-laying (Table 10). During egg-laying, incubation was shared almost equally by the adults (55 percent by females; 45 percent by males). After egg-laying, however, females spent more time on the nest (63 percent) than did males (37 percent). This difference likely reflects changes in foraging activities of females during and after egg-laying. Since egg-production in birds requires extra energy (King 1973), females must devote considerable time to feeding before and during egg-laying. Fjeldsa (1973c) found that female Horned Grebes fed twice as much as males during the five days prior to egg-laying. The present study indicates that females may increase the time available for foraging during the energy-demanding period of egg-laying by assuming a reduced role in incubation.

Incubation rhythm may also be influenced by factors related to territorial defense. Although both sexes defend the territory, males are generally more aggressive than females. Also, on the average, males

Table 10. Roles of the sexes in incubation.

	Mean Duration of Attentive Periods (min)			
	Females	(n)	Males	(n)
During Egg-laying[a]	39 ± 14	(8)	32 ± 5	(8)
After Egg-laying[b]	70 ± 14	(8)	41 ± 7	(9)

[a] $t' = 0.91$; 7 df; NS. (unequal variances)

[b] $t = 3.65$ 15 df; $P < 0.005$.

are larger than females (Table 11). Thus, males may be more effective in intraspecific territorial defense and in protecting the nest site against other species, many of which greatly outweigh the Horned Grebe. This may be one factor which accounts for the male's secondary role in incubation.

Attentive periods for males and females ranged from 17 to 102 minutes, with a mean of 45 minutes. The adaptive significance of such frequent changes on the nest is unknown. Drent (1973) suggested that an incubating parent must achieve a compromise between tending the eggs and leaving the nest to feed, but that antipredator measures were also involved. Long, unbroken attentive periods may be advantageous in minimizing activity near the nest, and therefore in reducing the probability of predators locating the nest. In this respect, frequent nest relief would be disadvantageous. Mean attentive periods of less than one hour have been reported for Pied-billed Grebes (Deusing 1939), Little Grebes (Hartley 1933), and Atitlan Grebes (*Podilymbus gigas*) (LaBastille 1974).

Nest Relief

Incubating Horned Grebes do not leave the nest until they are relieved by their mates, so that the nest is rarely left unattended. In over 650 visits to 139 nests during daylight hours (0500 - 2200 hr CDT), on only one occasion was a nest found unattended.

Unlike the courtship behaviour of the Horned Grebe, that associated with nest relief is simple and variable. During the period of egg-laying, copulations frequently occur on the nest platform when the male returns to relieve the incubating female. On two occasions, however,

Table 11. Sexual dimorphism of adult Horned Grebes at Minnedosa.

	Females		Males	
Character	$\bar{x}$	(n)	$\bar{x}$	(n)
Culmen[a] (mm)	23.0 ± 0.4	(26)	24.7 ± 0.5	(18)
Tarsus Length[b] (mm)	46.4 ± 0.5	(26)	49.2 ± 0.6	(19)
Wing Length[c] (mm)	142.4 ± 1.5	(26)	149.2 ± 2.3	(19)

[a] $t = 5.14$; 42 df; $P < 0.001$

[b] $t = 6.97$; 43 df; $P < 0.001$

[c] $t = 5.20$; 43 df; $P < 0.001$

I observed copulations during nest relief even after the clutch was complete. Both occurred within five days of laying of the last egg. Burger (1974b) observed copulations by Franklin's Gulls up to 12 days after egg-laying, and suggested that such continued copulations may decrease the time required to lay a replacement clutch in the event of nesting failure. Pairs that renest quickly would be favoured since there is high selection for early nesting and for synchrony within a colony (Burger *op. cit.*). Copulations after egg-laying by Horned Grebes may have similar adaptive significance. I discussed earlier (p. 44) that species breeding in habitats where nesting success is low will benefit from any reproductive trait that increases the potential number of nesting attempts in a season. Pairs that reduce the time between loss of a nest and initiation of a replacement clutch would be at a selective advantage.

During nest relief, Fjeldsa (1973d) reported courtship feeding by males of *P. a. arcticus*. I did not observe courtship feeding either during nest relief or during other activities. Perhaps this is another behavioural difference that separates *arcticus* from the North American subspecies.

Nest relief is often accompanied by nest-building activities. Generally, the relieved bird makes one or more dives to obtain nesting material before leaving the vicinity of the nest. The intensity and duration of nest-building are greatly influenced by water conditions at the nest site. Behaviour of relieved birds in relation to water conditions at the nest site was studied in four pairs in 1975 (Table 12). Under calm conditions (or when nests were sheltered from wave action), the grebes devoted less than three percent of their total time off the nest to nest-building. However, during periods when wind and wave

Table 12. Influence of water conditions at nest site on nest-building activities during incubation.

Water Conditions at Nest Site	Nest	Observation Period (min)	Time Devoted to Nest-building (min)	Totals
Calm	A	248	4	11/423[a] (2.6%)
	B	175	7	
Waves Disturbing Nest Platform	C	110	41	96/232[a] (41.4%)
	D	122	55	

[a] $x^2 = 138.2$; 1 df; $P < 0.005$.

action were disturbing the nest platform, nest-building increased significantly. On the average, grebes spent more than 41 percent of their time off the nest in collecting, transporting, and arranging nesting materials. The adaptive value of this behaviour is obvious. Because grebe nests are built directly on the water, they are subjected to considerable wave action. Proper maintenance of the nest platform throughout incubation is undoubtedly crucial for successful nesting. Increased nest-building under adverse weather conditions was reported by Broekhuysen and Frost (1968) for Black-necked (Eared) Grebes in Africa.

