

THE UNIVERSITY OF MANITOBA

The Breeding Cycle and Annual Production  
of the Common Loon (*Gavia immer*) in the  
Boreal Forest Region

by

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## ABSTRACT

The nesting ecology of Common Loons (*Gavia immer*) was studied on Hanson Lake in northern Saskatchewan. The irregular shoreline and numerous islands on Hanson Lake divided the lake into natural territories which were occupied at the commencement of spring breakup.

Egg-laying in the population was synchronous, particularly in late seasons, and peaked 4 to 9 days from the onset. All first clutches contained two eggs, unless laying was interrupted; occasionally only one egg was produced in late reneesting attempts. The incubation period was 26 days. Although laying spanned 40 days, 58% of young which fledged originated from clutches laid during the first 10 days. It was advantageous to nest early, as fluctuating water levels often flooded late nests. Replacement clutches made a small but important contribution to annual production.

Nest-site selection influenced nesting success. Predators and natural wave action were the main causes of clutch failure. Nest-sites on islands or concealed by vegetation were preferred as a means of reducing egg depredation. Shores sheltered by adjacent land masses were selected, a mechanism which minimized wave action at the nest.

Hatching within clutches was asynchronous, with a mean hatching interval of 17.3 hr. Egg I always hatched first, and the first chick always maintained an advantage in weight and vigor over its younger sibling. Most chick mortality occurred in the first 2 weeks, and 68% survived to fledging. Survival of second-hatched chicks was signifi-

cantly lower than all other chicks; this factor, and certain parental behaviors, suggested that Chick II is expendible. Young were abandoned at 10 to 13 weeks of age.

Foraging efficiency may regulate Common Loon populations. The availability of food may limit survival to fledging. Inferior foraging skills may result in heavy juvenile and sub-adult mortality on wintering areas.

Based on the breeding habits of the Common Loon, its sensitivity to recreational and commercial use of waterways was assessed. Although northern populations appear healthy, they are vulnerable to the effects of waterborne toxic chemicals. Fluctuating water levels during nesting could severely reduce annual production, and turbidity can render habitat unsuitable for visual foraging. Most outdoor recreation is compatible with loon populations, except for intensive boating during incubation.

