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BREEDING ECOLOGY AND PRODUCTIVITY OF
RED-NECKED GREBES IN TURTLE
MOUNTAIN PROVINCIAL PARK, MANITOBA

by

KENNETH D. DE SMET

BACHELOR OF SCIENCE, UNIVERSITY OF MANITOBA, 1977

A Thesis
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This thesis submitted by KENNETH D. DE SMET in partial fulfillment of the requirements for the Degree of MASTER OF SCIENCE from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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This Masters thesis meets the standards for appearance and conforms to the style and format requirements of the Graduate School of the University of North Dakota, and is hereby approved.

A William Johnson

Dean of the Graduate School

Title BREEDING ECOLOGY AND PRODUCTIVITY OF RED-NECKED GREBES IN TURTLE MOUNTAIN PROVINCIAL PARK, MANITOBA

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Degree MASTER OF SCIENCE

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Date June 24, 1983

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ABSTRACT

The breeding biology and productivity of the Red-necked Grebe (Podiceps grisegena) were studied in Turtle Mountain Provincial Park, Manitoba, during 1980 and 1981. Arrival dates ranged from mid-April to early June. Pre-nesting intervals ranged from 11 to 42 days and averaged about 20 days. Egg-laying commenced in early May and extended until mid-July. The average clutch size (4.95 eggs) was much larger than those found in other studies of the Red-necked Grebe in North America.

Although the nest success rate was low (26.2%), most failed pairs (83.5%) initiated at least 1 replacement clutch, and more than one-half of the observed pairs successfully hatched 1 or more chicks. Predators, primarily the Raccoon (Procyon lotor), were believed responsible for about half of the egg losses. High residue levels of several pesticides, particularly DDE and PCBs, were believed to have contributed to the low nesting success. About one-quarter of the viability-tested eggs during this study were considered inviable. Ratcliffe indices revealed that thin-shelled eggs were produced and several cracked eggs were found.

Average incubation periods calculated during this study (28-29 days) were longer than the 22-23 day incubation period generally recognized in the literature. Hatching occurred throughout June and July. Successful pairs hatched an average of 2.5 young, but raised only 1.9 young to the age of 1 month. High pesticide loads may have contributed to many of the losses that occurred during pre- and post-hatching stages. Later, intraspecific aggression probably

contributed to significant differences in individual mortality rates within large and small broods. Because losses during the second month were minimal, Red-necked Grebes during this study fledged 1.8-1.9 young/successful pair or about 0.9 young/breeding pair.

INTRODUCTION

The Red-necked Grebe is a Holarctic species with distinct western and eastern races separated by a wide gap in central Siberia. The nominate subspecies (Podiceps grisegena grisegena) occurs in eastern Europe and western Asia, whereas P.g. holboelii occurs in eastern Asia and northwestern North America. A third race (P.g. balchaschensis) has been described from Kazakhstan (Dolgushin 1960 in Sage 1973), although many believe it to be a long-winged form of P.g. holboelii (Cramp and Simmons 1977).

The North American breeding distribution of the Red-necked Grebe extends from northern Alaska and the Mackenzie Delta, south to Oregon and Idaho, and east to Wisconsin, Michigan, and Quebec (Fig. 1). In fall, the species migrates to the coast, wintering in 2 discrete areas: 1) along the Pacific coast from southwest Alaska to California; and 2) on the Atlantic coast from Newfoundland to central Florida (Fig. 1). Although banding data are limited, Palmer (1962) and Riske (1976) suspected that Red-necked Grebes wintering along the Pacific coast occupied the western portion of the breeding range, and birds wintering in the Atlantic nested primarily in the east.

My interest in the Red-necked Grebe stemmed from the fact that it has consistently appeared on American Bird's Blue List, a list designed to provide early warning for North American species experiencing long-term non-cyclical declines. Although population declines have been noted in Europe (Wobus 1964, Ahlen 1970, Fiala 1974, Cramp and Simmons 1977) and North America (Riske 1976, Tate 1981), minimal information is available regarding its reproductive biology and

Figure 1. North American breeding and winter ranges of the Red-necked Grebe (modified from Palmer 1962 and De Smet 1982). Turtle Mountain Provincial Park is indicated by an asterisk.


Breeding range
Winter range

productivity. In North America, Bent (1919) and Munro (1941) remain the most widely quoted sources, even though their information was based on casual observations of a few breeding pairs. Brief articles by Speirs et al. (1944), Cringan (1957), Mink and Gibson (1976), and Chamberlin (1977) dealt with nesting of isolated Red-necked Grebe pairs. Palmer (1962) summarized available information on the breeding biology of North American populations.

Probably the best sources of nesting information on the Red-necked Grebe in North America are unpublished graduate studies. These include a 2-year study of factors affecting the nesting dispersion of Red-necked Grebes on Astotin Lake, Alberta (Kevan 1970), and a 6-year study of human and environmental impacts upon the distribution, abundance, and reproductive success of 5 grebe species in central Alberta (Riske 1976). In Europe and Asia, the nesting biology of the Red-necked Grebe has been more extensively studied and was summarized by Wobus (1964), Dement'ev et al. (1968), Sage (1973), and Cramp and Simmons (1977). Comparisons between the European and North American subspecies are not always valid, however, because the nesting biology of European Red-necked Grebes is largely influenced by competition for resources with the larger Great Crested Grebe (Podiceps cristatus) (Fjeldsa 1973a, Cramp and Simmons 1977).

The objectives of this study were: 1) to assess factors influencing productivity of Red-necked Grebes in a relatively unmodified and undisturbed setting; and 2) to expand available knowledge on the reproductive biology of the North American subspecies.

METHODS

Turtle Mountain Provincial Park was considered an ideal site for this study because large numbers of Red-necked Grebes were known to nest there (De Smet and Smith 1979) and because lakes in the western half of the park were accessible yet experienced only limited recreational pressure. Field work was conducted from 3 May-22 August 1980 and from 9 April-4 September 1981. Roadways in the western half of the park were traversed daily, weather permitting, and nesting lakes were scanned with 10 x 50 binoculars or a 20-power spotting scope.

During the pre-nesting period, potential nesting lakes were scanned each day to determine arrival chronology, the pairing status of returning birds, and post-arrival activities. Clutch initiation was usually signaled by the presence of an incubating adult. Because premature incubation was common, however, eggs were only a certainty if they could be seen from shore or if the incubating adult shuffled onto its nest and opened its brood patch upon settling. During egg-laying, most nests were checked at 1-4 day intervals. Water depth, nest constituents, anchorage, and distance to the closest and farthest shores were usually determined during one of the initial nest checks. Distances up to 15 m were measured with a rope marked off at 1 m intervals; distances of 15-610 m were calculated with a rangefinder; and distances in excess of 610 m were determined from aerial photographs. At a later date, a compass and rangefinder were used to calculate the degrees of open water exposure for each nest at distances of 122, 366, and 610 m.

Exact egg-laying times were rarely obtained, but by checking nests at irregular intervals and noting the degree of nest-staining incurred by the most recent additions, egg-laying dates were determined for most eggs. Unmarked eggs were numbered in laying sequence with a waterproof marker and measured to the nearest 0.25 mm with Vernier calipers. Clutches were considered complete when subsequent nest checks revealed that no new eggs had been laid for at least 3 days. The maximum number of eggs found in a nest at any one time was recorded as the complete clutch size, even in cases where eggs were known to have disappeared prior to clutch completion. Although this practice deflated complete clutch size averages, it was deemed necessary because at least some early egg losses were replaced.

After clutch completion, the frequency of nest checks was reduced to about once every week. The nests continued to be monitored on a daily basis, however, through observations from a shoreline position. Because incubation was continuous beyond the second or third egg, a nest was suspected destroyed if neither adult was within the nest vicinity. Although no birds were color-marked or banded, daily observations confirmed that pairs usually remained on their respective territories after nesting losses. In instances where some doubt existed, the data for initial and replacement clutches were excluded.

Nests that were destroyed were usually examined immediately for clues to the causative agent. Depredation was suspected whenever eggshell fragments were found within or near a destroyed nest. "Probably depredated" clutches included those where no trace of eggshell fragments were found despite the entire clutch having disappeared between nest checks. Wave-related losses were suspected when nests were found in a largely disintegrated condition, particularly after high winds or storms. Deserted nests were detected by the presence of cool eggs and the unkempt appearance of the nest. Among other forms of egg loss, a distinction was made between single eggs disappearing between nest checks, more than 1 egg disappearing between nest checks, and eggs located beside unflooded nests (because differing factors were probably responsible for these losses).

During 1981, 29 eggs were collected next to active nests or from deserted clutches. Ratcliffe indices (Ratcliffe 1967) were calculated for these eggs after the shells had been rinsed with water, air-dried for several months, and weighed to the nearest 0.0001 g. The contents of these and 14 other displaced eggs were placed in aluminum foil or plastic bags and frozen. These were later packed in dry ice and sent to the Ontario Research Foundation where pesticide residue analyses were conducted. Due to financial restraints, the sample size for residue analyses was limited to 12 eggs. Among these, 8 were from clutches deserted during egg-laying or soon after completion, 2 were addled eggs from deserted partial clutches, and 2 were freshly-laid eggs collected beside an active nest and from a rarely observed clutch. Organochlorine and polychlorinated biphenyl (PCB) levels were determined utilizing capillary gas chromatography combined with electron capture techniques. Mercury analyses were carried out by cold vapor atomic absorption spectrophotometry. Although data are presented in wet and lipid weights, discussion on organochlorine and PCB residues are limited to lipid weight data because of great variations in the wet weight of eggs collected in different conditions of dessication and decomposition.

As hatching neared, 1-4 day intervals between nest checks were resumed. Hatching success and approximate hatching times were determined for most eggs by listening for peeping within the eggs, finding eggs during the pipping stage, or observing freshly-hatched eggshells. Although young chicks were not always visible, their presence was usually indicated by the puffed-up appearance of an incubating adult. Occasionally, an accurate count of the number of young was made when chicks peered out from underneath the adult's wing feathers or briefly got off the adult's back. Normally, however, brood size determinations were only feasible when a nest or guard relief occurred (at which time the young were temporarily dumped into the water or onto the nest rim). Consequently, the number of young in each brood was not determined on a daily basis and, in some instances, several days transpired between accurate brood counts. As a result, many eggs disappeared during the hatching period and were listed as "possibly hatched."

After the young began spending more time on the water, accurate brood counts were more readily obtained. Later, however, some families began splitting and the subgroups occasionally left the nesting territory for varying amounts of time. In large lakes or heavily populated bays, locating all the young and determining brood survival during this period was difficult to impossible. Although most families were monitored at irregular intervals throughout the first month, data on survival during the second month and on departure were only available for a few families each year.

Field data were statistically analyzed using tests described by Snedecor and Cochran (1967). Nomenclature of North American birds follows Peterson (1980). Scientific names for mammals and plants follow Banfield (1974) and Scoggan (1978), respectively.

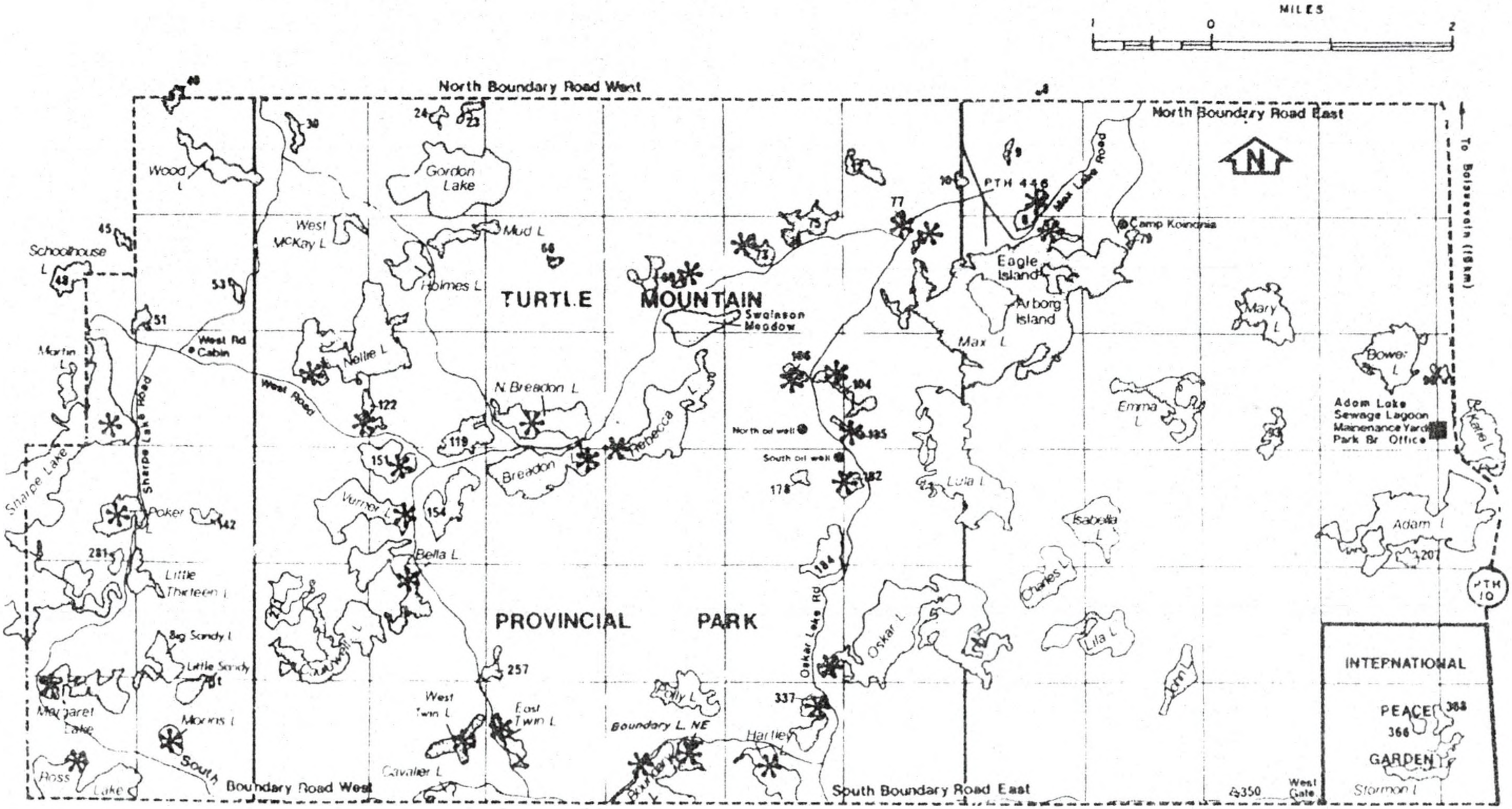
STUDY AREA

Turtle Mountain Provincial Park is located in southwestern Manitoba, immediately adjacent to PTH #10 and the International Peace Gardens on the east and the Canada/United States border on the south (Fig. 2). It is situated about 15 km south of Boissevain and 215 km southwest of Winnipeg. A large Community Pasture lies immediately east of PTH #10 and comprises much of the remainder of Manitoba's Turtle Mountains.

The Turtle Mountains are actually a range of morainic hills that rise 243 to 320 m above the surrounding plains (Cassel and Stewart 1968). The bedrock consists of Tertiary shale and limestone that has been covered with boulder fill (Weir 1960). The end moraine has resulted in a knob and kettle type of topography with numerous poorly drained depressions (Ransom 1969). Over 400 small to medium-sized lakes are located within Turtle Mountain Provincial Park. Because most of these were unnamed, a numbering system devised by De Smet and Smith (1979) was used in referring to unnamed study lakes.

Detailed discussions of the floral components of Turtle Mountain Provincial Park were presented in Disrud (1968), De Smet and Smith (1979), and Guinan and Rewcastle (1982). Upland areas are dominated by Trembling Aspen (*Populus tremuloides*), Beaked Hazelnut (*Corylus cornuta*), and Wild Sarsaparilla (*Aralia nudicaulis*). In imperfectly drained sites, these species are replaced by Balsam Poplar (*Populus balsamifera*), willows (*Salix* spp.), and sedges (*Carex* spp.). In open-water areas, Sago Pondweed (*Potamogeton pectinatus*), Clasping-leaf Pondweed (*P. richardsonii*), coontails (*Ceratophyllum* spp.),

Figure 2. Map of Turtle Mountain Provincial Park indicating the study lakes (marked with asterisks).


MILES
1
0
2
North Boundary Road West
North Boundary Road East
To Boissevain (15km)
TURTLE MOUNTAIN
PROVINCIAL PARK
Wood L
Gordon Lake
Schoolhouse L
West McKay L
Mud L
Holmes L
Swainson Meadow
PTH 446
Max Lake Road
Camp Koinonia
Eagle Island
Arborg Island
Max L
Mary L
Bower L
Emma L
Adam Lake
Sewage Lagoon
Maintenance Yard
Park Br Office
Karel L
Martin L
West Rd Cabin
West Road
Sharpe Lake Road
Sharpe Lake
Nellie L
N. Breadon L
Breadon
Rebecca L
North oil well
South oil well
Lula L
Verner L
Bella L
Poker
Little Thirteen L
Big Sandy L
Little Sandy
Margaret Lake
Morins L
Ross Lake
South Boundary Road West
South Boundary Road East
Cavalier L
West Twin L
East Twin L
Polly L
Boundary L. NE
Hartley
Oskar Lake Rd
Oskar L
Isabella L
Charles L
Lila L
John L
Adam L
PTH 10
INTERNATIONAL
PEACE
GARDEN
Stormon L
West Gate
40
30
24
23
45
48
53
51
66
73
75
77
10
9
8
79
106
104
105
102
122
119
151
154
142
281
178
184
257
337
93
207
366
388
350

water-milfoils (Myriophyllum spp.), duckweeds (Lemna spp.), stoneworts (Chara spp.), and filamentous algae prevail. Dominant shoreline emergents include Common Cattail (Typha latifolia), bulrushes (Scirpus spp.), bur-reeds (Sparganium spp.), Whitetop (Scolochloa festucacea), and sedges.

RESULTS AND DISCUSSION

SPRING ARRIVAL

a) Chronology

With the approach of spring, Red-necked Grebes begin to congregate on coastal waters in the central and northern portions of their winter range (Bent 1919, Palmer 1962). Although some lone birds venture inland as early as mid-February, these invariably depart within a few days (R. D. McRae pers. comm.). Even in years when the spring migration is advanced, influx at most inland locations is delayed until March (Table 1). On average, arrival dates range from mid-March to early April along the migration route to mid-April and early May at nesting lakes.