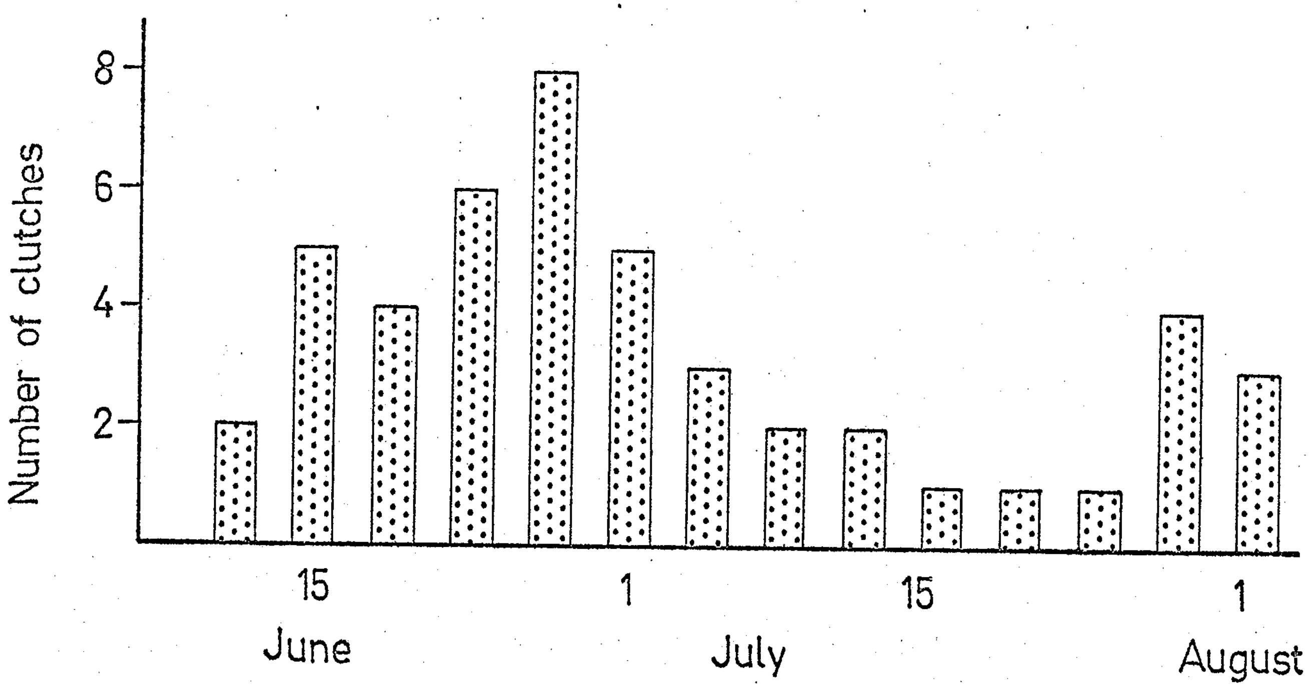
Hatching and Abandonment of the Nest

In 1974 and 1975 first eggs in 47 nests hatched from 10 June to 2 August (Figure 9). The wide range of hatching dates at Minnedosa reflects the protracted period of egg-laying which is due to the laying of up to three replacement clutches (and occasionally the laying of second clutches). Clutches hatching after 5 July represent successful renest or second nest attempts.

As effective incubation usually begins after the first egg of a clutch is laid, hatching is asynchronous and extends over a period of several days. Hatching periods for the three most common clutches are as follows: seven to eight days for a clutch of five eggs; eight to nine days for a clutch of six; and nine to ten days for a clutch of seven. Generally, the interval between hatching of consecutive eggs within a clutch reflects the laying interval; most chicks hatch from one to two days apart.

Hatching of individual eggs is a rapid process. In each of three Horned Grebe eggs at Minnedosa, emergence of the chicks from the

Figure 9. Distribution of hatching of first eggs in Horned Grebe clutches, 1974 and 1975. (Each bar represents a 4-day interval.)


Number of clutches
8
6
4
2
15
June
1
July
15
1
August

first signs of pipping took less than two hours. Under incubator conditions, the hatching process in Pied-billed, Eared, Red-necked, and Western Grebes at Delta, Manitoba ranged from 50 minutes to two hours (McAllister 1963). For Atitlan Grebes hatching was completed in about 1.5 hours (LaBastille 1974). Nice (1962) suggested that rapid hatching protects the grebe chicks against the danger of drowning in the wet nest.

Young grebes were classified by Nice (1962) as Precocial Category 4 (precocial chicks that follow parents and are fed by them). McAllister (1963), on the other hand, suggested that grebes be considered semi-precocial because the chicks do not follow the parents during the first week, but are brooded constantly, either at the nest or on the parents' backs. From an examination of the development of behaviour patterns in five species of grebes, McAllister (1963:128) concluded that grebes "would be better placed after the gulls as semi-precocial birds, birds which do not leave the nest although they are physically able to do so". The downy plumages of grebes (including the Horned) have been described by Storer (1967).