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## I. INTRODUCTION

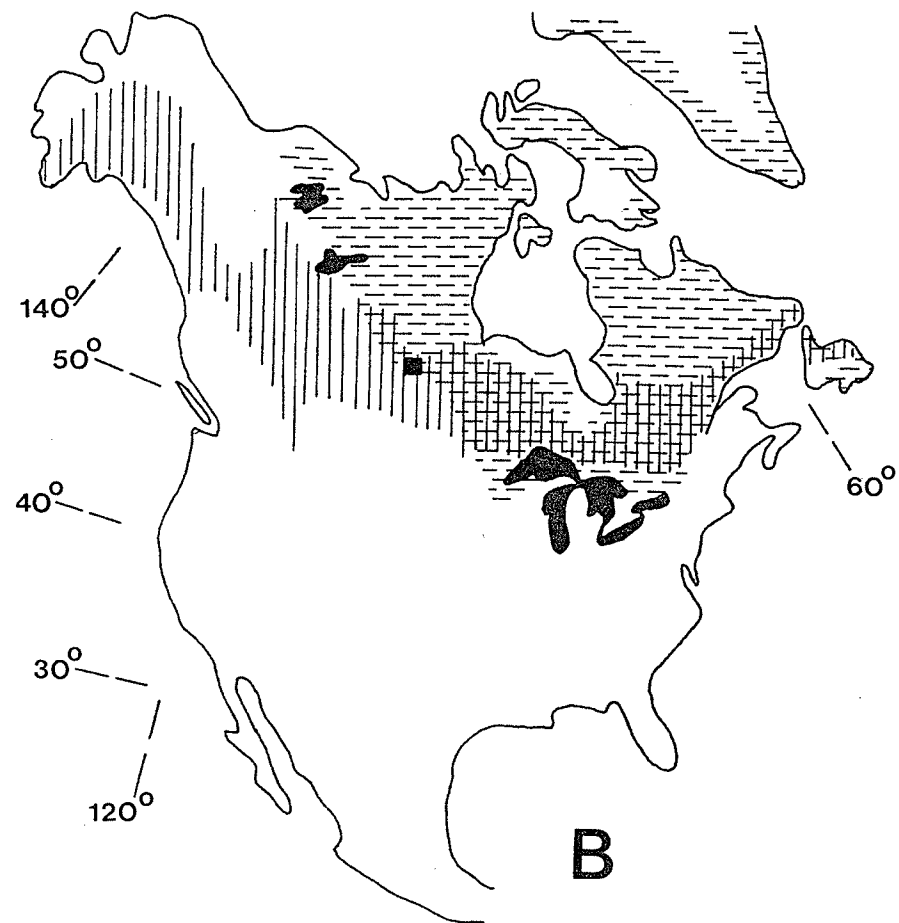
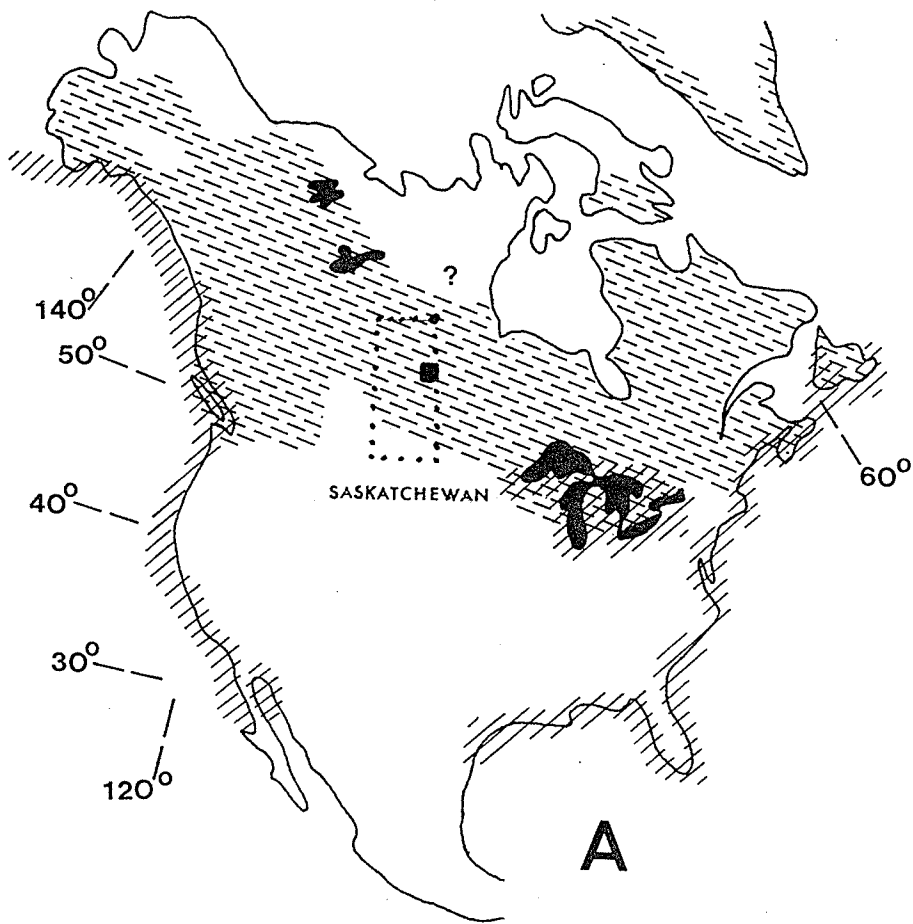
Four species of loons, which comprise the holarctic family Gaviidae (A.O.U. check-list 1957), breed extensively in North America. Although primarily maritime in winter and during migration, loons breed exclusively on inland fresh waters. In North America, the Common Loon (*Gavia immer*) has the most widespread and southerly breeding distribution, and is traditionally regarded as a bird of the northern wilderness.