Wobus (1964) contended that the arrival of Red-necked Grebes on nesting lakes in Germany was not determined by ice breakup dates. In western Ontario, however, Cringan (1957) noted that Red-necked Grebes arrived during ice breakup in 3 of 4 study years, and 3.5 weeks before breakup during an exceptionally cold spring. Riske (1976) also contended that arrival of Red-necked Grebes coincided with when the ice cleared in nesting lakes of central Alberta. A brief reconnaisance of the Turtle Mountain study area on 26 April 1980 revealed that all nesting lakes were free of ice, but only a few Red-necked Grebes were present. In 1981, lakes were open when field work commenced on 9 April, yet arrival was delayed until 18 April. Although these observations indicated that Turtle Mountain Red-necked Grebes arrived several days to weeks after spring breakup; unusually warm spring

Table 1. Red-necked Grebe arrival chronology at localities along the migration route and at probable breeding sites in Canada.

Locality	Reference	Number of years observed	Earliest arrival date	Average arrival date
Migratory sites				
Okanagan Lake, B.C.	Munro 1941	3	1-29 Mar	17 Mar
Okanagan Lake, B.C.	R. Cannings[a]	10	25 Feb-26 Apr	28 Mar
Alberta	Sadler and Myres 1976	7	22 Apr-12 May	28-29 Apr
Winnipeg, Man.	Lawrence 1933-1954	8	23 Apr-10 May	28 Apr
Winnipeg area, Man.	R. Koes[a]	6	13 Apr-4 May	24 Apr
Pinawa, Man.	Lawrence 1939-1940	2	26-29 Apr	27-28 Apr
Pinawa area, Man.	P. Taylor[a]	4	15 Apr	25 Apr
Barrie, Ont.	Devitt 1967 in J. M. Speirs[a]	11	-	10 Apr
Kingston, Ont.	R. Weir[a]	15	3 Mar	7 Apr
Toronto, Ont.	Saunders 1947 in J. M. Speirs[a]	15	4 Apr	22 Apr
Probable breeding sites				
Pike Lake, Alta.	Riske 1976	3	29 Apr-3 May	1 May
Astotin Lake, Alta.	Kevan 1970	1	29 Apr	-
Fort Sam, Sask.	Lawrence 1950-1953	4	22 Apr-11 May	29-30 Apr
Delta Marsh, Man.	Lawrence 1944-1945	2	20-23 Apr	21-22 Apr
Turtle Mountains, Man.	This study	1	18 Apr	-
Western Ontario	Cringan 1957	4	29 Apr-6 May	3 May
Manitoulin Island, Ont.	J. Nicholson[a]	7	30 Mar	16 Apr

[a] Personal communication

temperatures across the prairies during 1980 and 1981 (Gollop 1980, 1981) probably contributed to this phenomenon. During other years, it is possible that arrival and spring breakup dates are more closely linked.

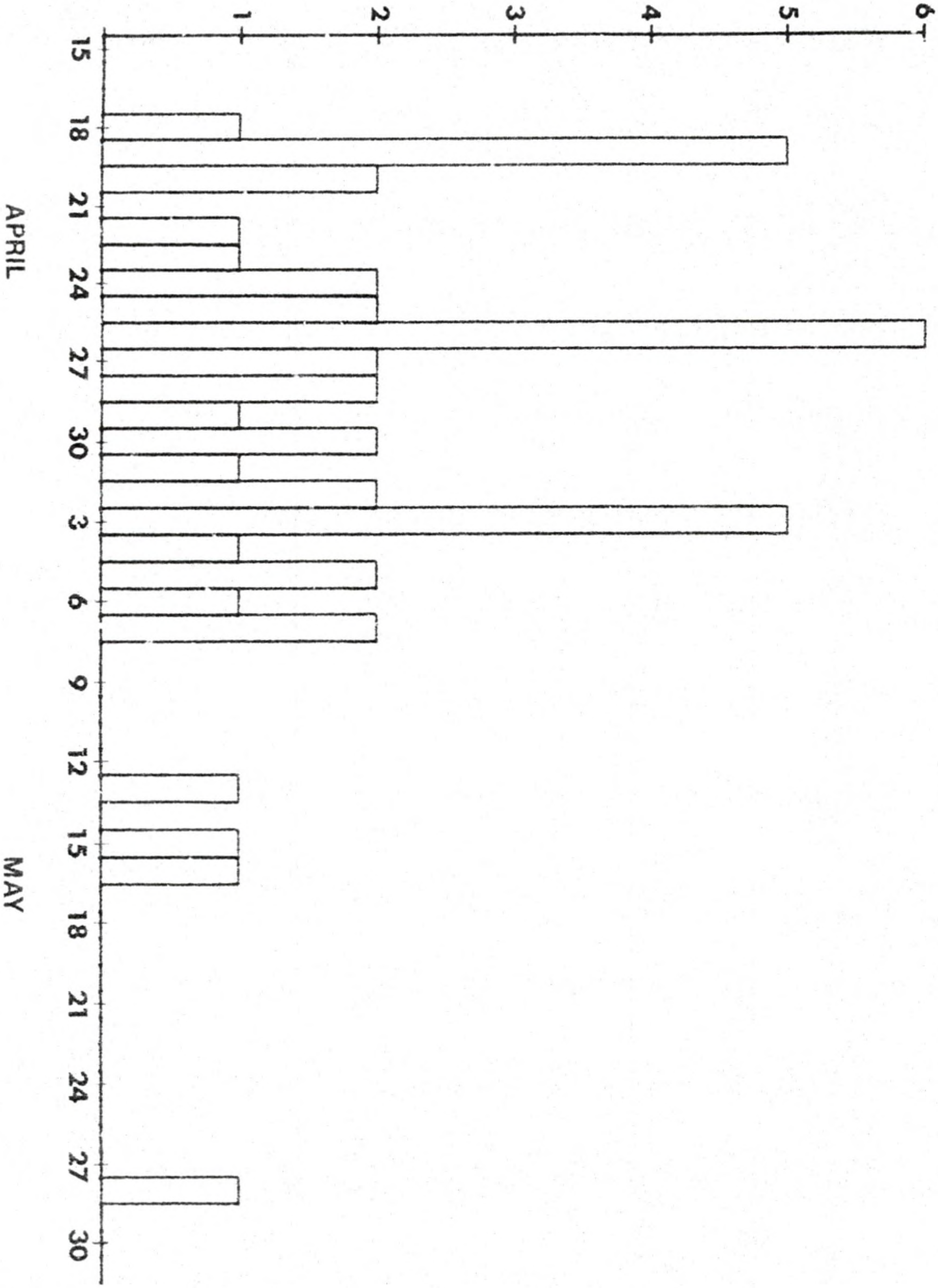
Arrival chronology for Red-necked Grebes on 45 territories in 1981 is indicated in Figure 3. More than one-quarter of the population returned within a week of the first arrivals and about one-half returned within 10 days. During both years, arrival progressed steadily until 7-10 May (at which time about 90% of the eventual nesting population were on territory), yet influx of breeding pairs continued until late May and early June.

b) Mate and Territory Fidelity

Since no long-term banding and recapture studies have been conducted on Red-necked Grebes, their mating status and territory fidelity is poorly documented. Although Bent (1919), Munro (1941), Yocom et al. (1958), and Palmer (1962) observed large numbers of unmated Red-necked Grebes during migration and on the wintering grounds, Dement'ev et al. (1968) and Sage (1973) maintained that Red-necked Grebe pairs migrated together and that they probably mated for life. Although it is likely that some Red-necked Grebes mate with the same partner in successive years, I believe that this is facilitated by territorial attachment rather than a year-round pairing. No Red-necked Grebes were banded during this study, but territory fidelity was demonstrated by at least 1 female (identified by a broken upper mandible) that nested within the same territory on Boundary Lake during both years. Because Turtle Mountain Red-necked Grebe pairs

Figure 3. Arrival dates for 45 Red-necked Grebes on nesting territories during 1981.

NEWLY OCCUPIED TERRITORIES



invariably emigrated separately after raising young (see page 87), sustained monogamy was unlikely. Ferguson (1981) also believed that Horned Grebes (Podiceps auritus) were not monogamous and suspected that territorial attachment facilitated pair-bond renewal.

During this study, Red-necked Grebes returned unpaired and subsequently mated in about 15% of the eventual territories. Upon returning, other pairs were unsynchronized in their actions and appeared recently mated. Several pairs were observed performing a Discovery Ceremony, a major element in the pair-forming process among grebes (Storer 1963, 1969, Fjeldsa 1973c), on their first day on territory. From this, I believe that many Red-necked Grebes in my study area paired upon or immediately preceeding arrival on their nesting lakes. Many of these probably mated within large assemblages along the migration route and subsequently dispersed to their nesting lakes. Such assemblages have been reported by Munro (1941), Palmer (1962), Kevan (1970), and Riske (1976), and one was noted on Rabb Lake (3 km southeast of my study area) during late April and early May, 1981 (Calvin Henry pers. comm.).

TERRITORY ESTABLISHMENT

a) Nest Site and Territory Selection

Soon after arrival, Red-necked Grebes began searching for potential nest sites around which they established their territories. At these sites, pairs usually constructed from 1 to several platforms, any one of which eventually became the nest. These platforms are essential for copulation, although Red-necked Grebes have been observed copulating on submerged logs (Johnstone 1953), on artificial nest structures (Kevan 1970), or in open water (Wobus 1964, Hemming 1968, this study).

On 3 occasions, I observed site-searching behavior by unmated Red-necked Grebes. These birds swam along shoreline emergents "bobbing" their heads back and forth in a coot-like manner similar to that displayed by Horned Grebes during nest site selection (Ferguson 1977). Occasionally they would stop near an emergent clump and dive, surfacing within or just outside the emergents. At other times, they peered beneath the surface, presumably checking the underwater environs of potential nest sites. The idea that this behavior constituted nest site selection was reinforced by later observations of pairs conducting similar diving, peering, and bobbing behavior after destruction of an earlier clutch.

b) Territory Types and Sizes

Within the Turtle Mountains, type A (mating, nesting, and feeding) territories were predominant in all lakes. Even where 3 or 4 pairs occupied a lake, type A territories were adhered to and the adults rarely ventured from their territories. Type B (mating and nesting) territories were occasionally noted when several pairs nested within the bay of a large lake. In such situations, non-incubating adults often swam into undefended areas outside the bay during feeding sessions. Although Wobus (1964) and Kevan (1970) reported some type D (nesting only) territories, none were noted in the Turtle Mountains.

In the Turtle Mountains, single pairs of Red-necked Grebes nested in lakes ranging from 1.8 to 25.9 ha in size (Table 2). Riske (1976) also noted few Red-necked Grebe pairs nesting in lakes of less than 2.0 ha, but Wobus (1964) reported Red-necked Grebes nesting on lakes as small as 0.4 ha. As maximum breeding densities for Europe, Wobus (1964) recorded 5 pairs (3 breeding) on a 4.8 ha lake and noted other nesting populations with densities of 3 pairs on a 1.1 ha lake, 5 pairs on 1.8 ha lake, and 30-35 pairs on a 68 ha lake. Within the Turtle Mountains, maximum breeding densities were found on Morins Lake (3 pairs within 8.8 ha) and Bella Lake (8-9 pairs within the 22.6 ha south arm and southwest bay). The densest nesting population was found on North Breadon Lake during 1980, however, where 9 pairs held territories within an area of about 20 ha on the west side and 4 occupied territories within an area of less than 4 ha in the westernmost end.

c) Intraspecific Territoriality

Despite numerous reports of Red-necked Grebes nesting within colonies, few articles present a thorough analysis of internest distances and relations between pertinent pairs. Early reports by Silloway (1902), Currier (1904), and Bent (1919) referred to Red-necked Grebe nesting colonies, but they presented little data. Among more

Table 2. Turtle Mountain lake or bay sizes and associated Red-necked Grebe pair densities during 1980 and 1981.

	Area (ha)	Breeding pairs		Regularly observed pairs	
		1980	1981	1980	1981
Lake E of Lake # 69	1.8	0	1	0	1
Lake E of Lake # 77	2.5	0	1	0	1
Max Lake (NE bay)	3.3	1	1	0	1
Lake # 105	3.5	1	1	1	1
Bella Lake (SW bay)	4.4	2	2	0	1
Lake # 77	4.7	1	1	1	1
Lake # 104 (N end)	5.1	1	2	0	1
Lake # 106	5.2	1	1	1	1
Boundary Lake Northeast	6.1	1	2	1	2
Lake # 182	8.1	1	1	1	1
Morins Lake	8.8	3	3	3	3
Margaret Lake (W end)	9.8	1	2	1	2
Lake E of Lake William[a]	10.1	1	0	1	0
Oscar Lake (W bay)	10.8	1	1	1	1
Lake # 6	11.2	2	3	2	3
East Twin Lake	11.4	2	2	1	2
West Twin Lake	11.6	2	2	1	1
Lake # 73	11.6	1	1	1	1
Lake # 122	13.4	1	1	0	1
Little Thirteen Lake	13.7	1	1	0	0
Bella Lake (S arm)	18.3	7	6	6	6
Lake # 337	21.9	4	3	4	3
Lake # 151	24.4	2	3	2	3
Poker Lake	25.9	1	1	1	1
Bella Lake (N arm)	26.1	1+	2+	1	1
Breadon Lake (E bay)	27.7	4	3	4	3
Boundary Lake (N bay)	33.8	2	5	2	5
North Breadon Lake	44.1	10	2	10	2
Verner Lake	51.2	5+	2+	1	2
Breadon Lake (minus E bay)	52.4	0	2	0	0
Max Lake (minus SE bay)	>60.0[b]	0+	1+	0	1
Rebecca Lake (SW end)	>60.0[b]	4+	2+	3	2
Nellie Lake (W end)	>60.0[b]	1+	7	0	1
Sharpe Lake (N end)	>60.0[b]	2+	5+	1	1
Ross Lake (N side)	>60.0[b]	0+	3+	0	2
Hartley Lake (NW end)	>60.0[b]	1	0	1	0
Totals		68+	76+	52	58

[a] Situated within the Turtle Mountain Community Pasture

[b] Exact lake size was not determined

detailed references, Cowan (1939) reported 61 Red-necked Grebes and many nests in a 0.4 ha emergent clump, and Munro (1941) found nests as close as 9 m apart. These, plus other references to Red-necked Grebe coloniality (i.e., Palmer 1962, Wobus 1964, Godfrey 1966, Harrison 1975, Cramp and Simmons 1977, Tessen 1977), made no mention of intraspecific relations within colonial-nesting populations.

Within the Turtle Mountains, territorial behavior was studied at a small (about 10 x 40 m) open-water clump of flooded willow stumps on North Breadon Lake. During the 1980 nesting season, 5 Red-necked Grebe pairs initiated 1 or more nests at this clump with up to 4 pairs nesting simultaneously. Most active nests were located at least 15 m from each other, but some were as close as 4 m. Territoriality between neighboring pairs was demonstrated throughout the breeding season, however, and probably contributed to 21 of 75 eggs (26.9%) laid at this site eventually being found in the water beside active clutches (compared to only 2.6% found in the water beside other Red-necked Grebe clutches from the Turtle Mountains).

Although territorial aggression occurred between all pairs occupying this clump, many involved one particularly aggressive pair (pair D). This pair continuously interfered with the late establishment of 2 pairs (F and X) about 20 m away. During one observation, I witnessed a confrontation where the non-incubating adult from pair D pecked the incubating adult from pair F until it vacated its newly-established nest. When F returned to its nest, it seemed unusually excited and occasionally peered into the water beside the nest. Two days later, a nest check revealed 2 eggs in the water beside this nest. Although no further encounters between these pairs were witnessed, at least 1 more egg rolled off F's nest before they moved to the other side of the clump. The other subordinate pair (X) also attempted to establish a nest in this area, but was unsuccessful due primarily to interference from pair D. Although pair X remained near the clump throughout June and was observed in several territorial conflicts with pairs D and F, 1 egg found near a platform that they had built was believed to be the extent of this pair's nesting efforts.

These observations confirm that territoriality exists within nesting aggregations that might appear colonial. In fact, colonialism in the true sense of the word (Welty 1962, p. 260) is probably never achieved by Red-necked Grebe nesting populations. Welty (1962, p. 259) noted "in certain cases large aggregations may not be true communities, but represent association forced by a lack of suitable nest sites." Fjeldsa (1973b) found colonial nesting aggregations of Norwegian Horned Grebes only where the birds might compensate for their small territories by utilizing extensive shallow-water feeding areas. In reference to populations of colonial grebes, Fjeldsa (1973b, p. 144) stated "a few cases could not be explained by a deficiency of normal nest sites, so social factors may also play a role." This may be true among some Great Crested Grebe populations; Harrison and Hollom (1932) noted nests placed so close together that they touched, in some lakes territoriality had largely disappeared, and up to 30 nests were found in clumps as small as 10 x 14 m. Among Red-necked Grebes, however, Kevan (1970) noted that the terms "solitary" and "colonial" have so far indicated only that in some areas the birds are more numerous than in others. Hence, until sociality among some Red-necked Grebe populations is demonstrated, use of the term "colonial" should be avoided in reference to nesting aggregations of this species.

d) Interspecific Territoriality

High levels of interspecific territoriality have been documented for several grebe species (Harrison and Hollom 1932, Kilham 1954, Kirby 1976, Riske 1976, Ferguson 1977). Munro (1941) and Wobus (1964), however, reported only isolated incidents where Red-necked Grebes attacked other species and Sage (1973) and Chamberlin (1977) observed interspecific conflicts only after the young had hatched. In contrast, nearly half of the regularly observed Red-necked Grebe pairs in the Turtle Mountains displayed some interspecific aggression. Although 82.1% of the observed interspecific encounters occurred during the pre-nesting and brood rearing phases (Table 3), these percentages were probably biased because more intensive observations were conducted during these stages.