The behaviour of newly-hatched Horned Grebes at Minnedosa is similar to that described by Simmons (1968) for Great-crested Grebes. Shortly after hatching the chick scrambles onto the incubating parent's back where it is brooded among the feathers between the adult's slightly raised wings. At the nest, grebe chicks are not brooded underneath the parent. During the hatching period the parents continue to share the incubation duties. One adult incubates the remaining eggs and broods the chicks while its mate provides food for the young. Horned Grebe chicks accept food (and feathers) during the first day and are totally dependent on the adults for food during their first two weeks. Towards the end of the hatching period the first-hatched chicks spend brief periods in the water near the nest, and sometimes rest on the nest platform beside the incubating parent. I have also observed chicks scramble down into the water to drink, defecate, or regurgitate a pellet.

The function of feather-eating by grebes and its relationship to pellet-casting have been discussed by Simmons (1956) and by Storer (1961, 1969). Published reports of pellet-casting by grebes are few. I observed pellet-casting by Horned Grebes on 17 occasions, 11 times by adults and six times by young (ranging in age from three days to seven weeks). At Minnedosa, the diet of Horned Grebes consists largely of aquatic insects and other invertebrates since most potholes are devoid of fish (see p. 11). (Food habits of the Horned and other North American grebes are presented by Wetmore (1924).) According to Storer (1969:185), "grebes living on fishless bodies of water and depending on arthropods for much of their diet rapidly accumulate indigestible chitin in the stomach. This requires rather frequent pellet-casting...". He concluded that the feathers ingested by grebes prevent indigestible material from entering the intestine by forming a plug in the pyloric lobe.

After the final egg of a clutch has hatched, the extent to which the parents use the nest platform to brood the young is variable. Many pairs abandoned the nest within two days, while others continued to brood on it for brief periods from four to seven days after hatching. The maximum time observed for abandonment of a nest was 11 days (in two pairs). In southern Alaska, Sage (1973) observed a pair of Red-necked Grebes using a platform other than the nest for brooding the young. He suggested that it may have been one of the pairing platforms built earlier in the season. I have no observations of Horned Grebes using platforms other than nests for brooding young.

Significance of Asynchronous Hatching in Grebes

Asynchronous hatching and the resulting age differences of chicks within broods are usually regarded as adaptations to a variable and unpredictable food supply (see Cody 1971; Lack 1954, 1966). The adaptive significance of asynchronous hatching and the mechanism that adjusts brood size to the availability of food resources are summarized by Ricklefs (1973a). Because they are larger, first-hatched young compete more effectively for food provided by their parents than do their younger siblings and when feeding conditions are poor, the smallest brood members often starve. "Selective starvation brings the energy requirements of the brood into line with the food gathering rate of the adults and ensures that all of the young raised are adequately nourished" (Ricklefs 1973a:253). Differential mortality of young has been documented in more than 20 families of birds (including several fish-eating species) where asynchronous hatching occurs (reviewed by Davis 1972). Mortality rates of smaller, late-hatched young are generally higher than those of their older siblings. I was unable to examine age-related mortality of young Horned Grebes because of the difficulty I encountered in capturing and marking chicks.

Apart from Simmons' (1970, 1974) work on the Great-crested Grebe, a species which feeds predominantly on fish, the significance of asynchronous hatching in grebes has not been discussed. The establishment of a dominance hierarchy within Great-crested Grebe broods, and a feeding preference by the adults for certain chicks (the 'in-chicks') ensures the survival of at least part of the brood (Simmons 1974). It is possible that asynchronous hatching allows the adjustment of brood size to feeding conditions by the adults' desertion of a nest before all eggs have hatched (Simmons op. cit.). Although abandonment of viable eggs has been documented in Great-crested Grebes (see Hanzak 1952), it has not been shown that such behaviour is adaptive (Simmons 1974).

In grebes, it is likely that the incubation pattern itself has selective advantage. Constant incubation after the first egg is laid undoubtedly increases both the safety of the nest and the probability of nesting success. Unlike the elaborate over-water nests of the diving ducks (Aythyinae), for example, grebe nests are rather poorly constructed and are more vulnerable to wave action. If left unattended during the laying period, probably most would be destroyed before laying was completed. Another advantage of this incubation pattern is that it reduces the time that the first eggs of a clutch are exposed to potential hazards. At Minnedosa, the first egg in a Horned Grebe nest normally hatches 23 days after clutch commencement. If incubation had not begun until the clutch was complete, however, the first egg would have been exposed for at least 30 days (in clutches of five or more eggs) before hatching. For birds nesting in unstable habitats where nest losses are high, selection favours a reduction in length of nest periods (see Ricklefs 1973b). Thus, although Lack's (1954) theory adequately explains the adaptive value of asynchronous hatching to piscivorous species of grebes, its value to species which feed largely on invertebrates (presumably a more predictable food supply) may be secondary to the incubation pattern. Asynchrony in the latter group may not have direct adaptive significance, but may be merely a consequence of the incubation pattern. This is supported by indirect evidence obtained in the present study. Many aspects of parental behaviour of Horned Grebes appear to be adaptations for reducing the competitive disparity among brood members caused by asynchronous hatching (see p. 79).