Although the Arctic Loon (*G. arctica*) and the Red-throated Loon (*G. stellata*) breed sympatrically with *G. immer* across much of their range, well-defined habitat differences result in ecological separation (Davis 1972). Breeding ranges of the Common Loon and the Yellow-billed Loon (*G. adamsii*) are largely allopatric, although more records are required to delimit their respective ranges in areas of possible sympatry (Godfrey 1966). Mayr and Short (1970) revoked specific status from *G. adamsii* due to its morphological similarity and contiguous allopatry with *G. immer*.

In North America, the Common Loon winters off coasts between latitudes 25° and 60°, with a small population wintering inland on the Great Lakes (Palmer 1962). It breeds throughout most of Canada (Fig. 1A). Its breeding range coincides closely with the wide belt of Northern Coniferous Forest, and extends peripherally north into the Taiga-Tundra transition zone and southward into the mixed woodlands of the Great Lakes, Maritimes and Pacific Coastal regions (Fig. 1B). The breeding range covers all of the Precambrian Shield, except Keewatin (Fig. 1A) where the regular occurrence of neither *G. immer* nor *adamsii* has been substantiated.

Figure 1. Distribution of the Common Loon in North America.

A. breeding and winter ranges (after Godfrey 1966, Palmer 1962); B. extent of the Boreal Forest (after Bartholomew 1974, Canada Dept. E.M.R. 1974) and Precambrian Shield (after A.A.P.G. and U.S.G.S. 1967, Williams 1958).




 BREEDING RANGE

 WINTER RANGE

 HANSON LAKE, SASK.

 BOREAL FOREST

 PRECAMBRIAN SHIELD

 HANSON LAKE, SASK.

Considering the prominence and trophic position of the Common Loon in the Boreal Forest community, it has been surprisingly little studied and much of its biology is poorly understood. Olson and Marshall (1952) provided the first comprehensive review of Common Loon reproductive biology based on studies in Minnesota. Local declines in populations, the widespread use of toxic chemicals, and the questionable tolerance of loons to increasing recreational use of lakes have generated recent concern for the species. This concern provided the impetus for several studies of Common Loon biology. Barr (1973) examined the feeding ecology of Common Loons in southeastern Ontario. In Minnesota, McIntyre (1975) assessed its adaptability to man-induced habitat deterioration. The Canadian Wildlife Service has undertaken toxicological studies on the species in the Great Lakes Region (J. Barr, pers. comm.).

Although Boreal Forest lakes, particularly the oligotrophic lakes of the Precambrian Shield, are the breeding habitat for most of the Common Loon population in North America, detailed studies of Common Loon biology have been conducted only along the southern periphery of its range. The objectives of this study were to evaluate the reproductive potential of a Common Loon population in its primary habitat, to determine the factors which influence breeding success under natural conditions, and to provide a framework for the future management of loon populations.

## II. METHODS

Hanson Lake was selected for this study because the population was large, the lake was accessible yet commercially undeveloped, and all areas of the lake were navigable by boat under most weather conditions. Data were collected during the summers of 1973, 1974 and 1975, following preliminary studies in 1972. Each year field studies commenced during spring breakup of lake ice and terminated in late August or early September. The study area was travelled in a boat equipped with outboard motor.

Commencing in May 1973, water levels of the lake were monitored from a stake placed permanently in the water; fluctuations were measured in relation to a zero reference point marked below the surface. Meteorological data for Hanson Lake were obtained from the Flin Flon Airport, 80 km to the east (Canada D. of T., 1963 to 1975).

Terms have been defined in the text and have been underlined where they first appear. The Common Loon has often been referred to as loon or loons; the family name has always been used where reference to any or all other species was intended. Taxonomic nomenclature for mammals, birds, fishes and flora follows Banfield (1974), Godfrey (1966), Scott and Crossman (1973), and Moss (1966), respectively.

Elementary statistical procedures outlined by Sokal and Rohlf (1969)

and Steel and Torrie (1960) were followed. Analyses of directional data followed methods given by Batschelet (1965). Statistical significance was accepted at a probability of 0.05, and non-significance has been denoted NS.