Among the purported functions of grebe interspecific territoriality, Kilham (1954) and Kirby (1976) felt that species displaced by Pied-billed Grebes (Podilymbus podiceps) were morphologically similar or had identical food requirements. Ferguson (1977) witnessed a peak in Horned Grebe interspecific territoriality during egg-laying and incubation and listed 3 probable functions for this behavior: 1) defense of the pairing and nest platforms; 2) reducing competition for overwater nest sites; and 3) reducing the amount of egg depredation by opportunistic species. In the Turtle Mountains, dabbling ducks frequently rested or preened on Red-necked Grebe platforms, and platform defense probably accounted for most dabbling duck displacements. Mallards were the most frequently

Table 3. Number of interspecific encounters between Red-necked Grebes and other species during various stages of the nesting cycle.

Displaced species	Nesting stage				
	Pre-nesting	Egg-laying	Incubation	Brood rearing	Totals
Western Painted Turtle (*Chrysemys picta belli*)	-	1	-	-	1
Common Loon (*Gavia immer*)	-	-	-	1	1
Pied-billed Grebe (*Podilymbus podiceps*)	7	1	1	2	11
Horned Grebe (*Podiceps auritus*)	1	-	-	-	1
Eared Grebe (*Podiceps nigricollis*)	3	-	-	-	3
Double-crested cormorant (*Phalacrocorax auritus*)	2	-	-	-	2
Mallard (*Anas platyrhynchos*)	8	4	4	16	32
Blue-winged Teal (*Anas discors*)	2	-	-	7	9
Gadwall (*Anas strepera*)	2	1	-	-	3
Canvasback (*Aythya valisineria*)	4	2	-	-	6
Redhead (*Aythya americana*)	2	-	-	-	2
Ring-necked Duck (*Aythya collaris*)	8	1	1	5	15
Lesser Scaup (*Aythya affinis*)	2	-	-	-	2
Bufflehead (*Bucephela albeola*)	5	-	-	4	9
Hooded Merganser (*Lophodytes cucullatus*)	1	-	2	7	10
Ruddy Duck (*Oxyura jamaicensis*)	1	-	-	-	1
American Coot (*Fulica americana*)	1	1	-	1	3
Black Tern (*Chlidonias niger*)	1	-	-	-	1
Red-winged Blackbird (*Agelaius phoeniceus*)	1	-	-	-	1
Muskrat (*Ondatra zibethicus*)	2	2	-	-	4
Totals	53	13	8	43	117

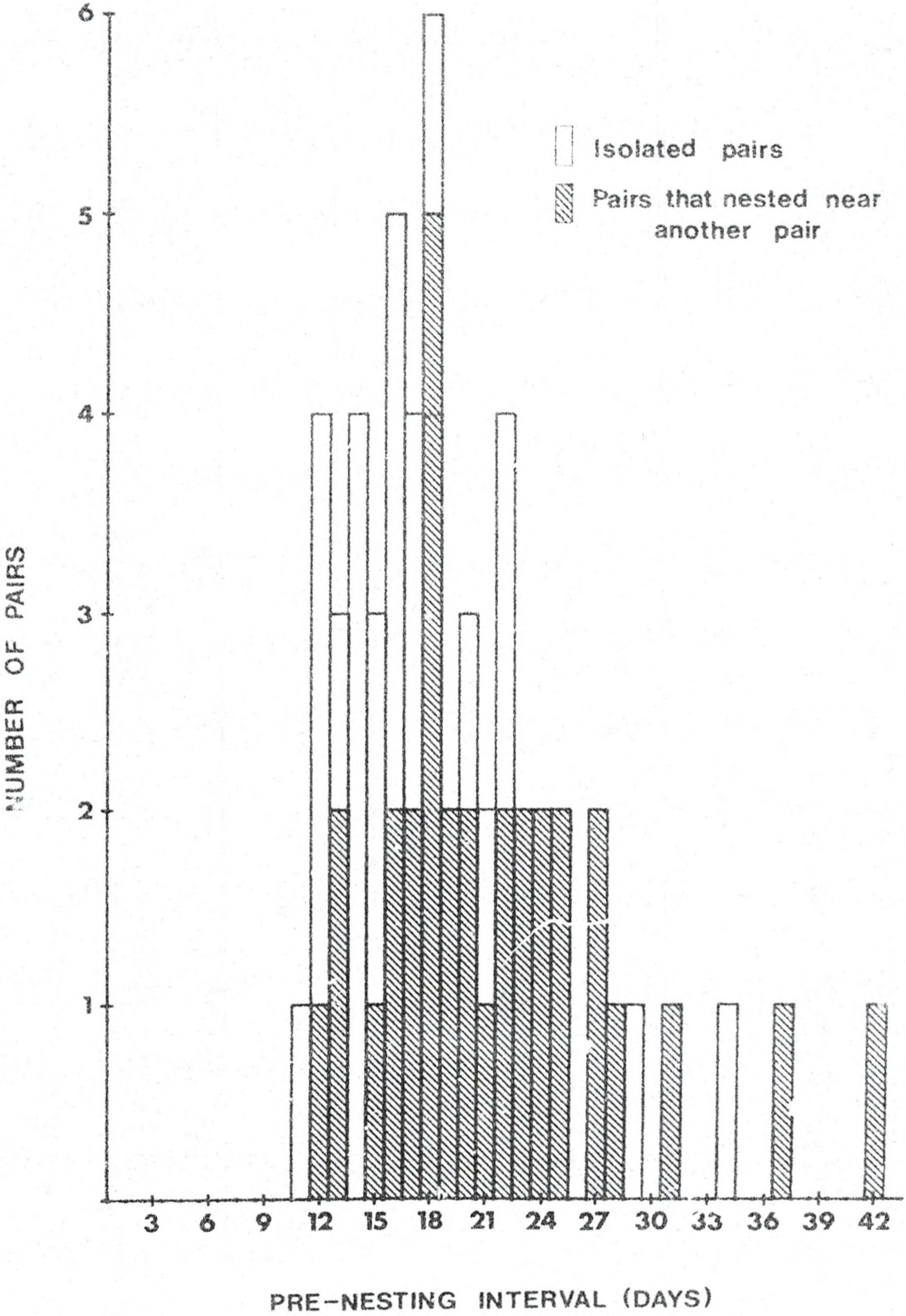
displaced species (Table 3), probably because they were the most plentiful duck in the park (De Smet and Smith 1979). Lone incidents where a Black Tern, Red-winged Blackbird, and Western Painted Turtle were displaced were also attributed to defense of the nesting platform.

During this study, I noted that Red-necked Grebes were more tolerant of dabbling duck species, but displaced most Pied-billed Grebes, Eared Grebes, Canvasbacks, Ring-necked Ducks, Buffleheads, and Hooded Mergansers that encroached upon their territory. These species were probably displaced because they are competitors for food and/or nesting sites. In instances where Redheads and Ruddy Ducks were displaced, however, the Red-necked Grebes may have been guarding against parasitism. Many Canvasback nests found in the Turtle Mountains during this study had been parasitized by Redheads and Ruddy Ducks, and 1 instance of Redhead parasitism on an active Red-necked Grebe nest was noted.

e) Pre-nesting Intervals

The pre-nesting interval refers to the length of time from arrival on a nesting lake until clutch initiation. Even when Red-necked Grebes arrived paired, Wobus (1964) found that they delayed clutch initiation for 2 or more weeks. In the Turtle Mountains, pre-nesting intervals determined for 55 Red-necked Grebe pairs ranged from 11 to 42 days and averaged 19.7 days (Fig. 4). On several occasions, pre-nesting intervals of less than 1 week were recorded; however, these invariably occurred on larger lakes that were not scanned completely. I later noticed that many pairs on larger lakes relocated after originally

Figure 4. Pre-nesting intervals for Red-necked Grebe pairs as related to the degree of isolation.


6
5
4
3
2
1
NUMBER OF PAIRS
Isolated pairs
Pairs that nested near another pair
3
6
9
12
15
18
21
24
27
30
33
36
39
42
PRE-NESTING INTERVAL (DAYS)

establishing in other areas of the lake. Consequently, arrival dates and pre-nesting intervals were only accepted for pairs on lakes that had been thoroughly scanned on a daily basis.

Among other grebe species, long pre-nesting delays have been attributed to several factors, including: 1) fluctuations in the food supply (Harrison and Hollom 1932, Fjeldsa 1973b, Simmons 1974); 2) high levels of intraspecific aggression (Harrison and Hollom 1932, Fjeldsa 1973b); 3) insufficient growth of emergent cover (Harrison and Hollom 1932, Fjeldsa 1973b, Simmons 1974); 4) delayed reproductive development of first-year birds (Fjeldsa 1973b); 5) water level fluctuations (Simmons 1974); and 6) inclement weather conditions (Simmons 1974, Ferguson 1977). Causes for pre-nesting delays among Red-necked Grebes have rarely been determined, although Kevan (1970) contended that intraspecific aggression was responsible in some instances.

Two factors that were probably responsible for delays in clutch initiation dates in the Turtle Mountains were high winds and intraspecific aggression. On many occasions, completed platforms were destroyed by waves during 1 or 2 days of high winds. Following this, most Red-necked Grebe pairs initiated construction of a new platform in a more sheltered portion of their territory. Intraspecific aggression probably contributed to significantly shorter pre-nesting intervals for 23 isolated Red-necked Grebe pairs ($\bar{X}$=17.1; SD=5.57) than for 32 pairs that nested near 1 or more other pairs ($\bar{X}$=21.5; SD=6.60) ($P<0.01$) (Fig. 4). Behavioral observations at dense-nesting sites (see page 22) also indicated that considerable interference occurred between pairs nesting near each other.

NEST PLACEMENT AND COMPOSITION

a) Placement and Anchorage Sites

Nest site selection by most grebes involves a response to the interrelated variables of water depth, proximity to open water, vegetation density, wave action, and proximity to shore (Gotzman 1965, Nuechterlein 1975, Ferguson 1977). Nest sites selected generally offer: 1) relatively unobstructed visibility and maximum distance to shore for protection against land predators; 2) proximity to deep, open water allowing easy access to and from the nest; and 3) solid anchorage, maximum distance to open water, and minimum distance to the opposite shore for protection against wind and waves.

Many studies report a nesting preference by Red-necked Grebes for smaller lakes or for bays connected to large lakes (Munro 1941, Wobus 1964, Kevan 1970). Gotzman (1965) contended that this apparent preference was due to suitable nesting habitat existing primarily within bays. Although this may be true on certain lakes, I believe that Red-necked Grebes in the Turtle Mountains selected territories with minimal amounts of wind and wave exposure. The data presented in Table 4 reveal that nests located in lakes smaller than 20 ha in size were significantly less exposed at distances of 366 m and 610 m than those in 20-30 ha lakes or those within bays of larger lakes. A fourth category of nests, those located within lakes exceeding 30 ha but not within well-enclosed bays, was significantly more exposed than nests within any of the other 3 categories ($P<0.001$). Nests within large lakes received additional wave protection by being situated in shallower water ($\bar{X}=50.1$; $SD=18.18$) than those in lakes of less than

Table 4. Average exposure measurements at Red-necked Grebe nests located within lakes of various sizes.

		Degrees of open-water exposure beyond:					
Lake size	N	122 meters		366 meters		610 meters	
		Mean	SD	Mean	SD	Mean	SD
<20 ha	74	96.26[a]	54.34	7.08[b]	12.18	0.88[c]	4.44
20-30 ha	47	124.11	60.46	26.26	21.87	2.49	5.47
Bays of larger lakes	42	109.98	57.03	27.12	24.01	5.81	9.46
>30 ha	57	176.86[d]	89.98	57.72[e]	39.24	28.18[f]	18.46

[a] Compared to mean for 20-30 ha ($P<0.001$)
Compared to mean for bays (NS)

[b] Compared to mean for 20-30 ha ($P<0.001$)
Compared to mean for bays ($P<0.001$)

[c] Compared to mean for 20-30 ha ($P<0.05$)
Compared to mean for bays ($P<0.001$)

[d] Compared to mean for 20-30 ha ($P<0.001$)
Compared to mean for bays ($P<0.001$)

[e] Compared to mean for 20-30 ha ($P<0.001$)
Compared to mean for bays ($P<0.001$)

[f] Compared to mean for 20-30 ha ($P<0.001$)
Compared to mean for bays ($P<0.001$)

30 ha ($\bar{X}$=60.0; SD=21.13) (P<0.001) (Fig. 5).

In addition to being protected from wind and waves, grebe nests should ideally be firmly anchored, readily accessible, and situated a safe distance from shore. In the Turtle Mountains, Red-necked Grebes met these requirements by nesting within open-water submergents (29.2%), by nesting within open-water emergent clumps or near the open water/emergent vegetation interface (25.6%), or by anchoring their nests to sticks, stumps, or to the lake bottom (23.7%) (Table 5). Even nests located within emergent bands (21.5%) were rendered accessible by being situated in sparse to medium-density vegetation and/or next to an open-water channel. Average distance to the closest shore ranged from 12.0 m for nests anchored to beaver food caches to 38.5 m for nests anchored to flooded willow stumps.

b) Water Depths

Water depths at 219 Red-necked Grebe nests located during this study averaged 54.9 cm (Table 5). Variability in average water depths found among studies of the Red-necked Grebe are probably related to local habitat differences. In the Turtle Mountains, nests anchored to beaver food caches were in much deeper water ($\bar{X}$=79.3 cm) than those anchored to the lake bottom ($\bar{X}$=38.7) or to flooded willow stumps ($\bar{X}$=42.5) (Table 5). On Astotin Lake, Kevan (1970) found most Red-necked Grebe nests within sedge clumps and reported a shallow average water depth (42 cm). Gotzman (1965) and Ricke (1976) reported average water levels of about 60 cm at Red-necked Grebe nests and a preponderance of nests within bulrush. In Manitoba's Waterhen region, Bent (1919) reported unusually high average water depths (90-122 cm)

Figure 5. Water depths at 107 Red-necked Grebe nests in smaller lakes compared to depths at 112 nests in larger lakes of the Turtle Mountains.

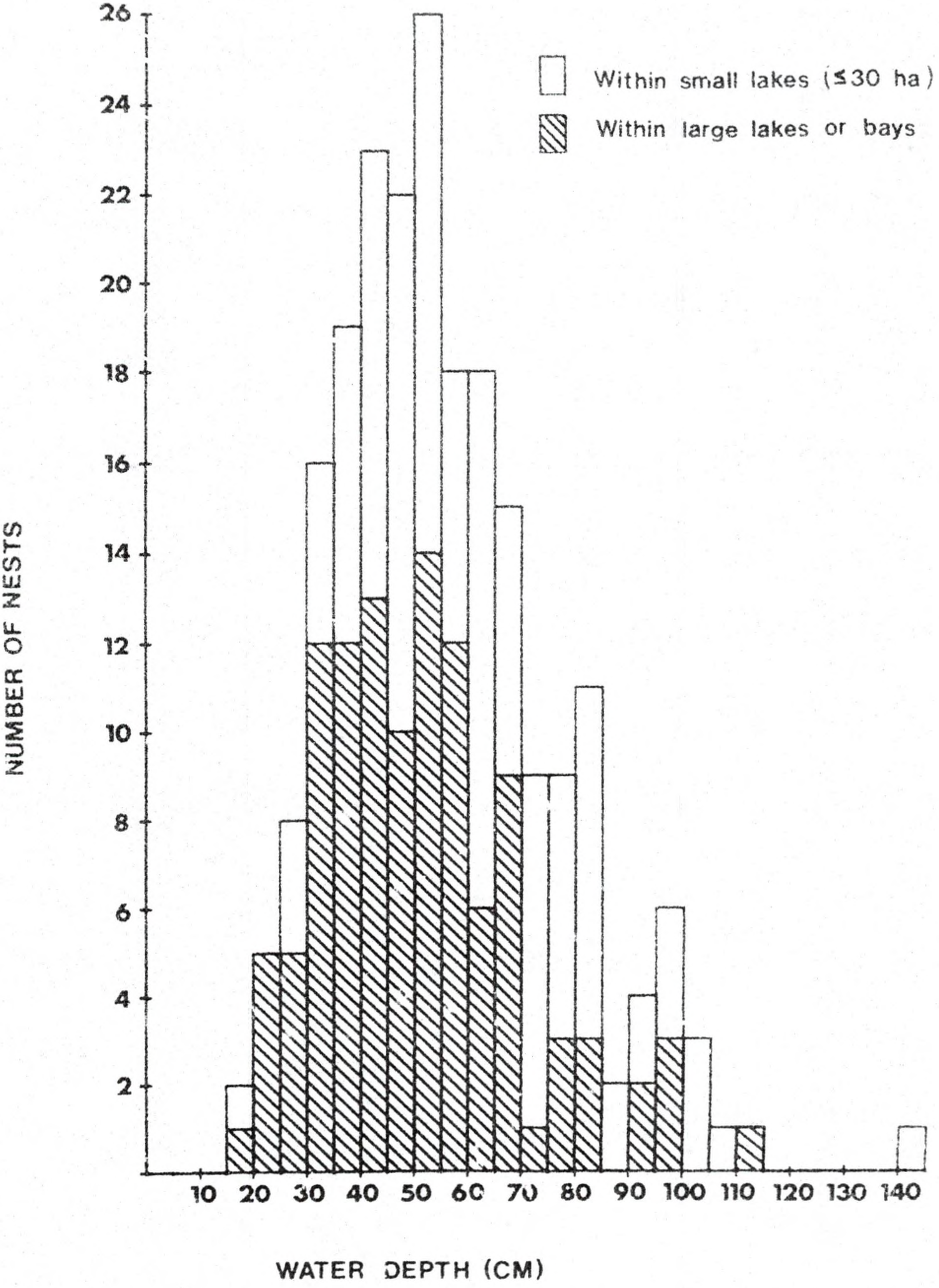

NUMBER OF NESTS
26
24
22
20
18
16
14
12
10
8
6
4
2
10 20 30 40 50 60 70 80 90 100 110 120 130 140
WATER DEPTH (CM)
□ Within small lakes (≤30 ha)
▨ Within large lakes or bays

Table 5. Red-necked Grebe anchorage sites and associated nest site characteristics for 219 nests in the Turtle Mountains. Data are presented in order of ascending distance to the closest shore. Sample size is given in parentheses when it differed from N.