Hatching Success

In calculating hatching success, I used only those nests (n = 133) that were found either before or during the first week of laying. Nests located after this time (n = 8) were excluded due to the bias they introduce in a population estimate of nest success (Mayfield 1975). Overall hatching success of Horned Grebes in 1974 and 1975 was low (Table 13). There was no significant annual difference in hatching success, and success was independent of laying date (Table 14). Predation and wave action accounted for 71.2 percent of the total egg loss.

Nests were grouped on the basis of proximity to shoreline into four arbitrary classes (Table 15). Although success and predation rates do not differ significantly among the classes, the data show that nests located nearest the shoreline were most susceptible to predation, and were least successful. (A successful nest is one in which at least one egg hatched.) Mean distance to shore of successful nests (7.9 ± 1.3 m) was significantly greater than that of nests destroyed by predators (6.1 ± 1.0 m) ($t = 2.20$; 85 df; $P < 0.05$). Also, successful nests were located in deeper water ($\bar{x} = 41.3 \pm 4.1$ cm) than nests destroyed by predators ($\bar{x} = 36.4 \pm 2.9$ cm) ($t = 1.99$; 89 df; $P < 0.05$).

Identification of nest predators was based on the appearance of eggshell remains as described by Rearden (1951). I did not observe any eggs actually being eaten. Potential mammalian predators on the study area include Raccoon, Striped Skunk (_Mephitis mephitis_), Red Fox (_Vulpes vulpes_), American Mink (_Mustela vison_), and Franklin's Ground

Table 13. Egg success of Horned Grebes at Minnedosa, 1974 and 1975.

	1974	1975	
Fate of Eggs	Number	Number	Totals
Hatched	99[a] (27.9%)	94[a] (33.3%)	193 (30.3%)
Taken by predators	173[b] (48.7%)	68[b] (24.1%)	241 (37.8%)
Washed out	29[c] (8.2%)	46[c] (16.3%)	75 (11.8%)
Rolled into water	17 (4.8%)	16 (5.7%)	33 (5.2%)
Failed to hatch	8 (2.3%)	11 (3.9%)	19 (3.0%)
Deserted	6 (1.7%)	7 (2.5%)	13 (2.0%)
Unknown loss	23 (6.4%)	40 (14.2%)	63 (9.9%)
Totals	355	282	637

[a] $x^2 = 1.54$; 1 df; NS.

[b] $x^2 = 25.19$; 1 df; $P < 0.005$

[c] $x^2 = 8.84$; 1 df; $P < 0.005$

Table 14. Hatching success of Horned Grebe nests in relation to laying date.

Clutch Initiation	Number of Nests	Hatching Success[a]
15 - 31 May	54	90/277 (32.5%)
1 - 15 June	40	63/200 (31.5%)
after 15 June	39	40/160 (25.0%)

[a] Hatching success = eggs hatched/eggs laid.

x^2 = 2.02; 2 df; NS.

Table 15. Nesting success in relation to proximity of nests to shoreline.

Distance to Shore (m)	Number of Nests Successful[a]	Number of Nests Destroyed by Predators[b]
0 - 3.0	2/14 (14%)	8/14 (57%)
3.1 - 6.0	14/43 (33%)	17/43 (40%)
6.1 - 9.0	13/31 (42%)	9/31 (29%)
> 9.0	13/27 (48%)	8/27 (30%)
Totals	42/115 (36.5%)	42/115 (36.5%)

[a] $x^2 = 3.32$; 3 df; NS.

[b] $x^2 = 2.56$; 3 df; NS.

Squirrel (*Spermophilus franklinii*). Of these, only Raccoon and Mink regularly destroy nests in aquatic or wet marshy areas (Rearden *op. cit.*). The manner in which the eggs were eaten indicates that Raccoons were responsible for most of the predation on Horned Grebe nests. Most destroyed eggs were characterized by an opening in the large end of the shell which suggested that the end had been bitten off. The Raccoon's reputation as a predator on over-water nests in the Minnedosa district is well-known (Kiel *et al.* 1972). Potential avian predators include Common Crow (*Corvus brachyrhynchos*) and Black-billed Magpie (*Pica pica*), as well as opportunistic species such as American Coot, Black Tern, and Yellow-headed Blackbird. Egg loss to avian predators, however, is considered to be low because Horned Grebes rarely leave their nests unattended and both sexes are very aggressive.

Egg predation was significantly higher in 1974 than in 1975 (Table 13), but the reason for this difference is not known. Water levels in 1975 were similar to those in the previous year and there were no obvious differences in distribution or abundance of nesting cover. Mean water depth at 1975 nests (40.8 ± 3.5 cm) did not differ from that at 1974 nests (38.1 ± 2.7 cm) ($t = 1.25$; 117 df; NS). Similarly, there was no difference in mean distance to shoreline between 1975 nests (7.3 ± 1.2 m) and 1974 nests (6.6 ± 0.9 m) ($t = 0.95$; 113 df; NS). Circumstantial evidence suggests that the annual difference in predation rates may be due to differences in foraging activity of the Raccoon. Canvasbacks nesting on the study area also suffered higher egg losses to Raccoons in 1974 than in 1975 (J. Serie, pers. comm.).