#### 1. ARRIVAL AND TERRITORY OCCUPATION

Within the limitations imposed on boat travel by ice, spring arrival of loons was monitored in 1973 and 1974. A portion of Hanson Lake (Bertrum Bay) was censused daily in 1973 from breakup until the population stabilized at the onset of nesting. This was repeated at three-day intervals on Bertrum Bay in 1974.

The limits of territories were determined by charting all observations of Common Loons prior to and during the nesting period. Ten adults individually marked with coloured patagial markers during June, 1975, (both members of three pairs and one member of four additional pairs) were observed repeatedly until departure to determine whether territories were occupied by the same individuals over the course of a summer.

Each territory was visited weekly throughout the summer. More frequent visits were made as individual breeding cycles dictated. Where possible, territories were visited daily during egg-laying and early brood-rearing, at six hour intervals during hatching, and every three to four days during incubation.

## 2. POPULATION SURVEYS

All adult loons observed during the nesting period were accorded a status based on their reproductive activities. A pair was assigned breeding status only when a clutch or brood was observed. In the absence of conclusive evidence of breeding, non-breeding status was given only to pairs which showed neither attachment to shoreline areas during the nesting period on all visits to the territory, nor agitation or wariness to the observer when shoreline vegetation was searched. Pairs which showed shoreline attachment and agitation were classed as probable-breeding. Those behaving ambiguously or observed infrequently were classed as undetermined. Single adults were presumed non-breeding and were classed as unmated.

## 3. THE NEST-SITE AND EGG LAYING

An attempt was made to locate and map each nest during or prior to laying. Nests were visited daily during laying and hatching, and each nest was visited at least every 5 days during incubation. Records taken from each nest included topographic features, nest dimensions, percent composition of nest materials, substrate supporting the nest, distance to water from leading edge of nest, the presence and density of both aquatic and terrestrial vegetation (with supporting photographs), and a chronological log of visits. Eggs were marked with a grease pencil, and weights and dimensions were recorded. First and second eggs were marked "I" and "II" where the laying sequence was known, and "A" and "B" where the sequence was unknown. These designations were also

applied to the young which hatched.

Two crude estimates of vegetation cover were made at each nest. These estimates assessed the visibility of the nest from the vantage point of a predator. Vertical cover was the estimated proportion ( $\pm 10\%$ ) of the nest obscured from the view of an observer standing directly over the nest. The percentage of lateral cover was estimated ( $\pm 10\%$ ) from looking outward from the nest.

Common Loons are known to replace failed clutches. Initial clutches were eggs from the first laying cycle of a specific female in a given year which were deposited in the first nest in which laying occurred. Replacement clutches were eggs from any additional laying cycles or those deposited in any additional nest. In the event a partial clutch was lost during cycle I and laying proceeded uninterrupted at the same nest, the resulting clutch was considered an initial clutch. However where laying did not continue at the normal interval, or where the laying cycle proceeded at another nest, all subsequent clutches were considered replacements. Thus while the failure of at least one cycle I egg (two in most cases) was a prerequisite for replacement, it was possible for a replacement clutch to contain only cycle I eggs.

Laying times for individual eggs, based on daily visits, were estimated ( $\pm 12$  hr) to be the mid-point between successive visits during which a particular egg appeared. Estimates of hatch times were also derived by daily visits, but were based on published descriptions of the hatching sequence (Beebe 1907, Rand 1954) and on two instances in which

Hanson Lake young were hatched in captivity. In this way it was possible to narrow down hatch time ( $\pm$  3 hours) to one of 4 quarters of the day, and estimates of incubation period carried confidence limits of  $\pm$  15 hours.

Care was taken to minimize the effect of the investigator at the nest-site. Nests were approached slowly by boat from a conspicuous position, which allowed incubating birds to leave the nest secretively. Nests were not visited when rough water threatened flooding, nor when gulls or corvids were observed in the vicinity of the nest. Surrounding areas were scanned for aerial scavengers before approaching the nests.