Anchorage site	N	Distance to closest shore (m)	Distance to farthest shore (m)	Water depth (cm)
To a beaver food cache	9	12.0	142.2	79.3
Edging a shoreline emergent band	19	12.7	95.7	54.1
Within open-water emergent clumps	37	14.8 (35)	79.6 (35)	50.0
Within a shoreline emergent band	11	15.2	79.6	57.3
To the lake bottom (offshore reef)	6	20.5	33.6	38.7
To a log or branches in open water	8	33.9 (6)	95.5 (6)	53.9
Within an open-water emergent band	36	37.2	115.3	58.3
To submergents	64	38.1	158.3	58.9
To flooded willow stumps	29	38.5 (28)	180.5 (28)	42.5
Means	219	24.0 (214)	125.6 (214)	54.9

and located Red-necked Grebe nests primarily in reeds (<u>Phragmites</u> spp.). This was probably related to the fact that reeds are dense, shallow-water emergents that provide suitable anchorage only during temporary periods of high water (Nuechterlein 1975). Within the Turtle Mountains, no Red-necked Grebe nests were anchored to reeds.

Red-necked Grebe nests in the Turtle Mountains were found in water depths of 15-140 cm, yet more than 96% of the nests were in water depths of 20-100 cm (Fig. 5). Kevan (1970) also gave 20 cm as a minimum depth for Red-necked Grebe nests and recorded 3 instances where nests in shallow water were stranded following a drop in water level. Hence, Red-necked Grebes probably select sites of greater than 20 cm to avoid stranding nests during incubation and to allow swimming access to and from the nest throughout incubation. Maximum water depths were usually limited by availability of suitable anchorage objects, but even when deep-water anchorage sites were available, Red-necked Grebes usually preferred depths of less than 1 m. I attributed this preference to an apparent positive correlation between water depth and wave action.

c) Nest Constituents

The nest materials in 217 Red-necked Grebe nests found during this study were separated into major components (the predominant nest constituent) and minor components (those which occurred within a nest but did not constitute the major component) (Table 6). Bulrushes and decayed vegetation were the major component in about one-quarter of the nests. Other major components that occurred in 5-15% of the nests were filamentous algae, Sago Pondweed, Clasping-leaf Pondweed, coontails,

Table 6. Composition of 217 Red-necked Grebe nests during 1980 and 1981 indicating the percentage of nests where each constituent occurred as a minor or major component.

Nest components	Minor components(%)		Major components(%)	
	1980	1981	1980	1981
Submergents				
Filamentous algae	20.2	15.0	10.6	1.8
Stoneworts (*Chara* spp.)	6.7	3.5	1.9	4.5
Sago Pondweed (*Potamogeton pectinatus*)	20.2	14.2	8.6	14.2
Clasping-leaf Pondweed (*P. richardsonii*)	8.6	4.5	7.7	2.7
Other pondweeds	9.7	2.7	4.8	0.9
Coontails (*Ceratophyllum* spp.)	18.3	20.4	7.7	6.2
Duckweeds (*Lemna* spp.)	-	0.9	-	-
Pond-lily (*Nuphar variegatum*)	2.9	2.7	-	-
Water-milfoils (*Myriophyllum* spp.)	1.9	16.5	1.9	19.4
Bladderworts (*Utricularia* spp.)	3.8	-	-	-
Subtotal submergents			43.2	49.8
Emergents				
Horsetails (*Equisetum* spp.)	-	1.8	-	1.8
Cattails (*Typha* spp.)	1.9	15.9	2.9	1.8
Bur-reeds (*Sparganium* spp.)	-	-	1.0	-
Reed (*Phragmites communis*)	-	0.9	-	-
Whitetop (*Scholochloa festucacea*)	-	2.7	1.0	1.8
Bulrushes (*Scirpus* spp.)	20.2	25.7	23.1	21.2
Sedges (*Carex* spp.)	1.9	0.9	3.8	-
Spike rushes (*Eleocaris* spp.)	1.0	-	-	-
Subtotal emergents			31.8	26.6
Other components				
Decayed vegetation	26.0	15.0	24.0	23.9
Mud and roots	26.0	9.7	-	-
Sticks	36.5	39.8	1.0	-
Subtotal other components			25.0	23.9

and water-milfoils. Although sticks were rarely the major component, they represented a minor component in more than one-third of the nests. Other nest materials that occurred as a minor component in more than 15% of the nests were filamentous algae, Sago Pondweed, coontails, bulrushes, decayed vegetation, and mud.

Red-necked Grebe nests and courtship platforms were generally composed of materials found within a few meters of the nest. Nevertheless, adults often swam out some distance during nest-building activities, apparently searching for preferred components. During early nest-building stages, buoyant materials were selected to provide the nest with its floating capability. Bulrushes appeared to be preferred because they were often common in nests at least 50 m from emergents. Even more noticeable, however, was the Red-necked Grebe's preference for sticks. During nest building bouts, adults were frequently observed tugging at the same stick time and again until it was freed or a piece broke off. Occasionally, sticks were carried in from such a distance that several minutes and the participation of both adults was required to carry them to the nest.

LAYING DATES AND CLUTCH SIZES

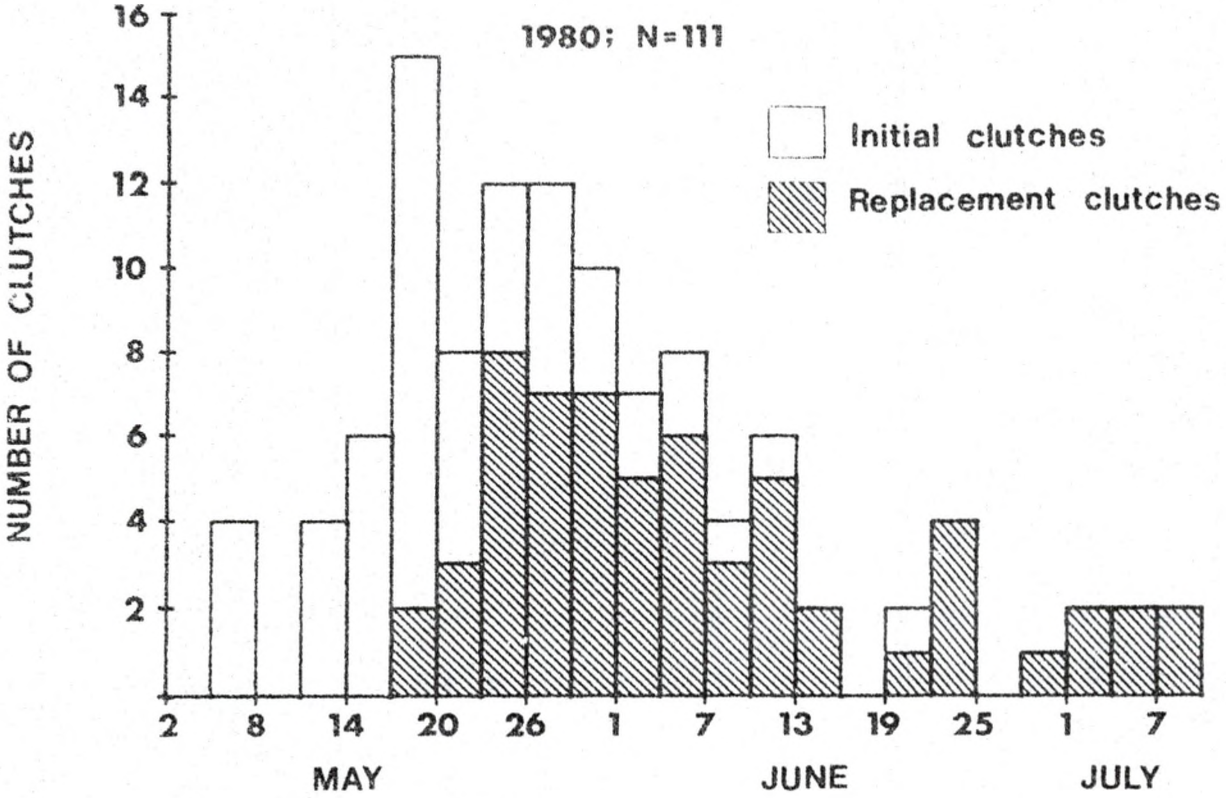
a) Clutch Initiation Dates

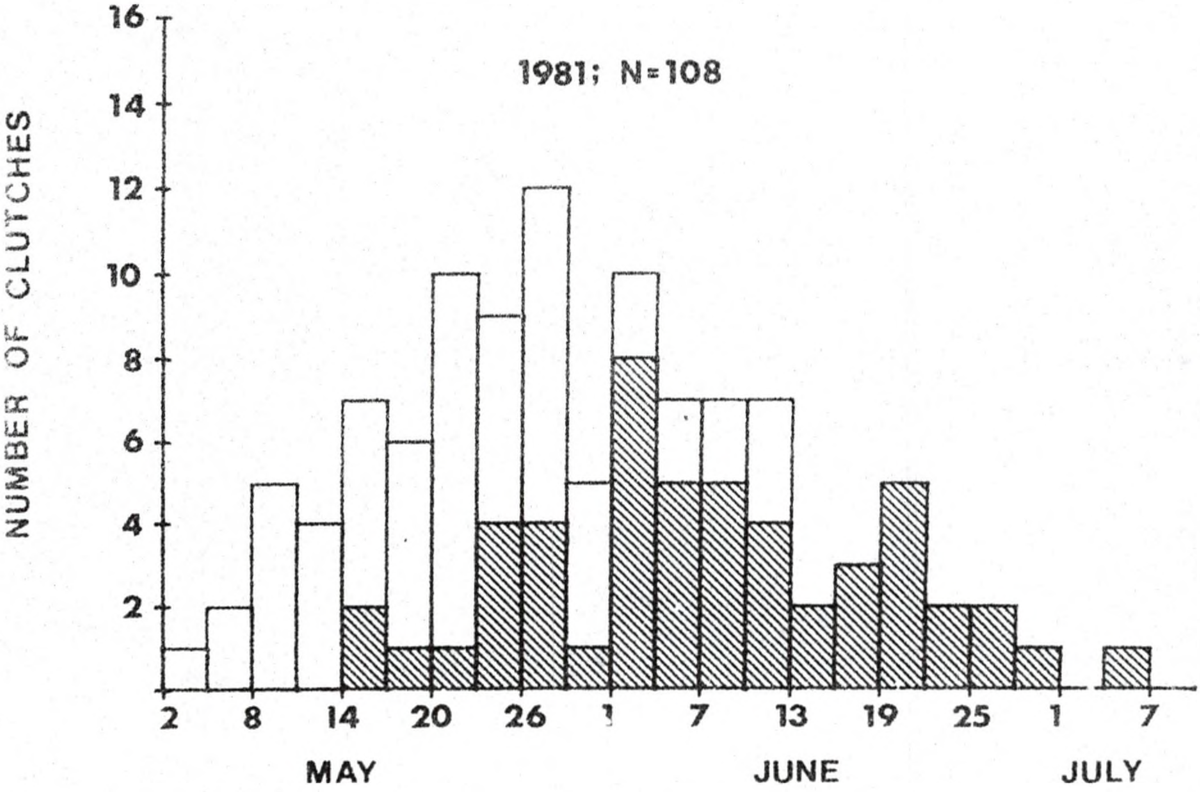
Clutch initiation dates for the initial and replacement nests of 108 Red-necked Grebe pairs that were regularly observed are indicated in Figure 6. Nesting commenced on 5 May 1980 and 4 May 1981. More than 85% of the population began nesting before the end of May and no initial nests were established beyond 19 June 1980 and 12 June 1981. Renests constituted 30.3% of the nests initiated in May and 81.6% of the nests initiated during June and July. Final replacement clutches were initiated on 9 July 1980 and 6 July 1981.

b) Egg-laying Intervals

Wobus (1964) noted that even in cases of great disturbance, the interval between successive Red-necked Grebe eggs was 2 days. In the Turtle Mountains, the egg-laying interval for Red-necked Grebes frequently was less than 2 days. Several instances were noted where new eggs appeared every 1 to 1.5 days. This was best illustrated by a pair on Breadon Lake that produced a 6-egg clutch in less than 6 days and produced 2 eggs in between nest checks 22.5 hours apart. In many instances, the egg-laying cycle was reduced by at least 1 day (i.e., 4-egg clutches were laid in 5 days, 5-egg clutches in 7 days, and 6-egg clutches in 9 days). Rarely was the egg-laying interval extended beyond 2 days. In some instances where extended intervals were noted, this was followed by a spurt in egg production (2-3 eggs appearing in rapid succession). On other occasions, the entire cycle was prolonged.

Figure 6. Three-day totals for the number of clutches initiated by regularly observed pairs of Red-necked Grebes during 1980 and 1981.


1980; N=111
Initial clutches
Replacement clutches
NUMBER OF CLUTCHES
16
14
12
10
8
6
4
2
2
8
14
20
26
1
7
13
19
25
1
7
MAY
JUNE
JULY


1981; N=108
NUMBER OF CLUTCHES
16
14
12
10
8
6
4
2
2
8
14
20
26
1
7
13
19
25
1
7
MAY
JUNE
JULY

c) Complete Clutch Sizes

In the Turtle Mountains, complete clutch sizes ranged from 2-9 eggs, with 95% of the clutches containing 3-7 eggs (Table 7). The average size of complete clutches from the Turtle Mountains ($\overline{X}$=4.95) was significantly larger than the average clutch size for Red-necked Grebes from Pike Lake, Alberta ($\overline{X}$=3.97) (Table 7). Red-necked Grebe clutch sizes on Astotin Lake, Alberta, were smaller ($\overline{X}$=4.62), but this difference was not significant ($P>0.05$).

Reasons for the larger average clutch size of Turtle Mountain Red-necked Grebes were not obvious. The mean clutch size for "early" nests (initiated in May or early June) from the Turtle Mountains was 5.10, compared to "early" means of 5.18 reported by Kevan (1970) and 5.05 found by Riske (1976). In all 3 studies, 5-egg clutches were predominant and 4- to 6-egg clutches comprised the majority (71-83%) of the early nests. Although "late" nests (initiated after 15 June) in the Turtle Mountains were larger ($\overline{X}$=3.86) than those for Astotin Lake ($\overline{X}$=3.14) or Pike Lake ($\overline{X}$=3.46), this difference was not significant (Table 7). Among late nests, 4-egg clutches were the mode during this study, compared to modes of 3 eggs in both Alberta studies.

Although Wobus (1964), Kevan (1970), and Riske (1976) noted seasonal declines in Red-necked Grebe clutch sizes, regression coefficients and exact data on initial and replacement clutch sizes were lacking. Utilizing complete clutch sizes from the Turtle Mountains, regression coefficients of -0.05 and -0.06 eggs per day were calculated for 45 initial and 55 replacement clutches, respectively (Fig. 7). Although replacement clutch sizes tended to be larger than

Table 7. Complete clutch sizes for "early" (initiated during May or early June), "late" (initiated after 15 June), and all Red-necked Grebe nests from the Turtle Mountains compared to those from Alberta populations.

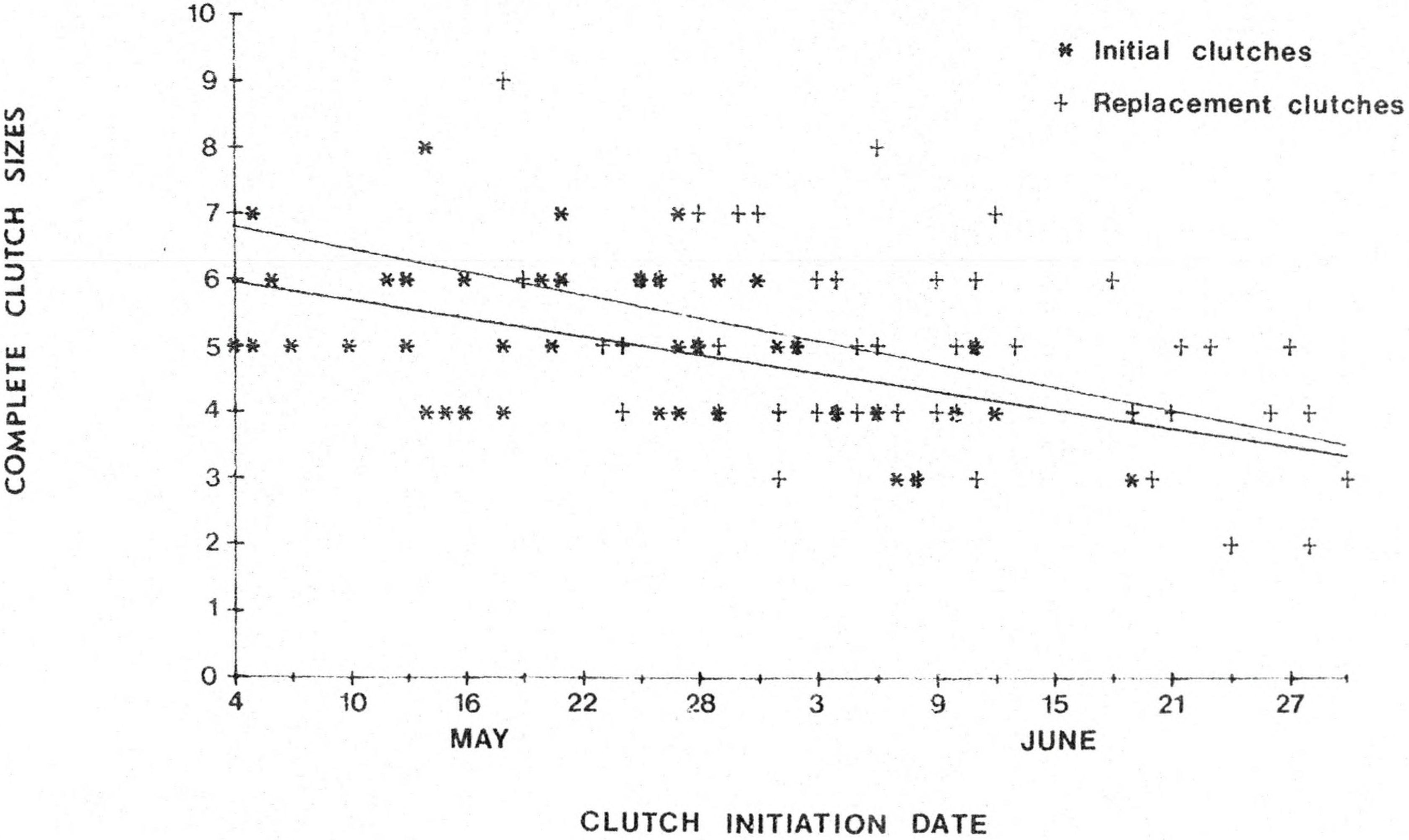
Study site (Reference)	Type of nest	N	Complete clutch size									Mean clutch size	SD
			1	2	3	4	5	6	7	8	9		
Turtle Mountains, Manitoba (This study)	Early	86	–	–	5	24	26	21	7	2	1	5.13[a]	1.22
	Late	14	–	2	3	5	3	1	–	–	–	3.86[b]	1.17
	Total	100	–	2	8	29	29	22	7	2	1	4.95[c]	1.28
Astotin Lake, Alberta (Kevan 1970)	Early	56	–	2	5	9	18	13	6	2	1	5.18	1.45
	Late	21	2	5	6	5	2	1	–	–	–	3.14	1.31
	Total	77	2	7	11	14	20	14	6	2	1	4.62	1.68
C. Alberta lakes and potholes (Riske 1976)	Early	40	–	–	4	7	17	9	2	–	1	5.05	1.20
	Late	46	–	6	21	12	6	1	–	–	–	3.46	0.96
	Total	86	–	6	25	19	23	10	2	–	1	4.20	1.34

[a] Compared to Astotin Lake mean (NS)
Compared to central Alberta mean (NS)

[b] Compared to Astotin Lake mean ($P<0.1$)
Compared to central Alberta mean ($P<0.1$)

[c] Compared to Astotin Lake mean ($P<0.1$)
Compared to central Alberta mean ($P<0.001$)

Figure 7. Red-necked Grebe clutch size variation in relation to the start of egg-laying within 45 initial and 55 replacement clutches from the Turtle Mountains.