Egg loss to wave action was significantly greater in 1975 than in 1974 (Table 13). On two days between 19 and 26 June, 1975, wind speeds reached 50 km/hr, and on a third day wind speeds exceeded 80 km/hr. Six nests (containing 30 eggs) were destroyed by wave action during this period. This accounted for 65 percent of the total number of eggs washed out in 1975. Waves generated by winds exceeding 50 km/hr are generally sufficient to wash out nests, regardless of the density of emergent cover. In 1975, many peripheral stands of emergent vegetation were flattened by the 80 km/hr winds of 26 June.

The present study supports the predictions of nesting success based on water levels and habitat availability proposed by Nuechterlein (1975) for Western Grebes. He predicted that abiotic factors such as wind and wave action would reduce greatly the nesting success of grebes in years when water levels and availability of quality nesting habitat were low. Water levels on the Minnedosa study area were high in 1974 and 1975. Emergent vegetation (particularly bulrush, cattail, and whitetop) responded to the high water conditions and provided an abundance of nest sites well-protected from wind and wave action. Horned Grebes sustained low egg losses to wave action in 1974 and 1975 (Table 13).

Parental Care and Chick Development

At one-to-three day intervals throughout the brood-rearing period of 1975, I made extensive observations on 19 Horned Grebe families. As the brood-rearing activities of each pair were confined to one pothole and, in all cases, each pothole supported only one pair of nesting grebes, individual broods could be surveyed from hatching until the young fledged. Recognition of individual broods permitted parental care and chick development to be studied.

Chick Development

During their first three days, Horned Grebe chicks are brooded almost constantly on the adults' backs, either on the nest platform or in the water. As the chicks get older they spend an increasing amount of time in the water and by eight or nine days of age they no longer require brooding. McAllister (1963) reported that functional preening and oiling in a captive Horned Grebe chick first appeared on the sixth and seventh days, respectively. Thus, the age at which chicks take to the water corresponds to the age at which preening and waterproofing become functional. The development of thermoregulation is likely involved also, as small chicks may lose considerable body heat through their short down and through their feet and legs.

On several occasions I observed one parent carrying as many as five young on its back. However, as the first-hatched chicks of a brood are often a week old before the nest is abandoned, one adult rarely carries this many young for extended periods. The larger (older) chicks soon take to the water and follow their parents rather than being carried by them. The carrying period ends when the youngest chick has reached the age of eight or nine days.

The carrying period in Great-crested Grebes lasts up to three weeks (Simmons 1974). The presence of large, predatory fish in lakes where Great-crested Grebes breed may be one factor promoting the extended carrying period in this species. Harrisson and Hollom (1932) and Simmons (1974) reported that predation by Pike (*Esox lucius*) was a major factor causing mortality of grebe chicks in England. An extended carrying period may have survival value by reducing chick losses to underwater predators. At Minnedosa and throughout the Canadian prairies, typical breeding habitats of the Horned Grebe lack large, predatory fish.

Following the carrying period, young Horned Grebes follow their parents until the chicks are capable of obtaining about 50 percent of their own food, usually at 16 to 18 days of age. Chicks of this age rarely associate with other members of the family. This is partly due to the aggressive behaviour of their parents towards them, especially when the parents are also feeding smaller young (see p.78). At 12 to 13 days of age chicks make their first successful feeding dives (chicks inexperienced in feeding themselves bring their prey to the surface before swallowing them). At 19 to 21 days most chicks are independent of parental care, although the smallest brood members frequently are fed until they are 21 to 24 days old.

Parental Feeding

Adaptive aspects of parent-chick relationships of the Horned Grebe are best understood when they are compared to those of the Great-crested Grebe. Simmons (1970, 1974) suggested that many features in the reproductive biology of Great-crested Grebes are adaptations for raising young either at a time of food shortage, or in habitats with an unpredictable food supply. This is accomplished, in part, by a system of chick favouritism, where parents selectively feed certain chicks (the 'in-chicks') at the expense of other brood members (the 'out-chicks'). Such behaviour ensures, if possible, the survival of at least some chicks. In contrast, parental feeding by Horned Grebes at Minnedosa reduces the competitive advantage that some brood members have over others as a result of age differences among chicks.

During the carrying period, Horned Grebe parents share the brooding and feeding duties. Most often one parent carries the young while its mate feeds them. Occasionally, small chicks are 'dumped' into the water by the brooding parent who then assists its mate in feeding the brood. And, on rare occasions, I have observed adults feeding young while carrying chicks. Although parents carrying young are unable to obtain food by diving, they capture prey near the surface by submerging only the neck and head. These prey are then offered to the chicks being carried.

The begging and submissive behaviour of Horned Grebes is similar to that of Great-crested Grebes (see Simmons 1968). Chicks being brooded at the nest or in the water simply wait on the parent's back while the other parent approaches with food. However, soon after they have taken to the water, they develop an elaborate begging display. As soon as the feeding parent surfaces from a dive with prey in its bill, the chicks assume a submissive posture and swim toward the approaching adult. The submissive posture is often accompanied by loud begging calls and by splashing movements of the feet and legs, especially when the chicks are older than two weeks.

During the carrying period, the first chick to reach the feeding parent generally receives the food - the adults do not show a preference for certain chicks. But, owing to the age differences among chicks, some brood members compete more effectively for food than others. Older chicks in the water have a feeding advantage over their smaller siblings that still require brooding. Frequently, however, a feeding parent ignored the chicks in the water, even though they were begging loudly, and presented food to the young being carried by the second parent. This behaviour ensures that the older chicks do not receive all the food and reduces the competitive advantage that they have over other brood members.