#### 4. FATES OF EGGS

Fates of eggs were determined by inspecting the nest site and, if necessary, adjacent areas. Where shell fragments were found, eggs were recorded as either hatched or depredated (following Girard 1939). Where shell fragments were not found, fate was recorded as disappeared although predators were probably responsible in many cases. Where possible, the work of mammalian and avian predators was separated (based on Rearden 1951). Flooded or wave-damaged nests were recorded as washed out, and recovery of eggs from the water often confirmed this. Washout by boats was distinguished from natural washout by the condition of the nest structure.

## 5. BROOD REARING

Care was taken to avoid unnecessary handling or disruption of broods. In 1975, the young from 13 two-chick broods of known hatching sequence were marked to determine survival. Testor's airplane dope was applied thinly to the tips of the down on the back and crown. Chick I was marked with white; Chick II was marked with pale yellow. Some marked young were recaptured and marked again once marks became faint at about two weeks of age.

To determine the age at which chicks disappeared, broods were surveyed daily until they were four days old, at three day intervals until two weeks old, and thereafter at least once a week. The time of mortality was calculated to the nearest day as the midpoint between the last observation of a chick and its first apparent absence from a brood. As the presence of young can at times be overlooked, the disappearance of chicks was confirmed by noting the absence of a chick on three successive surveys.

## 6. FLEDGING AND DEPARTURE

Field studies usually ended before most young had fledged or adults departed from the territories. In 1974, surveys of Hanson Lake continued until 3 October, to observe the break-up of family units.

### III. THE STUDY AREA

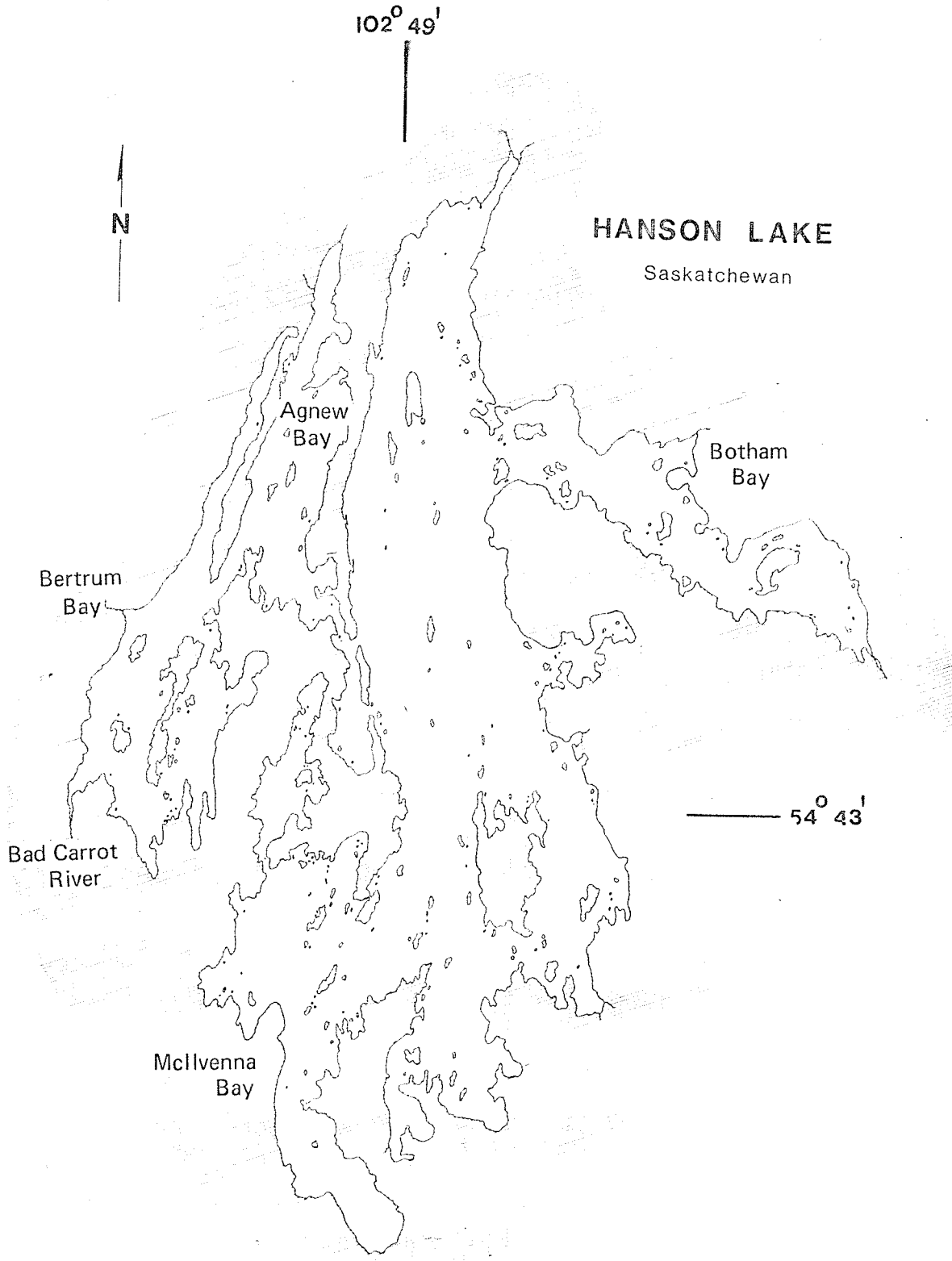
Hanson Lake (Fig. 1) is situated at the northern extremity of the Saskatchewan River drainage basin in east-central Saskatchewan (lat.  $54^{\circ} 43'N$ , long.  $102^{\circ} 49'W$ ), approximately 80 km west of Flin Flon, Manitoba. The lake is located centrally in the Boreal Forest and lies within the southern reaches of the Precambrian Shield (Fig. 1). Hanson Lake has a surface area of 4 123 ha, of which islands form 276 ha.