COMPLETE CLUTCH SIZES
10
9
8
7
6
5
4
3
2
1
0
* Initial clutches
+ Replacement clutches
4
10
16
22
28
3
9
15
21
27
MAY
JUNE
CLUTCH INITIATION DATE

initial clutch sizes on any given date, covariance analysis indicated that this tendency was not significant (F=3.37; 1,97 df; P>0.05). Fjeldsa (1973b) also found that Horned Grebe renests contained more eggs than initial nests established at the same time. He postulated that previous experience, behavioral coordination between the mates, and success in establishing territories contributed more to the final clutch size than calendar date.

Red-necked Grebe clutches exceeding 7 eggs are reportedly rare. Kevan (1970) located 3 nests with 8-9 eggs on Astotin Lake that she believed were not the result of joint laying. Others, including Cringan (1957), Palmer (1962), Sage (1973), Riske (1976), and Cramp and Simmons (1977), however, suspected that Red-necked Grebe clutches containing more that 6 eggs were "dump" nests (i.e., having been laid by more than one female). In all instances where 7-9 eggs constituted the complete clutch size during this study, I was reasonably certain that no dumping had occurred. The 9-egg clutch, for example, was produced by 1 of 3 pairs on Morins Lake during 1981. In this clutch, 10 eggs were laid at approximate 2-day intervals between 18 May and 4 June, but the seventh egg rolled out of the nest soon after it was laid. Daily observations revealed that this pair began continuous incubation soon after clutch initiation, and allowed neither of the other Red-necked Grebe pairs onto their territory. Likewise, in other larger clutches produced during this study, egg-laying occurred at approximate 2-day intervals and no territorial breakdowns were observed.

d) Egg Sizes

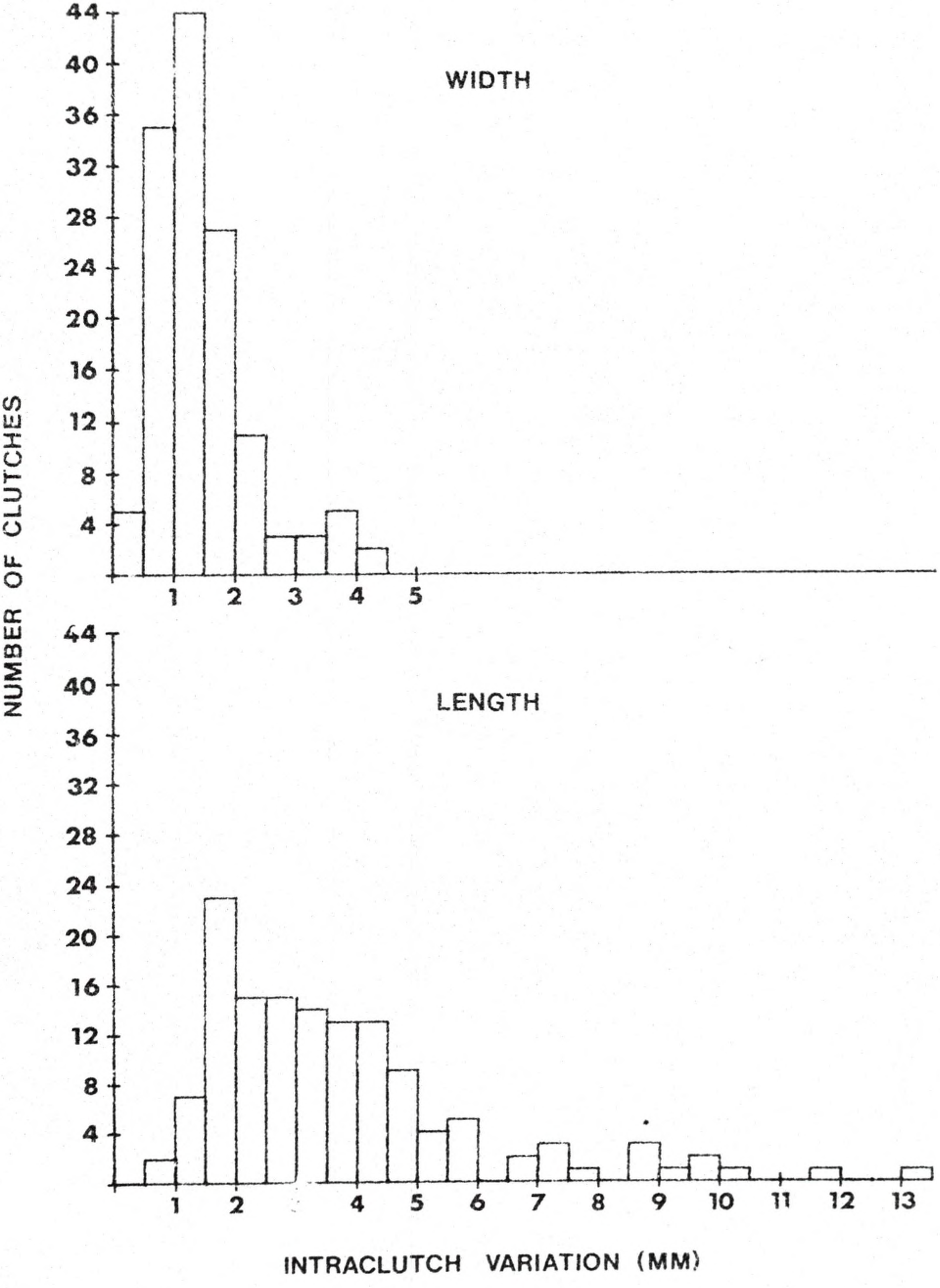
Mean length and width of 923 Red-necked Grebe eggs from the Turtle Mountains were 54.3 mm and 35.8 mm, respectively. These values were slightly shorter and wider than the combined average for 182 Red-necked Grebe eggs from previous North American studies (Table 8). Excluding 2 unusually small eggs (43.5 x 29.0 mm and 42.0 x 31.0 mm) that may have been laid in active Red-necked Grebe nests by nearby Pied-billed Grebes, and 1 small egg (29.3 x 22.0 mm) that was probably laid by a Red-necked Grebe, Turtle Mountain eggs ranged in length from 45.[illegible]-52.5 mm and in width from 32.5-39.5 mm.

Kevan (1970) indicated that intraclutch variation in egg length and width of Astotin Lake Red-necked Grebes was slight (maximum of 7 mm and 5 mm, respectively). These figures were quite substantial, however, when compared to the maximum length and width variance in her entire sample (10 mm and 9 mm, respectively). In the Turtle Mountains, maximum intraclutch variation in length (13.25 mm) was more pronounced than maximum intraclutch width variation (4.25 mm) (Fig. 8). Among 135 Red-necked Grebe clutches with 4 or more eggs, intraclutch variation in length averaged 3.6 mm (SD=2.27), compared to an average width difference of only 1.3 mm (SD=0.82). One pair that consistently alternated between a small egg and a large egg throughout its laying cycle, had length differences of up to 13.25 mm between successive eggs and corresponding width differences of only 3.25 mm.

Table 8. Measurements for 923 Red-necked Grebe eggs from the Turtle Mountains compared to those for 182 eggs from other North American studies.

Reference	N	Egg length (mm)		Egg width (mm)	
		Mean	SD	Mean	SD
This study	923	54.3	2.63	35.8	1.13
Bent (1919)	60	53.7	-	34.5	-
Palmer (1962)	20	55.7	2.25	36.1	1.24
Kevan (1970)	102	54.9	2.20	35.7	1.67

Figure 8. Width and length variation within 135 Red-necked Grebe clutches composed of 4 or more eggs.


WIDTH
LENGTH
NUMBER OF CLUTCHES
44
40
36
32
28
24
20
16
12
8
4
1
2
3
4
5
44
40
36
32
28
24
20
16
12
8
4
1
2
4
5
6
7
8
9
10
11
12
13
INTRACLUTCH VARIATION (MM)

NEST LOSSES

a) Egg Success and Causes for Nest Losses

Among 697 eggs found in regularly observed Red-necked Grebe clutches during this study, at least 550 (78.9%) failed to hatch (Table 9). In less frequently observed clutches, the percentage of eggs that were unsuccessful (71.5%) was similar taking into account the higher proportion of possibly hatched eggs. In total, Red-necked Grebe egg success in the Turtle Mountains ranged from 16.4 to 22.3% (depending on whether "possibly hatched" eggs were excluded or included, respectively).

Although low nesting success by grebes has rarely been attributed to depredation, I contend that predators were the primary reason for the low egg success recorded during this study. In regularly observed clutches, 197 eggs (28.3%) were depredated, 13 eggs (1.9%) were deserted after an adult was killed on its nest, and 6 eggs (0.9%) were deserted after partial clutch depredation. In addition, 75 eggs (10.8%) from regularly observed clutches were listed as "probably depredated," and predators may have contributed to losses of 104 eggs (14.9%) that disappeared during incubation, 39 eggs (5.6%) found in the water beside unflooded nests, and 49 eggs (7.0%) that were deserted as entire clutches (perhaps after the death of one of the adults). In clutches that were infrequently observed, fewer nest checks resulted in more eggs disappearing, but percentages of predator-related losses were similar. In these, 6.6% of the losses were definitely predator-related, 28.5% were listed as "probably depredated," and predators may have contributed to losses among 34.3% more. Hence,

Table 9. Fate of 834 Red-necked Grebe eggs from 179 regularly observed clutches (88 pairs) and 29 infrequently observed clutches (20 pairs) from the Turtle Mountains.

Fate	Regularly observed clutches		Infrequently observed clutches	
	N	%	N	%
Eggs hatched	116	16.6	21	15.3
Eggs possibly hatched	31	4.4	18	13.1
Entire clutch depredated	197	28.3	9	6.6
Entire clutch probably depredated	75	10.8	39	28.5
Eggs deserted after an incubating adult was killed	13	1.9	0	0
Eggs deserted after partial clutch depredation	6	0.9	0	0
Eggs deserted after partial clutch hatching	48	6.9	3	2.2
Eggs deserted during egg-laying or incubation	49	7.0	14	10.2
Eggs located beside an active or unflooded nest	39	5.6	2	1.5
Single eggs disappeared between nest checks	62	8.9	7	5.1
More than 1 egg disappeared between nest checks	42	6.0	24	17.5
Nest flooded by waves	17	2.4	0	0
Eggs broken during handling	2	0.3	0	0

predators were believed responsible for about one-half of the egg losses in regularly and infrequently observed Red-necked Grebe clutches from the Turtle Mountains.

A discussion of potential predators in the Turtle Mountains was presented by De Smet (1982). Circumstantial evidence suggested that the Raccoon (*Procyon lotor*) was the major predator on Red-necked Grebe nests. Other species that were believed responsible for some egg and nest losses included Muskrats, American Coots, and Pied-billed Grebes. Losses to these species were especially prominent during early egg-laying stages, when incubation was incontinuous and interspecific boundaries were not yet clearly defined. Although several observers attributed major losses by nesting grebes to crow depredation (Rowan 1924, Simmons 1955, Cringan 1957, Wobus 1964, Riske 1976), egg-thieving by American Crows (*Corvus brachyrhynchos*) in the Turtle Mountains was considered rare. During this study, 3 incubating Red-necked Grebes were killed, probably by Mink (*Mustela vison*) or Great Horned Owls (*Bubo virginianus*).

Major nesting losses to wave action have been reported for several grebe species (Munro 1941, Speirs et al. 1944, Hanzak 1952, Glover 1953, McAllister 1958, Chabreck 1963, Broekhuysen and Frost 1968, Burger 1974, Nuechterlein 1975, Riske 1976). Monthly wind speed data for southwestern Manitoba issued by Atmospheric Weather Services (Winnipeg), however, revealed that wind speeds during the summer months of 1980 and 1981 were about 20% below normal. Accordingly, wind-related losses were slight and accounted for only 2.0% of the egg losses noted during this study.

Minor losses were also attributed to intraspecific conflicts and to incubating adults knocking eggs off their own nest. High rates of intraspecific aggression were noted where nests were dense, and were believed to have contributed to many eggs being found beside active nests at these sites (see p. 22). In addition, 69 single eggs disappeared from active clutches between nest checks. Incidental observations suggested that some of these were knocked out of active clutches during nest reliefs or while the adults adjusted nest materials (De Smet 1982).

b) Pesticides and Environmental Contamination

Physiological repression of reproduction due to pesticides manifests itself in numerous ways including reduced sperm production, delayed ovulation, decreased clutch sizes, eggshell thinning and breakage, altered incubation behavior, developmental abnormalities, and increased rates of pre- and post-hatching mortality (Riske 1976, Feerer and Garrett 1977). Most of the literature on grebes, however, indicates high egg fertility and little or no pesticide-inhibition of reproductive success. In European studies, infertility of grebe eggs was reported as rare to occurring in less than 5% of the eggs (Harrison and Hollom 1932, Hanzak 1952, Simmons 1955, Wobus 1964, Fjeldsa 1973b). Studies of the Western Grebe (Aechmophorus occidentalis) in North America (Nuechterlein 1975, Lindvall and Low 1980) revealed few abnormally thin-shelled or broken eggs. Riske (1976), however, located several thin-shelled and addled Red-necked Grebe eggs and contended that biocidal residues were partially responsible for population declines of 50-75% and production declines of 55-80% in central Alberta from 1970-1976. A second study that revealed possible pesticide inhibition dealt with the effects on Western Grebes of direct application of DDD into Clear Lake, California. No young were produced in this colony for 11 years following application of the pesticide, but by 1970 residue levels had dropped and reproduction was again approaching normal levels (Rudd and Herman 1972). A follow-up study in 1975, however, revealed large population declines, a 13% drop in average clutch size, significant eggshell thinning, several addled eggs, and abnormal incubation behavior (Feerer and Garrett 1977).

The viability of Red-necked Grebe eggs from the Turtle Mountains was assessed by determining the eventual fate of 191 eggs from 58 successful clutches (Table 10). Among these, 78.5% were viable and 21.5% were inviable. Egg inviability appeared to be the primary cause for egg abandonment following partial clutch hatching by Turtle Mountain Red-necked Grebes. Among 44 eggs deserted after partial clutch hatching, 18 were addled or undeveloped, 9 had died during development, 7 were probably inviable (subsequent eggs in the clutch had hatched prior to their disappearance), and only 10 (22.7%) were viable.

Even in instances where viable eggs were deserted, inviability among earlier eggs frequently contributed to their abandonment. Chicks begin peeping within Red-necked Grebe eggs 12 to 36 hours before they hatch (McAllister 1963 in Kevan 1970). This presumably prevents premature abandonment of viable eggs (Wobus 1964). If an inviable egg was the next egg scheduled to hatch, however, no peeping would occur for 1-3 days. The adult grebes might interpret this as a signal that the remainder of the clutch was inviable and consequently desert it. This was suspected on 3 occasions during this study when pairs with 2

Table 10. Percentages of viable and inviable eggs in successful Red-necked Grebe clutches from the Turtle Mountains.

Egg viability	N	%
Viable		
Definitely hatched	137	71.7
Eggs deserted after partial clutch hatching	10	5.2
Eggs located beside an unflooded nest	2	1.0
Egg broken during handling	1	0.5
Subtotal	150	78.5
Inviable		
Addled or undeveloped eggs deserted after partial clutch hatching	18	9.4
Eggs that advanced to the peeping or pipping stage but did not hatch	9	4.7
Eggs deserted after partial clutch hatching (probably inviable since subsequent eggs had already hatched)	7	3.7
Addled or undeveloped eggs located beside an unflooded nest	7	3.7
Subtotal	41	21.5

to 3 young abandoned their last 2 eggs. Upon examination of the abandoned eggs, the penultimate egg was addled but the final egg was viable. In another case, a pair with 2 young abandoned 3 viable eggs (No. 7-9) after 2 addled eggs (No. 5 and 6) failed to hatch.

Comparison of Ratcliffe indices for Red-necked Grebe eggs from the Turtle Mountains to those from other studies revealed that thin-shelled eggs were being produced. Ratcliffe indices calculated for 29 Turtle Mountain eggs from 21 clutches averaged 1.72 (SD=0.17). This mean was significantly less than the mean of 1.84 (SD=0.11) calculated by Faber and Hickey (1973) for 112 Red-necked Grebe eggs laid before 1947 ($P<0.001$). Riske (1976) calculated an even greater average index for 186 Red-necked Grebe eggs from central Alberta ($\bar{X}$=1.86), but statistical comparisons were impossible because a standard deviation was not given. Only one other collection, a 10-egg Red-necked Grebe sample collected in Wisconsin and Ontario (Faber and Hickey 1973), had equally low Ratcliffe indices ($\bar{X}$=1.66) when compared to those found in the Turtle Mountains.