First-hatched young in Great-crested Grebe broods have a similar feeding advantage during the hatching and carrying periods. This advantage is enhanced by the establishment of a dominance hierarchy within broods. Aggressive encounters between chicks were most frequent when they approached the same parent to obtain food (Simmons 1974). I found no evidence to suggest that a dominance hierarchy was established within Horned Grebe broods. Aggressive disputes between chicks were rare and competition for food was relaxed. This is likely due to an abundance of invertebrate prey in the potholes and to the relative ease with which it is obtained. Data on duration of feeding dives (presented on p.53) show that parents are very proficient in obtaining food for their young. Preliminary observations of feeding rates of adults indicate that a pair of Horned Grebes at Minnedosa is capable of providing its young with up to 465 prey in one hour of foraging. For three broods (containing three, four, and six young) being fed by both parents, feeding rates ranged from 7.5 to 7.8 prey per minute of foraging time.

Following the carrying period, participation of adults in caring for their young depends on brood size. In broods of fewer than four chicks, one parent generally leaves the territory (pothole) shortly after the carrying period is over, usually within five days. The other parent remains with the young until the smallest chick is independent of parental care. Either parent may remain with the brood. In four families where the parents were individually marked, the female remained to care for the young in two cases; the male stayed with the young in the other two cases.

In broods of four or more, the young are divided between the parents within three days of the end of the carrying period. This system of brood-division is similar to that observed in the Great-crested Grebe. Brood-division results "in the formation of two family sub-groups with each parent usually feeding only its 'own' young and showing hostility to the 'other' young if they approach closely. The two sub-groups typically associate only loosely, mainly when loafing, and may sometimes separate more or less entirely" (Simmons 1974:424). In Horned Grebes there is a gradual weakening of the adult pair-bond following hatching and, unless a second nest is attempted, the pair-bond dissolves soon after brood-division is established. Brood-division does not always involve the entire brood. In broods of five or more young, where the age difference between first- and last-hatched chicks is often as great as eight or nine days, the oldest one or two chicks are nearly independent when brood-division is established. In these families brood-division often involves only part of the brood and the adults direct their attention to the smaller chicks. Thus, regardless of brood size, one parent is rarely in charge of more than two chicks for any length of time.

Within each family sub-group, all chicks are fed equally during the first two or three days of brood-division. The chick nearest its parent after it surfaces from a dive generally receives the food. However, as the larger chicks reach 16 to 18 days of age (the age at which they forage for about half of their own food), the feeding behaviour of the parent changes. These chicks are now often threatened or chased by the parent when they approach for food, especially if the parent is feeding smaller chicks. In the early stages of development of parental aggression, the larger chicks continue to beg for food. Later on, in response to the repeated hostility of the parent, they spend an increasing amount of time away from their family sub-group. At 19 to 21 days of age they are independent of parental care. Thus, when the larger chicks are nearly self-sufficient, parents focus their attention on the smaller brood members in an effort to maximize production.

Two observations concerning parental aggression towards young are of particular interest. First, parental aggression occurs only if the sub-group contains more than one chick. A parent tending a single chick will continue to feed it until the chick is fully independent. Secondly, in sub-groups of two or more chicks, parental aggression is rarely directed toward the smallest young, even when it is the last chick receiving parental care. In fact, parental feeding of the smallest young frequently continues until the chick is 21 to 24 days of age. This prolonged period of parental care for the smallest chick may compensate for any competitive disadvantage that it experienced earlier in the brood-rearing period.

Through the combined effects of brood-division, parental aggression, and prolonged feeding of smaller brood members, Horned Grebes effectively reduce the competitive disparity that exists within broods as a result of age differences among chicks. Age differences and, presumably, differences in competitive ability are more pronounced as brood size increases. However, chick survival to fledging in 1974 and 1975 was independent of initial brood size (Table 16).

Table 16. Chick survival to fledging in relation to initial brood size.

Initial Brood Size	Number of Young Hatched	Number of Young Fledged[b]	Percent Survival to Fledging
2 - 3 (6)[a]	14	10	71
4 - 5 (17)[a]	78	48	62
6 - 7 (10)[a]	63	44	70

[a] Number of broods.

[b] $x^2 = 0.44$; 2 df; NS.

Departure of Adults and Young

Departure of adults from the territory is influenced by brood size. Small broods are usually tended by only one parent; its mate leaves the territory shortly after the end of the carrying period. If the brood is large and divided, each parent remains on the territory until all chicks in its sub-group are independent.