Hanson Lake is oligotrophic with depths over 30 m. The lake is a complex network of bays, channels and islands (Fig. 2). Of 221 islands, 86 percent (190) are smaller than 1.0 ha and 49 percent (109) are smaller than 0.1 ha; in addition, islets  $10\text{ m}^2$  or less are numerous. Although shoreline development is high ( $D_L$ , as defined by Hutchinson 1957), shores are not conducive to littoral productivity. Most shoreline is rock which drops abruptly, thus providing only a narrow littoral zone.

#### 1. BREAKUP

The arrival of Common Loons in spring coincides closely with the break-up of ice on the lakes on which they breed (McIntyre 1975, Munro 1945, Olson and Marshall 1952). Initial breakup is defined as the day on which the first large scale shifting and disintegration of ice cover occurred; ice-off is defined as the first day on which no ice remained; the breakup period extends from initial breakup until ice-off.

Figure 2. Map of Hanson Lake showing islands and shoreline topography.



Kilometers

The dates of these events at Hanson Lake are summarized in Table 1. The chronology and pattern of breakup showed annual consistency, with a maximum of eight days variation between any two years during this study. In relation to 1974, 1975 was an early year and 1973 was a late year.

## 2. WATER LEVELS

On Hanson Lake, seasonal and annual fluctuations in water levels were very small, which was a favourable environment for loons which nest in close proximity to water. Water levels were remarkably consistent both within and between years (Fig. 3). The maximum fluctuation during this study was 22.5 cm, which was small in relation to surrounding lakes which may fluctuate more than 200 cm within a season (Sawchyn 1967).