Direct evidence that thin-shelled Red-necked Grebe eggs were being produced in the Turtle Mountains was collected in the form of broken eggs found in 2 clutches that were deserted during late egg-laying stages. Although Red-necked Grebe eggs were rarely handled during this study (except during egg-laying and hatching stages), I located 7 eggs within active clutches that were cracked. Because these eggs invariably disappeared soon after, many of the single eggs that disappeared in between nest checks (8.3%) may have been fragile eggs that broke under the weight of an incubating adult.

Analyzed Red-necked Grebe eggs from the Turtle Mountains contained appreciable residue levels of several pollutants (Table 11). The most concentrated of these were PCBs ($\overline{X}$=194.8 ppm) and DDE ($\overline{X}$=74.3 ppm). Average residue levels of 1-10 ppm were also noted for hexachlorobenzene HE, dieldrin, DDD, oxychlordane, and mirex. Although the wet weight data for mercury also indicated an appreciable residue level, data for several of the eggs were of questionable value because some samples appeared to have thawed and incurred slight albumen losses prior to processing.

Table 12 compares DDE, DDD, and PCB levels in eggs from the Turtle Mountains to those reported in other North American grebe investigations. The highest residue levels noted in any of these studies were from 3 Red-necked Grebe eggs collected in Rush Lake, Wisconsin, during 1970 (Faber and Hickey 1973). Unfortunately, circumstances surrounding the collection of this small sample were not reported. Other grebe studies have recorded DDE and DDD levels similar to or slightly higher than those found in the Turtle Mountains, but none recorded PCB levels as high as those found during this study. In fact, DDE and PCB levels found in eggs from the Turtle Mountains were more than 3 and 4 times greater than those found in eggs from a purportedly troubled population of Red-necked Grebes in central Alberta (Riske 1976). Although the effects of PCBs are still poorly understood, Dustman et al. (1971) concluded that populations laying eggs with PCB levels of 10 ppm or more should be investigated for population problems. Because Red-necked Grebe eggs from the Turtle Mountains contained more than 19 times that amount of PCBs, plus high levels of DDE and several other contaminants, pesticide residues probably contributed to the low reproductive success experienced by this population.

Table 11. Pollutant concentrations in 12 eggs collected from Red-necked Grebe clutches during 1981.

Pollutant	Wet weight conc.(ppm)		Lipid weight conc.(ppm)	
	Mean	SD	Mean	SD
1,2,3,5/1,2,4,5 - chlorobenzene	0.002	0.004	0.02	0.042
DDT	0.002	0.006	0.02	0.052
1,2,3,4 - chlorobenzene	0.003	0.003	0.03	0.028
Pentachlorobenzene	0.01	0.012	0.14	0.125
γ- chlordane[a]	0.05	0.033	0.48	0.369
α- chlordane	0.05	0.041	0.60	0.489
β - HCH	0.05	0.029	0.65	0.339
Mercury	0.11	0.025	–[b]	–[b]
DDD	0.11	0.075	1.18	0.926
HE[a]	0.15	0.093	1.79	1.118
Oxychlordane	0.17	0.111	2.02	1.273
Hexachlorobenzene (HCB)	0.18	0.113	2.01	1.254
Dieldrin	0.19	0.154	2.09	1.651
Mirex	0.58	0.494	8.11	8.655
DDE	6.30	4.358	74.26	43.488
PCB 1254/1260 (peak 2)	16.32	11.788	194.79	123.907
PCB 1254/1260 (peaks 1 & 2)	19.94	14.266	240.26	158.201

[a] Sample sizes for γ-chlordane and HE reduced to 10 and 4, respectively, because of the presence of an interfering peak.

[b] Lipid weight data not applicable because mercury is associated with proteins rather than lipids.

Table 12. DDE, DDD, and PCB residues (lipid weight basis) in Red-necked Grebe eggs from the Turtle Mountains compared to those in grebe eggs analyzed by other investigators.

Species Study site (Reference)	N	Average residues (ppm)		
		DDE	DDD	PCB
Pied-billed Grebe				
Wisconsin (Faber and Hickey 1973)	9	82.6	-	77.6
Horned Grebe				
Battleford, Sask. (Vermeer and Reynolds 1970)	10	88.4	-	-
Alberta potholes (Riske 1976)[a]	4	53.0	1.5	-
Central Alta. potholes (Riske 1976)	10	32.0	0.0	59.2
Eared Grebe				
Old Wives Lake, Sask. (Vermeer and Reynolds 1970)	10	6.9	-	-
Bassano, Alta. (Riske 1976)[a]	1	51.3	1.7	-
Calgary, Alta. (Riske 1976)	10	13.2	0.0	2.7
Watt Lake, Alta. (Riske 1976)	10	15.2	0.0	10.2
Western Grebe				
Clear Lake, Cal. (Herman et al. 1969)	17	142.2	298.7	-
Clear Lake, Cal. (Rudd and Herman 1972)	28	47.9	117.4	-
Cold Lake, Alta. (Vermeer and Reynolds 1970)	10	87.2	-	-
Jackfish Lake, Sask. (Vermeer and Reynolds 1970)	10	57.9	-	-
Duck Lake, B.C. (Riske 1976)[a]	11	57.2	6.0	-
Lac Ste Anne, Alta. (Riske 1976)	20	42.4	3.7	86.7
Bear River, Utah (Lindvall 1976)	40	76.5	14.9	4.0
Red-necked Grebe				
Rush Lake, Wis. (Faber and Hickey 1973)	3	646.8	-	744.6
Fort Saskatchewan, Alta. (Riske 1976)[a]	1	9.0	0.1	-
Pike Lake, Alta. (Riske 1976)	17	7.5	0.0	6.0
Other C. Alta. lakes (Riske 1976)	29	29.5	0.5	63.5
Turtle Mountains, Man. (This study)	12	74.3	1.2	194.8

[a] Eggs collected by R. W. Fyfe

RENESTING

a) Renesting Parameters

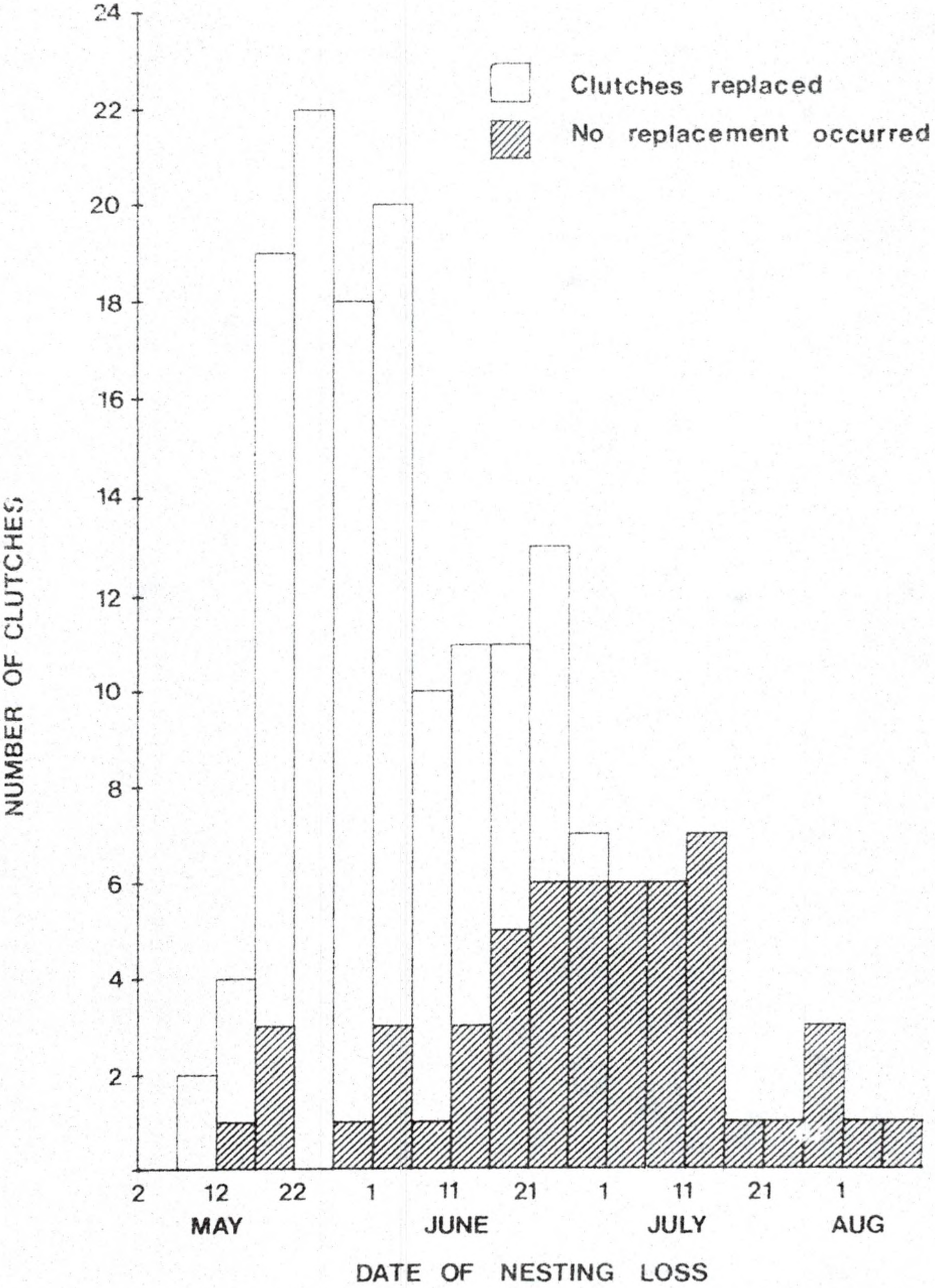
Although 79 of 110 regularly observed Red-necked Grebe pairs failed in their initial nesting attempts during this study, most (83.5%) initiated at least 1 replacement clutch and 6 pairs produced at least 5 clutches during a nesting season. Among the 13 pairs that did not renest, 5 abandoned their nesting lakes soon after nest losses during May. The other 8 pairs that failed to renest were among the small percentage of pairs that started egg-laying in June, half of which lost their initial nests in July and probably failed to renest due to time constraints. The rest incurred early to mid-June losses and remained on their nesting lakes, but they appeared to lack the drive to initiate a replacement clutch.

Figure 9 indicates the percentage of pairs that renested following losses at different stages of the nesting season. Of the clutches lost prior to June, 92.4% were replaced, and between early and mid-June, 82.9% of the lost clutches were replaced. After 15 June, however, percentages decreased sharply and none were replaced following losses later than 26 June. Among 7 renests initiated in early July, 6 were abandoned before clutch completion.

b) Replacement Intervals

The replacement interval refers to the number of days between destruction of a nest and initiation of a renest. Replacement intervals for Red-necked Grebes from the Turtle Mountains averaged 5.38 days, but varied according to the stage of nesting during which the

Figure 9. Parameters of renesting for Red-necked Grebes in the Turtle Mountains as indicated by 5-day total number of clutches replaced and not replaced following May to August nest losses.


Clutches replaced
No replacement occurred
NUMBER OF CLUTCHES
24
22
20
18
16
14
12
10
8
6
4
2
2
12
22
1
11
21
1
11
21
1
MAY
JUNE
JULY
AUG
DATE OF NESTING LOSS

previous loss occurred (Table 13). Losses incurred within a week of clutch initiation were replaced in an average 4.8 days, whereas losses incurred during the second, third, or beyond the third week of nesting were replaced in average times of 5.5, 6.0, and 8.9 days, respectively. Differences between replacement intervals during the first week, compared to beyond the first week were significant ($P<0.05$). When losses occurred during the first week of incubation, the laying cycle often was not interrupted and laying proceeded in a new nest within 1 or 2 days. When destruction occurred near clutch completion, however, the last egg(s) were occasionally deposited on a nearby platform and were not incubated. Other pairs built a new nest for their final egg(s) and eventually supplemented these with eggs from the next laying cycle. Upon destruction of complete clutches, 4-10 days usually elapsed before the female began egg-laying again.

c) Partial Replacement and Late Additions

Replacement of eggs in partially destroyed clutches has been reported for Horned Grebes (Ferguson 1977) and Red-necked Grebes (Riske 1976). In the Turtle Mountains, 1 or more eggs were added to at least 10 Red-necked Grebe clutches that incurred losses, but continued incubation and replacement after partial clutch losses was not universal. Abandonment occurred in at least 7 instances where partial clutch losses were incurred, usually when more than half of a larger clutch was suddenly decimated. When losses were more gradual, however, pairs often continued incubating even when only 1 egg remained.

Replacement following partial clutch losses was evident in at least 4 instances during this study. In 3 of these clutches,

Table 13. Replacement intervals following losses at various stages of egg-laying or incubation.

Stage of egg-laying or incubation when loss occurred	N	Replacement interval (days)	
		Mean	SD
During the first week	65	4.77	3.80
During the second week	20	5.50	3.10
During the third week	10	5.95	1.76
Beyond the third week	9	8.94	4.28

egg-laying began within a week after 3-5 eggs were lost, and 4 eggs were added. In the fourth instance, replacement commenced within a week after 6 of 7 eggs disappeared, but this clutch was destroyed soon after. In 6 other clutches that incurred losses of 1 or 2 eggs, however, the addition of a single egg well into incubation may not have been a deliberate attempt to replace former losses, but merely represent late additions.

Occasionally grebes add eggs to their clutch well after completion (see Lindvall 1976, Riske 1976, Ferguson 1977). Although these late additions are often assumed to be replacements for earlier losses, my research indicated that this was not always the case. On 3 occasions pairs added a single egg 1-3 weeks after clutch completion despite no losses having occurred. Another pair with a 5-egg clutch reinitiated egg-laying about a week after completion, producing a final clutch of 8 eggs. The possibility that these additions were laid by other females was considered remote because: 1) all 4 pairs were isolated; 2) incubating Red-necked Grebes seldom left their nests unattended following clutch completion; and 3) in no instance did incubating Red-necked Grebes allow an intruder near their nest.

The ultimate purpose of late additions to grebe clutches is not known. Riske (1976) speculated that these additions had a chance of contributing to overall production should most or all of the earlier clutch fail. Late additions to Turtle Mountain clutches, however, were invariably deserted following partial clutch hatching or disappeared along with the remainder of the clutch. I contend that many of the late eggs in the Turtle Mountains represented accidental or unpurposeful additions to the clutch. An autopsy of a female that was killed while incubating a completed clutch on Bella Lake revealed many developing ova of different sizes up to 20 mm in diameter. These ova probably contribute to rapid replacement after clutch losses; however, I believe that some ova develop in instances where no loss has occurred and these are added to completed clutches.

d) Second Clutches

Second clutches (those laid while raising some young from an earlier nest) are rarely found among Red-necked Grebes (Wobus 1964, Mink and Gibson 1976, Riske 1976). Within the Turtle Mountains, many pairs nested early and hatched only 1 or 2 young. In many instances, I expected these to initiate a second clutch, yet only 1 second clutch was attempted out of 110 pairs of Red-necked Grebes that were regularly observed.

Wobus (1964) and Simmons (1974) indicated that second clutches among grebes are usually initiated when young from the first clutch are more than a month old. Fjeldsa (1973b), however, found that Horned Grebes initiated second clutches from 13 to 69 days after hatching young from the first nest. In the second clutch that I located on Margaret Lake during 1981, 2 unusual occurrences took place. Eggs from both clutches were laid in the same nest, but laying of the second clutch commenced 1-2 days before hatching of the first. Unfortunately, this second clutch was destroyed soon after completion and the pair raised only 1 immature from the first clutch.

HATCHING

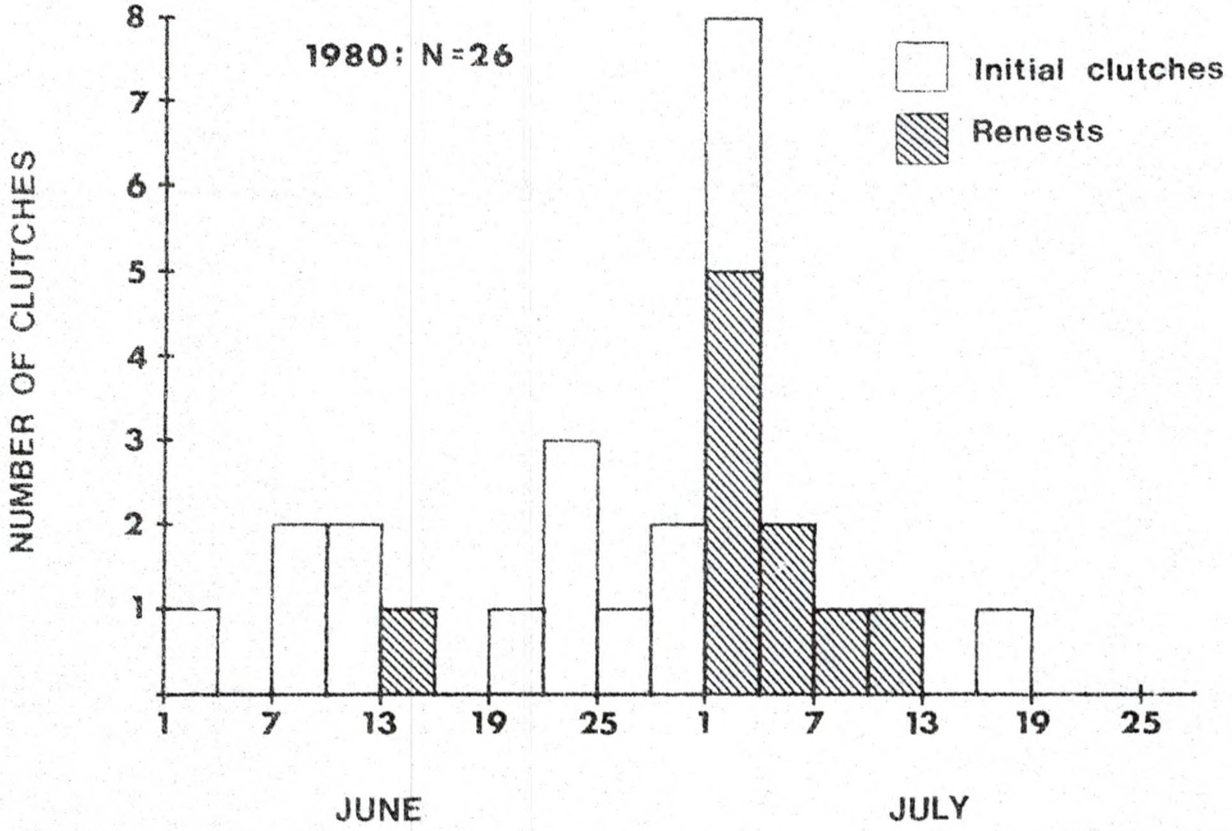
a) Hatching Chronology

Due to high rates of nest destruction and renesting, hatching initiation dates for Red-necked Grebe clutches in the Turtle Mountains extended throughout June and July (Fig. 10). Evidence from infrequently observed pairs indicated that hatching occasionally extended into August, as the first egg from a 5-egg clutch was peeping on 29 July 1981 and another pair carried 2 recently-hatched immatures on 11 August 1981. During both years, peak hatching occurred in late June and early July. Although initial clutches commenced hatching as late as 16 July and renests as early as 15 June, 76.7% of the clutches that started hatching in June were initial clutches and 70.4% of those hatching in July were replacement efforts.

b) Incubation and Hatching Periods

The incubation period refers to the number of days from laying to hatching of the last egg in a clutch, whereas the hatching period refers to the length of time required for any egg to hatch (Welty 1962). Hatching periods calculated for 140 eggs from 52 successful clutches during this study averaged 29.1 days (SD=2.85) (Fig. 11). A modified incubation period (including hatching periods for the last-hatched egg from all successful nests), averaged 29.0 days (SD=3.06). Due to high rates of disappearance and desertion of eggs, however, the last egg hatched in only 11 nests. The average incubation period for these 11 nests was 27.6 days (SD=2.76).