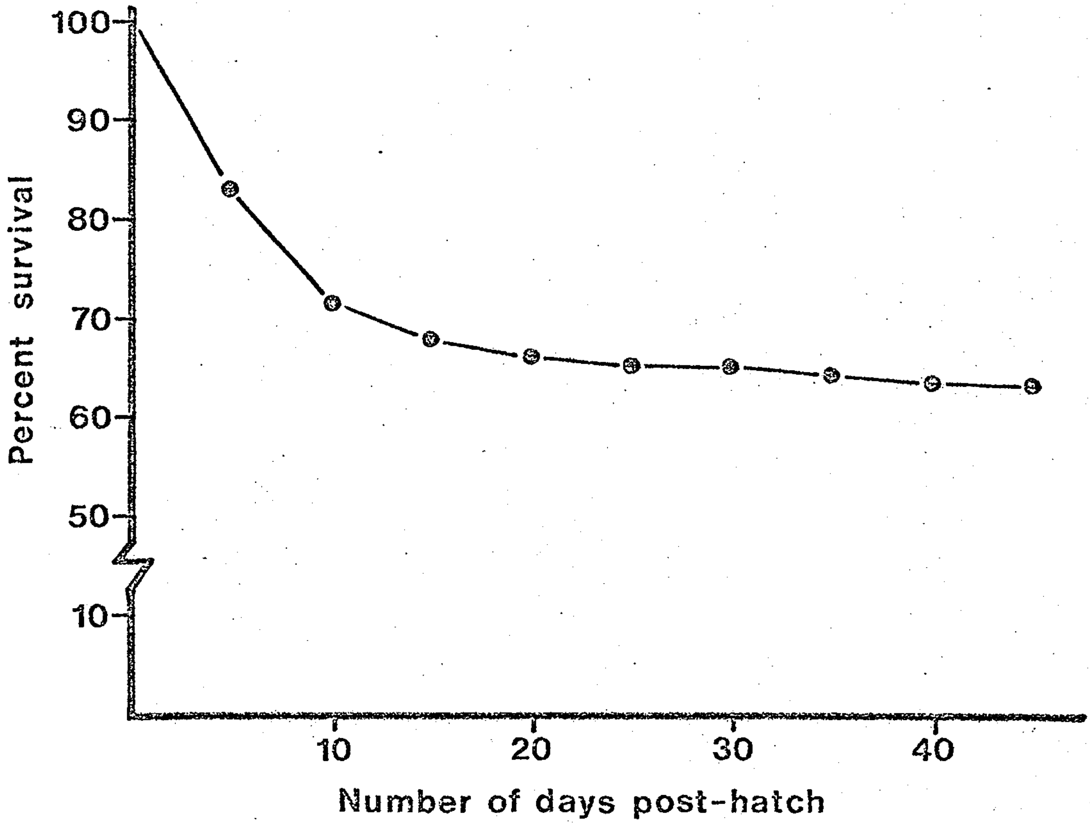
At Minnedosa, most chicks fledged at an age of 45 to 50 days; the older chicks left the natal pothole before their younger siblings. During the five days before their actual departure, chicks made frequent 'practice upwind flights' by pattering along the water surface in an attempt to become airborne. The youngest chicks that I observed in true flight were 41 to 42 days of age. In 1974 and 1975, fledging dates ranged from 1 August to 15 September.

Fledging Success

In 1974 and 1975, 38 broods (containing 165 young at hatching) were surveyed at one-to-three day intervals. From an average brood size of 4.3 chicks at hatching, 63.6 percent survived to fledging. As in most nidifugous species (Lack 1968), chick mortality was highest in the first few days after hatching (Figure 10). Only 71.5 percent survived the first ten days. The mortality which occurred during this period represents over 78 percent of all chick mortality to the time of fledging.

Causes of post-hatching mortality are generally unknown because few dead chicks were found. Newly-hatched chicks are feeble swimmers and are susceptible to drowning and exposure. Fjeldsa (1973c) obtained a correlation between early mortality of Horned Grebe chicks and inclement weather conditions during the hatching period. He

Figure 10. Survival to fledging of Horned Grebes, 1974 and 1975. (On the time scale, zero represents the mid-point in hatching of a clutch.)


Percent survival
100
90
80
70
60
50
10
10
20
30
40
Number of days post-hatch

indicated that fatigue and loss of heat were likely responsible for the deaths of small young. Mortality of young as a result of inclement weather has also been reported for other grebe species (see Kevan 1970; Munro 1941; Simmons 1974).

I have no direct evidence of chick loss to predators. However, Mink, Raccoon, and Great Horned Owls (*Bubo virginianus*) are present on the study area and may be responsible for some of the chick mortality.

GENERAL DISCUSSION

POTHOLE MARSHES AS UNSTABLE HABITATS

The concept of environmental stability is usually interpreted in terms of predictability of resources (Margalef 1968). Unstable environments are characterized by random fluctuations in availability of resources, largely as a result of climatic variability. Of all aquatic systems, prairie marshes are considered to be the least stable (Weller and Spatcher 1965). Because of the small size, shallow depth profile and small drainage basin of a typical pothole marsh, its water level varies directly with the amount of precipitation. In western Canada the area of wetland habitats in a given year correlates closely with the total annual precipitation (Kiel *et al*. 1972). In modern times the number of ponds throughout the prairie and parkland regions of western Canada have fluctuated from 1.6 to 7.1 million ponds in the driest and wettest years, respectively (Leitch 1975).

Apart from the direct loss of wetlands during periods of drought, short-term changes in the quality of marsh habitats are pronounced. Extensive changes in distribution, abundance and species composition of aquatic vegetation accompany the fluctuating water levels of prairie pothole marshes (Eisenlohr 1969; Kiel *et al*. 1972; Millar 1969). During years of subnormal precipitation and receding water levels, plant species characteristic of terrestrial communities often dominate the peripheral areas of pothole basins. In contrast, successive years of high water levels can eliminate much of the emergent vegetation through flooding (see Kiel *et al*. 1972).

Published accounts on the impact of fluctuating water levels on higher trophic levels are few. Recently, however, Voigts (1976) demonstrated that aquatic invertebrate populations were influenced by structural changes in aquatic vegetation. Increased structural complexity of the plant community (such as the interspersion of submerged vegetation with stands of emergent vegetation) in several Iowa marshes yielded a corresponding increase in invertebrate abundance and diversity. Since each trophic level is affected by changes in the levels beneath it, it is clear that all trophic levels of a pothole marsh will be affected by fluctuating water levels, either directly or indirectly.

ADAPTATIONS TO UNSTABLE HABITATS

Birds inhabiting prairie pothole marshes are subjected to an ever-changing environment where the availability of resources fluctuates widely. Successful breeding is contingent upon the availability of many resources, including nest sites, feeding areas and food supply, and shelter (Hilden 1965). In marsh habitats all these resources are alterable by fluctuating water levels.

Environmental change permits a measure of a species' adaptability. Relatively non-specialized groups, such as the icterids, are able to exploit alternative habitats and food resources when marsh habitats are unfavourable for nesting (Robertson 1972; Voigts 1973; Weller and Spatcher 1965). In contrast, species with specialized foraging techniques and/or limited flexibility in habitat selection are less tolerant of habitat changes. Fixed patterns of behaviour (locomotion, feeding and nest-building) that are determined by specialized anatomical structures often necessitate a certain type of habitat

(Hilden 1965). The impact of habitat changes on specialized, over-water nesting birds is clearly demonstrated during periods of drought. In dry years, receding water levels produce wide mudflats which separate the water from the shoreline vegetation. Ordinarily this vegetation would be available as emergent nesting cover. This lack of over-water nesting habitat may preclude nesting by some species of anatids almost entirely (Leitch 1964). Nesting success also is influenced by changes in availability of emergent cover. Although detailed studies of nest-site selection are lacking for most grebes, existing information indicates that they are dependent upon emergent vegetation for protection and support of over-water nesting platforms. The vulnerability of grebes' nests to wind and wave action has been documented for many species, including Eared (Broekhuysen and Frost 1968; McAllister 1958), Pied-billed (Chabreck 1963; Glover 1953), Western (Nuechterlein 1975) and Horned Grebes (present study). Nuechterlein (1975) demonstrated that Western Grebes suffered high nest losses to wave action when water levels and availability of quality nesting cover were low.

Birds adapted to varying environments are frequently termed fugitive or opportunistic species (see Cody 1971) because of their abilities to disperse and colonize new areas. For example, during years of deteriorating habitat conditions on the prairies a high proportion of the prairie waterfowl population emigrates to more stable marshes in Arctic regions (Crissey 1969; Hansen and McKnight 1964). For larids, McNicholl (1975) reported that site tenacity is poorly developed in species nesting in unstable habitats and that group adherence allows rapid colonization of newly-created habitat. Emigration by grebes from drought-affected areas has not been documented. Evidence of dispersal requires data on movements of banded individuals and on regional population censuses, both of which are lacking for North American species. Evidence of their pioneering abilities, however, has been documented. Weller and Spatcher (1965) demonstrated that Pied-billed Grebes colonized new marsh habitats in Iowa within two-to-three years after flooding. The authors suggested that the rate of colonization by this species was related to their dependence on animal foods which first must repopulate the marshes. Nuechterlein (1975) suggested that the social system of Western Grebes is one of colonial nomadism and that the unpredictable nature of their nesting habitats inhibits site tenacity and natal homing.

Apart from their pioneering abilities, species adapted to fluctuating environments often exhibit reproductive traits that promote rapid population growth. The evolution of reproductive parameters (or 'reproductive strategy') in relation to environmental stability has been reviewed by Cody (1971). In general, populations with a high value of 'r', the intrinsic rate of natural increase, are favoured under conditions of environmental instability. MacArthur and Wilson (1967) proposed the term 'r-selection' to denote the directional force of natural selection in varying environments.

Although information on many demographic parameters of the Horned Grebe is lacking, the present study suggests that many of its reproductive traits are adapted for maximizing its reproductive potential. Because of the changing nature of marsh habitats, Horned Grebes must rear young when habitat conditions are favourable since the probability of producing offspring in future years is uncertain. In the event of nesting failure, Horned Grebes renest persistently. Many behavioural adaptations minimize the time between nesting attempts, thereby increasing the nesting potential of a season. Copulations after egg-laying is complete, re-use of territories, and initiation of replacement clutches before nest construction is complete promote rapid replacement of destroyed clutches. An extension of the breeding season through molt-breeding overlap also increases the nesting potential.

In populations where 'r' is being maximized, MacArthur and Wilson (1967) stated that the emphasis is on production of offspring. In the Horned Grebe this is accomplished primarily by its large clutch size and parental behaviour. Theoretically, any increase in clutch size, up to a limit determined by the availability of resources, serves to increase the reproductive rate (Cody 1966). Mean clutch size of Horned Grebes at Minnedosa is 56 percent greater than that of *P. a. arcticus* which is adapted to northern climatic regions with low biological productivity (see Fjeldsa 1973a,c). The elaborate system of parental feeding observed at Minnedosa assists in increasing the production of young by reducing competition for food among brood members. The breeding strategy of the Horned Grebe reflects considerable evolutionary adaptation to fluctuating habitats and enables the species to exploit the high productivity of prairie marshes, despite their instability.

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