Figure 10. Three-day hatching initiation totals for 57 successful Red-necked Grebe clutches during 1980 and 1981.


8
7
6
5
4
3
2
1
NUMBER OF CLUTCHES
1980; N=26
Initial clutches
Renests
1
7
13
19
25
1
7
13
19
25
JUNE
JULY

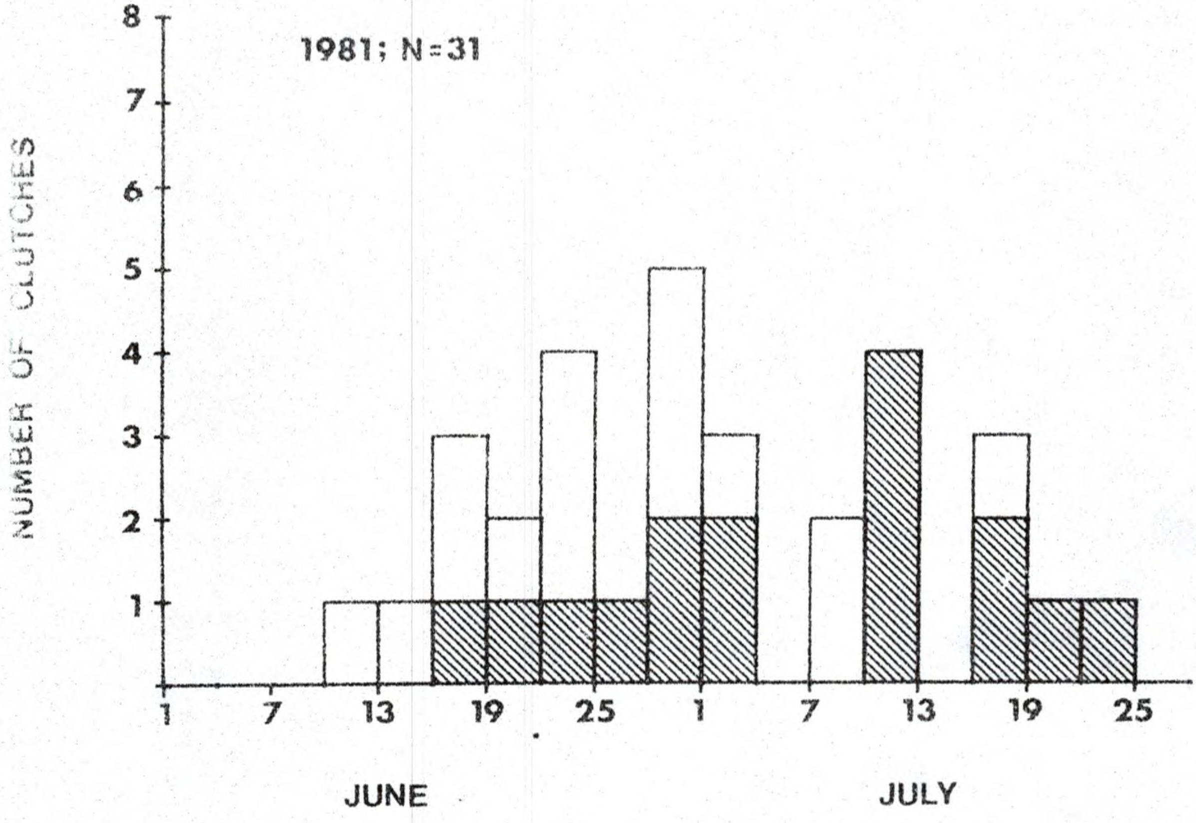
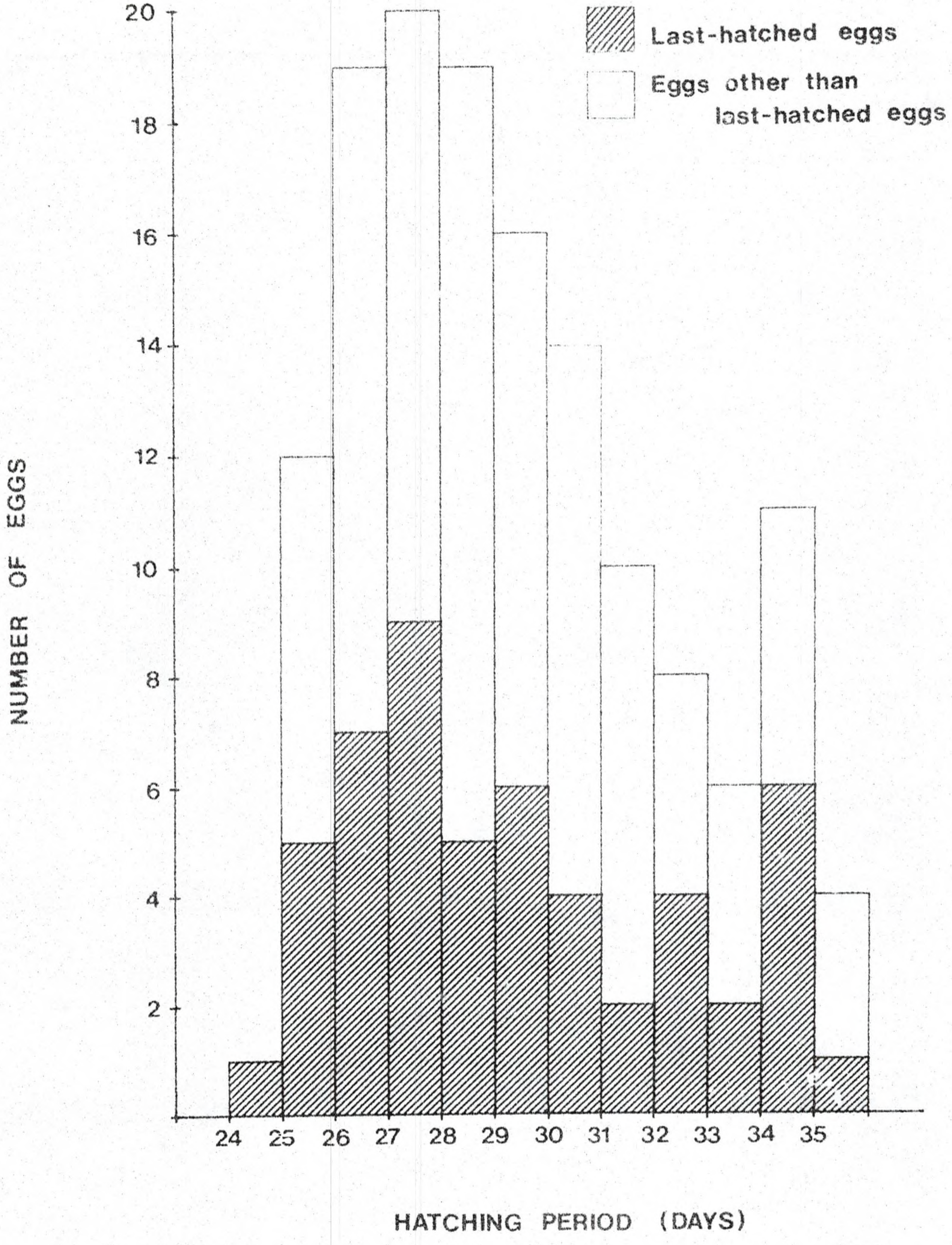

8
7
6
5
4
3
2
1
NUMBER OF CLUTCHES
1981; N=31
1
7
13
19
25
1
7
13
19
25
JUNE
JULY

Figure 11. Hatching periods for 140 eggs (including 52 last-hatched eggs) from Red-necked Grebe clutches in the Turtle Mountains.


20
18
16
14
12
10
8
6
4
2
NUMBER OF EGGS
Last-hatched eggs
Eggs other than last-hatched eggs
24
25
26
27
28
29
30
31
32
33
34
35
HATCHING PERIOD (DAYS)

The average incubation period for Red-necked Grebes in the Turtle Mountains (28-29 days) was considerably longer than that cited in the literature. Other studies of the Red-necked Grebe reported average incubation periods of 20-23 days (Sage 1973, Cramp and Simmons 1977), 22-23 days (Bent 1919, Harrison 1979), 23 days (Wobus 1964, Kevan 1970, Mink and Gibson 1976), and 22-25 days (Harrison 1978).

Reasons for the extended incubation periods of Red-necked Grebes in this study were not readily apparent. Although eggs in nests that were checked more frequently during egg-laying, incubation, and hatching tended to have longer hatching periods (Fig. 12), a regression analysis revealed no significant linear relationship between hatching periods and observer disturbance (F=0.83; 1,50 df; P>0.05). An alternative explanation was that the extended incubation periods recorded during this study were due to seasonal differences in the mean hatching date. High rates of early nest destruction combined with a reduced incubation drive late in the nesting season might skew the average upward. Indeed, a regression analysis revealed a significant linear relationship between hatching periods and the date of hatching for last-hatched eggs from clutches of Red-necked Grebes in the Turtle Mountains (F=5.51; 1,50 df; P<0.05) (Fig. 13). Because hatching dates were not presented in other studies of the Red-necked Grebe, however, it was impossible to compare mean hatching dates. Although high rates of early nest destruction and renesting may have resulted in a preponderance of late nests and an elevated average hatching period for eggs from the Turtle Mountains, hatching periods for early Turtle Mountain clutches were still much longer than those found in other studies.

Figure 12. Hatching periods in relation to the amount of disturbance (number of nest checks) during egg-laying, incubation, and hatching for last-hatched eggs from 52 Red-necked Grebe clutches.

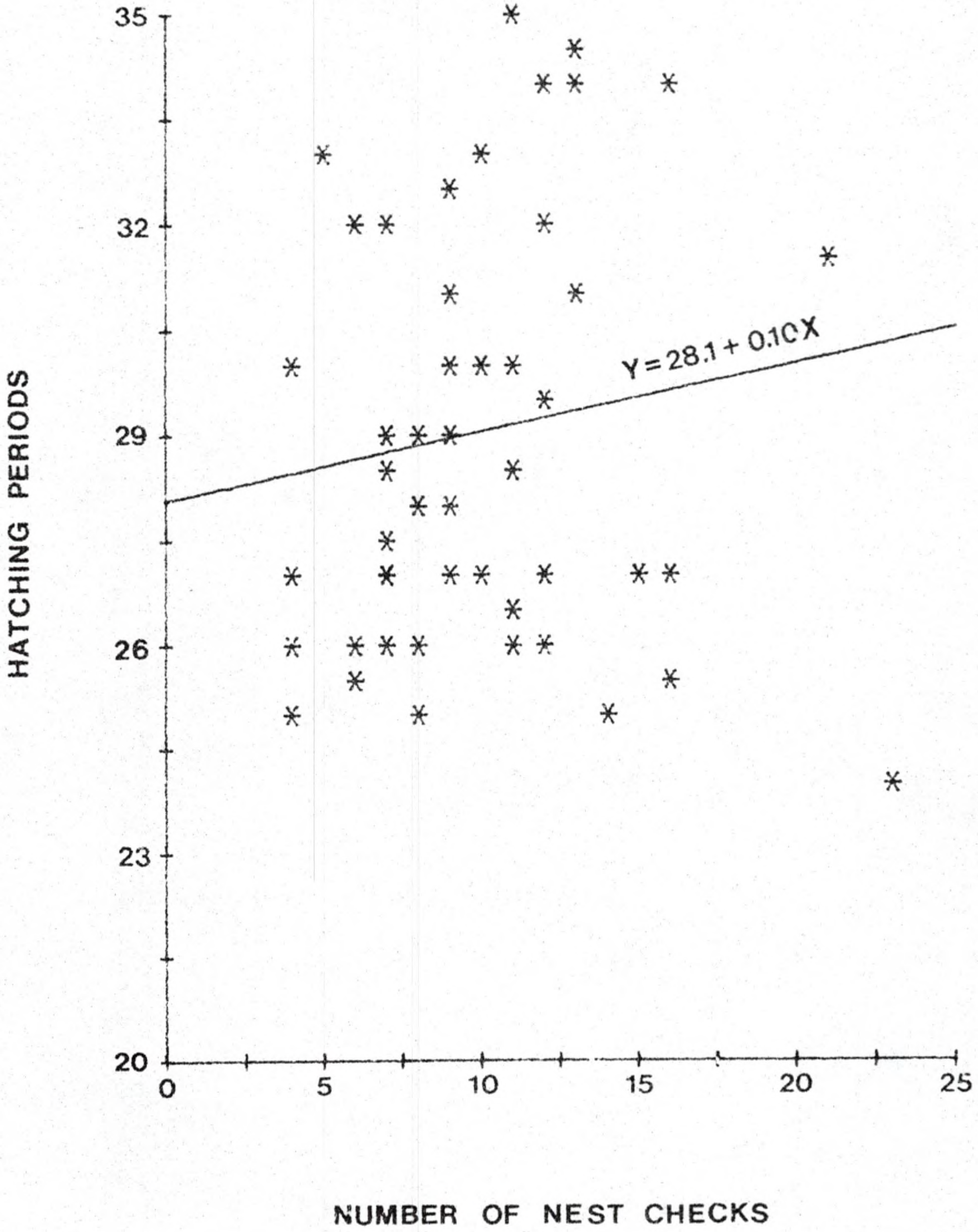
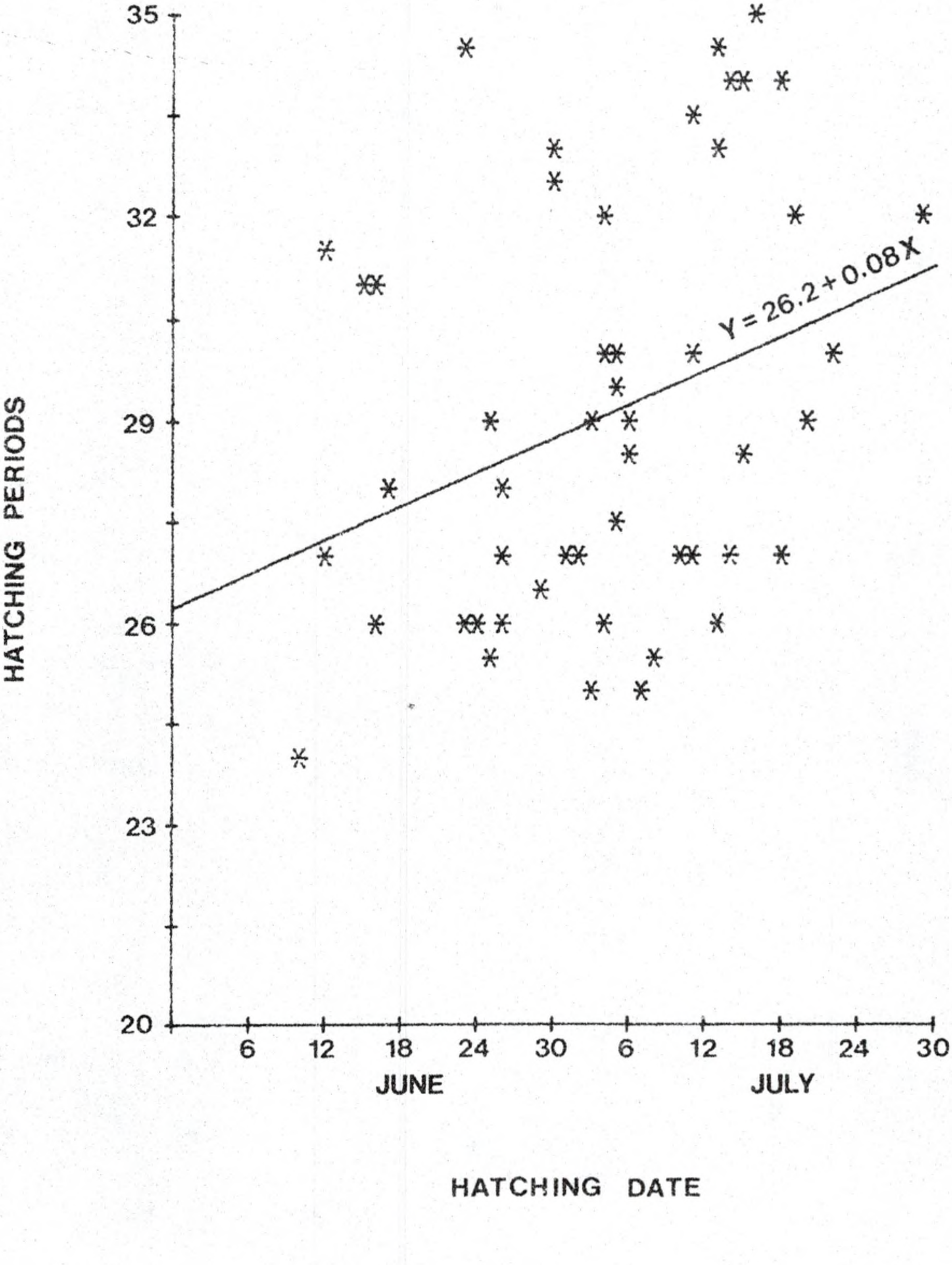

HATCHING PERIODS
35
32
29
26
23
20
0
5
10
15
20
25
Y = 28.1 + 0.10X
NUMBER OF NEST CHECKS

Figure 13. Hatching periods in relation to the hatching date for last-hatched eggs from 52 Red-necked Grebe clutches.


HATCHING PERIODS
35
32
29
26
23
20
6
12
18
24
30
6
12
18
24
30
JUNE
JULY
HATCHING DATE
Y = 26.2 + 0.08X

I believe that the main reason for the discrepancy in hatching and incubation periods between this study and others was that previous research relied on or was influenced by incubator-based data. In North America, few studies have field-tested Bent's (1919) estimated 22-23 day incubation period (based on hatching times within an incubator). According to Dement'ev et al. (1968), the incubation period for P.g. grisegena has been studied only in captive birds. Because eggs hatched within an incubator would not experience similar temperature fluctuations to those hatched in the wet surroundings of a nest, I suspect that incubator results represent the minimum amount of time in which the eggs could hatch. Hence, incubator-based data should not be relied upon in determining average incubation periods for grebes in a natural setting.

c) Hatching Intervals

Although asynchronous hatching occurs in all grebes, hatching of the first egg usually occurs at a faster rate than the laying rate. Wobus (1964) and Kevan (1970) observed this for Red-necked Grebes, but did not present supportive data. In the Turtle Mountains, the average hatching interval between successive eggs increased from 1.0 days between the first 2 eggs, to 1.7 and 1.8 days from the second to the fourth egg, and to 1.9 days between successive eggs beyond the fourth egg (Table 14). The difference in average hatching intervals before and after the second egg was very highly significant ($P<0.001$). Much of this difference was attributed to incontinuous incubation prior to laying of the second egg, although incomplete behavioral and physiological development during early incubation probably contributed.

Table 14. Average hatching interval between successive eggs from regularly observed clutches where 2 or more successive eggs hatched.

Eggs involved	N	Hatching interval (days)	
		Mean	SD
#1 and #2	22	1.05	0.41
#2 and #3	22	1.66	1.16
#3 and #4	21	1.79	1.17
#4 - #7	14	1.86	0.74
Total	79	1.56	0.98

During this study, I observed an adult that failed to "shuffle" onto its eggs (an action that opens the brood patch and brings it in contact with the eggs) during an early nest-relief, whereas another early-incubating adult possessed an insufficiently developed brood patch.

Throughout this study, the first eggs within a clutch often hatched on the same day or at 1-day intervals. In some clutches, the first 3 eggs were found peeping simultaneously and on one occasion, the first 4 eggs hatched within a day and a half. McAllister (1963 in Kevan 1970) noted one instance where an entire 6-egg Red-necked Grebe clutch hatched within 2 days, and Mink and Gibson (1976) observed a 5-egg second clutch that hatched within a single day.

During this study, successive eggs rarely hatched at intervals exceeding 2 days. Nevertheless, in one clutch, the hatching interval between the third and fourth eggs (laid within 2-3 days of each other) was 6 days. In another clutch, a lengthy hatching interval between the final 2 eggs was believed due to a delay between laying of the eggs and incontinuous incubation after the penultimate egg hatched. In both instances, it was suspected that the adults devoted most of their time caring for 2 previously hatched young and only rarely incubated their last egg.

d) Abandonment of the Nest

After hatching was completed, Red-necked Grebe pairs usually resorted to nearby open water where 1 adult (the guard adult) generally remained with the young while the mate foraged for and brought food to the young. In at least 3 instances, the empty nest was used as a brooding platform until 1-2 weeks after hatching. At least 8 other pairs of Red-necked Grebes constructed open-water brooding platforms 1-3 weeks after the young hatched. These platforms were used sparingly as a resting site for the young and occasionally the guard adult. Even though 20% of the successful pairs in this study brooded their young on the nest or a brooding platform, other studies of the Red-necked Grebe (Wobus 1964, Sage 1973) and other grebe species (Ashby 1933, Bird 1933, Simmons 1955) reported only isolated cases where the abandoned nest or a brood platform was used.

BROOD SURVIVAL AND DEPARTURE

a) Brood Survival

Among 114 pairs of Red-necked Grebes that were observed throughout June and into July, 58 (50.9%) were successful in hatching at least 1 young. Observations were discontinued on 7 families that moved to inaccessible areas before the young were a month old and on 3 families that disappeared (perhaps moved). For the remaining 48 pairs, an average of 2.5 eggs/nest hatched (or 3.3 eggs/nest if eggs that possibly hatched were included). By the time broods were 10 days old, average brood size dropped to 2.3/pair (Table 15). This was further reduced to 2.0 and 1.9 chicks/pair at 20 and 30 days after hatching, respectively. Thus, 24.2% of the chicks died during their first month (or 42.0% if eggs that possibly hatched were included).

Survival rates were much higher beyond the first month. Only 1 chick disappeared among 82 observed up to an age of 40 days, and none died among 51 observed up to 50 days of age. Because some broods began departing the nesting lakes soon after the chicks were 50 days old, no survival data were collected beyond that age.

b) Causes for Chick Losses

Although many studies have reported heavy losses of grebe chicks within a few days of hatching (McAllister 1958, Chabreck 1963, Wobus 1964, Fjeldsa 1973b, Ferguson 1977), causes for these losses were rarely identified. Extended periods of damp, cool, or stormy weather have been suspected for major losses among immatures of several grebe species (Harrison and Hollom 1932, Munro 1941, Chabreck 1963, Wobus

Table 15. Comparison of chick survival in relation to initial brood size for 48 Red-necked Grebe broods observed for at least 1 month. Number of broods in each category are given in parentheses.

Brood size	Number of days after hatching							Brood size	Number of days after hatching						
	0	5	10	15	20	25	30		0	5	10	15	20	25	30
6-chick broods								3-chick broods							
6	(1)	(1)	(1)	(1)	(1)	(1)	(1)	3	(11)	(10)	(10)	(8)	(8)	(8)	(8)
0-5	-	-	-	-	-	-	-	2	-	(1)	(1)	(3)	(3)	(2)	(2)
								1	-	-	-	-	-	(1)	(1)
								0	-	-	-	-	-	-	-
5-chick broods								2-chick broods							
5	(2)	(1)	(1)	(1)	(1)	(1)	(1)	2	(16)	(16)	(15)	(13)	(13)	(12)	(12)
4	-	(1)	-	-	-	-	-	1	-	-	-	(2)	(1)	(2)	(2)
3	-	-	(1)	-	-	-	-	0	-	-	(1)	(1)	(2)	(2)	(2)
2	-	-	-	(1)	(1)	-	-								
1	-	-	-	-	-	(1)	(1)								
0	-	-	-	-	-	-	-								
4-chick broods								1-chick broods							
4	(7)	(6)	(4)	(2)	(1)	(1)	(1)	1	(11)	(9)	(9)	(9)	(9)	(9)	(9)
3	-	(1)	(2)	(3)	(3)	(2)	(2)	0	-	(2)	(2)	(2)	(2)	(2)	(2)
2	-	-	(1)	(1)	(1)	(2)	(2)								
1	-	-	-	(1)	(1)	(1)	(1)								
0	-	-	-	-	(1)	(1)	(1)								
Chick totals	44	42	38	33	29	27	27	Chick totals	76	73	71	67	66	64	64

1964, Fjeldsa 1973b, Simmons 1974, McNicholl 1979). Other studies attributed depredation by fish, primarily pike (Esox spp.), to be a major limiting factor (Bent 1919, Harrison and Hollom 1932, Venables and Lack 1936, Simmons 1955, La Bastille 1974). Occasionally, diseases and parasites are blamed for losses among grebe young (Munro 1917, 1922, 1929, Kevan 1970).

In the Turtle Mountains, extended inclement weather during the hatching period was minimal and probably contributed to few deaths. Because few or no large predatory fishes resided within lakes where Red-necked Grebes nested, losses to these were considered minimal. No losses to diseases or parasites were identified.

Chick mortality due to high pesticide loads may have contributed to the deaths of some Turtle Mountain Red-necked Grebes during pre- and post-hatching stages. Rudd and Herman (1972) contended that direct accumulation of residues in the eggs followed by toxic manifestations as the yolk sac was absorbed by the young were the causes for much of the Western Grebe hatchling mortality observed at Clear Lake, California. In Alberta, Riske (1976) found high pesticide residues in several recently-hatched grebes and concluded that these had contributed to their deaths. In the Turtle Mountains, several embryos that died during the peeping and pipping stages may have succumbed to elevated pesticide residues. The high incidence of eggs disappearing during hatching in Red-necked Grebe clutches from the Turtle Mountains indicated that pre- and post-hatching mortality were more common than was observed.

Sibling rivalry probably contributed to many of the chick losses observed during this study. Harrison and Hollom (1932) first identified sibling rivalry within grebe broods, believing that some of the smaller Great Crested Grebe immatures starved as a result of older siblings consistently beating them in races to the feeding parent. In at least one instance, Wobus (1964) attributed mortality of a young Red-necked Grebe to starvation resulting from older siblings repeatedly attacking it during feeding sessions. Paul Hansford (pers. comm.) studied the feeding ecology of a Red-necked Grebe population in Alberta during 1980 and concluded that sibling rivalry was a major factor contributing to reduced productivity in this population. Nuechterlein (1981) believed that sibling rivalry resulted in dominant Western Grebe chicks gaining initial access onto their parent's back, contributing to increased exposure-related losses among younger siblings.

Within the Turtle Mountains, I frequently observed chick-chick and parent-chick interactions during feeding sessions. In one instance where mortality through sibling rivalry was suspected, 1 parent left about a week after the young had hatched, leaving its mate to care for 2 chicks. An observation of the 8-10 day old chicks revealed much sibling rivalry, resulting in the oldest chick obtaining most of the food procured during an entire feeding session. An hour-long observation 3 days later revealed much the same trend, as the smallest chick obtained only 1 of 53 food items brought by the adult and was pecked or chased by its older sibling or parent whenever it got near the feeding parent. For 15 minutes after the feeding session, the smallest chick attempted to climb onto its parent's back, but was prevented by attacks from both the adult and the older immature. Twice when it did manage to climb aboard, it was immediately shaken off and pecked by the adult. I left, convinced that the small immature would not survive. When I returned the following day, however, both young had vanished.

Chick-chick and parent-chick interactions were particularly common in large families and were believed to have contributed to significantly higher individual mortality rates within larger broods (Table 15). Individual mortality rates beyond 5 days of age were 35.7% for young within 4-6 chick broods, compared to a 12.3% mortality rate within 1-3 chick broods ($X^2=6.99$, 1 df; $P<0.01$). Significant differences were also noted in individual mortality rates for young within these two groups beyond 10 days of age ($X^2=5.46$; 1 df; $P<0.05$), and beyond 15 days of age ($X^2=4.61$; 1 df; $P<0.05$). Although sibling competition for resources probably was not the only factor involved in these differences, it may have been the most important.

c) Independence and Departure

Ferguson (1977) suggested that young Horned Grebes took to the water after preening and waterproofing became functional. Wobus (1964) indicated that young Red-necked Grebes were rarely found on the adult's back beyond 2 weeks, but Chamberlin (1977) observed this habit until 3 weeks of age. In the Turtle Mountains, 10-day-old Red-necked Grebe chicks spent more than half of their time on the water, but they continued to resort to the warmth and protection of the adult's back until they were at least 2 weeks of age. In about one-third of the families observed, the last immature was still seen on the adult's back more than 2 weeks after hatching, but only once was this seen in a natural setting beyond 17 days of age (a 20-day-old chick that scrambled onto its parent's back after the adult issued a warning "chuck").

Although young dive from danger on their first day, the earliest unprompted dive noted during this study was by a 5-day-old chick. By the time young were 2 weeks old, they were often observed diving during feeding sessions. These dives appeared to be exploratory, however, and few successful feeding dives were noted by young less than 4 weeks old. During the first month, young probably procured little of their own food except for the occasional item found on the water or picked off objects protruding from the water. Throughout their second month, immatures continued to beg for and receive food from their parents. By the age of 6-7 weeks, however, immatures that approached a feeding parent were often pecked at and driven off.

In all families under observation, 1 parent departed 1-3 weeks before its mate. If only a single chick was reared, departure of the first adult often occurred before the immature was a month old. In larger broods, the initial departure generally occurred when at least some brood members were partially independent (6-7 weeks of age). Although departure of the second adult occurred slightly earlier when smaller broods had been reared, it generally remained until the youngest brood members were at least 6-8 weeks of age.

During this study, departure data were collected from 11 broods of Red-necked Grebes. In these, immatures generally departed at 9-10 weeks of age, although a few left before they were 2 months old, and others remained beyond 70 days. As with the adults, most immature Red-necked Grebes departed their nesting lakes singly.

SUMMARY AND CONCLUSIONS

During this study, hatching success among eggs from Red-necked Grebes that were regularly observed ranged from 16.4 to 22.3% (depending on whether "possibly hatched" eggs were excluded or included, respectively). Although the nest success rate was low (26.2%), most pairs that failed on their first nesting attempt initiated at least 1 replacement clutch and some renested up to 4 times. Consequently, among 114 pairs observed throughout June and into July, 58 (50.9%) were successful in hatching at least 1 young. Successful pairs hatched an average of 2.5 young/pair. By 30 days of age, brood size had declined to a mean of 1.9 young/successful pair. Because losses during the second month were minimal, Red-necked Grebes in the Turtle Mountains fledged approximately 1.8-1.9 young/successful pair or about 0.9 young/breeding pair.

A major obstacle encountered in comparisons of reproductive success among grebe populations is the various observational techniques employed in productivity assessments. Depending on how frequently pairs, nests, and broods are observed throughout the nesting season, nesting success may be reported as: a) percentages of successful eggs; b) percentages of successful nests; c) percentages of successful pairs; d) number of young fledged/breeding pair; and/or e) number of young fledged/successful pair. Table 16 compares productivity measurements for Red-necked Grebes in this study to those found in other grebe studies.

Hatching success rates for Red-necked Grebes in the Turtle Mountains were lower than those recorded in all except 2 grebe

Table 16. Comparison of hatching and fledging success for Turtle Mountain Red-necked Grebes compared to those for other North American grebes. Sample sizes are in parentheses.

Species Study site (Reference)	Hatching success (%)			Fledging success (N young)	
	Successful eggs	Successful nests	Successful pairs	Per successful pair	Per breeding pair
Pied-billed Grebe					
Iowa (Glover 1953)	-	70.4	-	-	-
Texas (Cottam and Glazener 1959)	85.6-98.0	90.6 (32)	-	-	-
Louisiana (Chabreck 1963)	-	89.6 (107)	-	-	-
Alberta (Riske 1976)	-	-	100.0 (21)	3.04	3.04
Manitoba (Sealy 1978)	-	31.0 (42)	-	-	-
Horned Grebe					
Norway (Fjeldsa 1973b)	63.2 (1332)	75.5 (721)	-	-	-
Alberta (Riske 1976)	-	-	57.0 (125)	2.26	1.27
Manitoba (Ferguson 1977)	30.3 (637)	36.5 (115)	-	2.76	-
Western Grebe					
Manitoba (Nuechterlein 1975)	-	48.0 (115)	-	-	-
Utah (Lindvall and Low 1982)	-	21.0 (221)	-	1.7	0.35
Red-necked Grebe					
Germany (Wobus 1964)	-	-	-	1.96	1.05
Astotin Lake, Alta. (Kevan 1970)	-	-	58.4 (89)	1.95	1.1
Pike Lake, Alta. (Riske 1976)	-	-	20.0 (267)	1.39	0.38
C. Alta. potholes (Riske 1976)	-	-	66.0 (63)	1.63	1.06
Turtle Mountains, Manitoba (This study)	16.4-22.3 (834)	26.2 (210)	50.9 (114)	1.8-1.9	0.9-0.95

investigations. In Utah, Lindvall and Low (1982) reported low nest success rates, attributing most losses to avian depredation during observer disturbance of the Western Grebe nesting colonies. In the Turtle Mountains, predators were implicated in about half of the egg losses, but the contribution of human disturbance was believed minimal. Low nesting success was also reported for a Red-necked Grebe population on Pike Lake, Alberta (Riske 1976). Only 20% of the nests on this lake were successful; heavy losses were attributed to high pesticide residues, the detrimental impacts of human recreational activities, and wave-related losses. Although high pesticide residues were present in Red-necked Grebe eggs from the Turtle Mountains, wind and waves accounted for only 2.0% of the egg losses, and recreational use of the study lakes was minimal.

Because of the extremely low nesting success of Red-necked Grebes on Pike Lake, this population experienced an abnormally low fledging success rate (Table 16). Red-necked Grebe populations in Germany (Wobus 1964), Astotin Lake, Alberta (Kevan 1970) and Alberta potholes (Riske 1976), however, had fledging success rates that were similar to those recorded in the Turtle Mountains. Other Red-necked Grebe studies recorded annual fledging rates of 1.6 young/breeding pair in Sweden (Ahlen 1970), and 2.8 young/successful pair in Russia (Markuze 1965 in Fjeldsa 1973b).

Hence, with the exception of 2 European studies, most recent studies of the Red-necked Grebe indicate that about 2 young are fledged/ successful pair (or about 1 young/breeding pair). Among other large grebes, 1.7 young/breeding pair was considered normal for the Western Grebe (Rudd and Herman 1972) and was indicated as a continental average for European studies of the Great Crested Grebe (Melde 1973 in Simmons 1974). The scant amount of data on productivity of smaller grebe species also indicates that these generally have higher fledging rates than the Red-necked Grebe (Table 16). Why this is so, despite the Red-necked Grebe possessing one of the largest average clutch sizes among grebes (Palmer 1962, Cramp and Simmons 1977), remains unknown. While this study revealed possible clues, more research is required on productivity and causes of nesting losses among populations throughout the breeding range. Extensive banding programs are needed to provide information on site and mate fidelity, longevity, and rates of adult mortality. Limnological studies, combined with research on feeding ecology, might reveal insights regarding habitat preferences and reproductive potential of certain populations. It is hoped my findings will stimulate such research and spark renewed interest in the reproductive biology of this species.

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