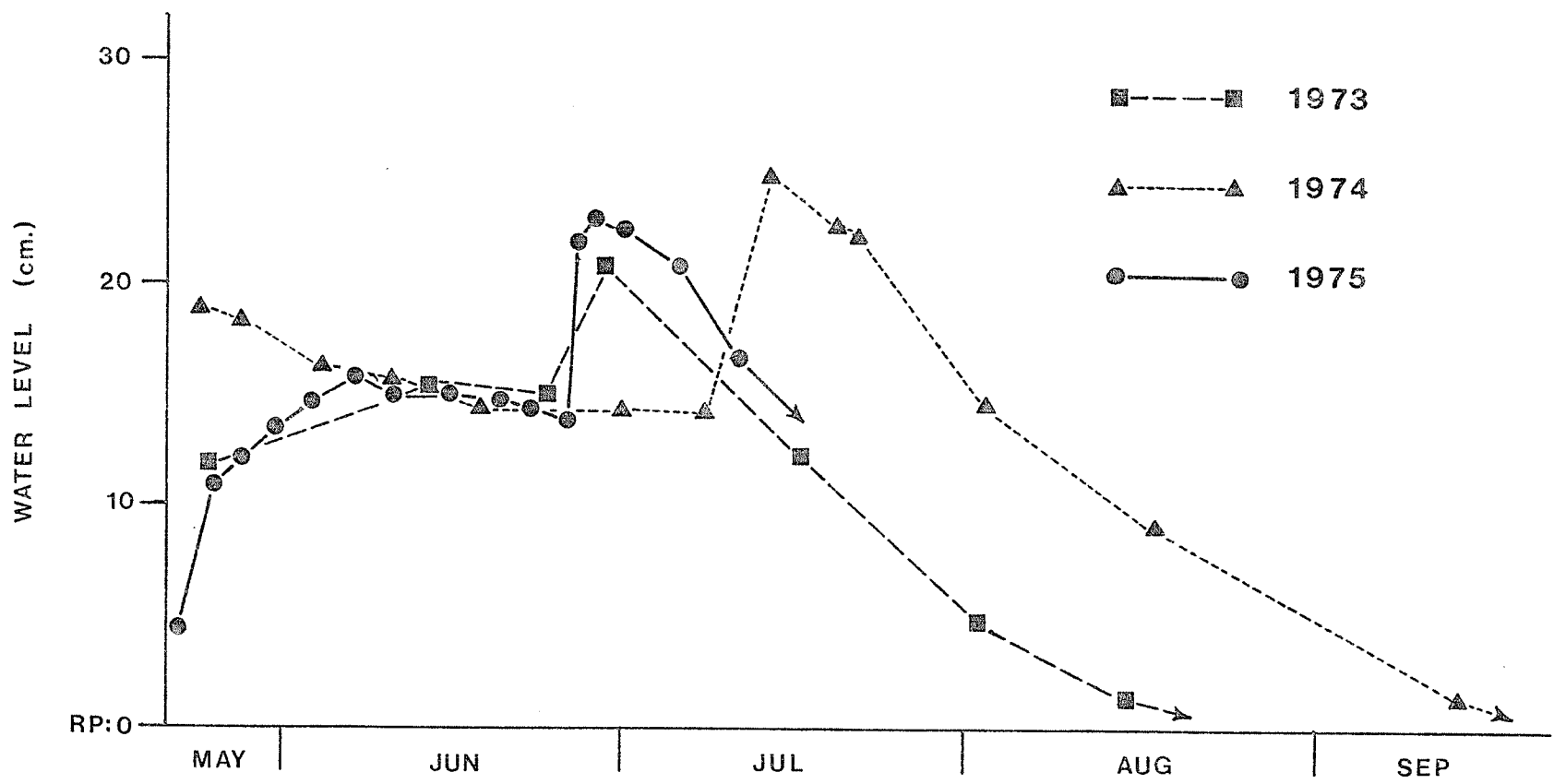
The stability of Hanson Lake is attributed to its relative isolation from a major waterway; it is a headwater lake with a local drainage area of 208 km<sup>2</sup> (Sawchyn 1967). The lake is fed mainly by the Bad Carrot River, a stream which receives only meltwater and muskeg drainage and which stagnates by mid-summer. The lake is drained through marshy lowland areas and through a narrow outlet which forms the headwater of the Hanson River.

Each year breakup on Hanson Lake was followed by a two week period of gradual stabilization to a level 14 to 16 cm above the zero reference point (Fig. 3). Precipitation caused an abrupt rise in water levels each summer commencing late June to mid-July, but the maximum increase

TABLE 1. Chronology of breakup of Hanson Lake, Saskatchewan  
from 1973 to 1975.

	1973	1974	1975
Date of initial breakup	15 May	11 May	8 May
Breakup period	7 days	7 days	5 days
Date of ice-off	22 May	18 May	13 May

Figure 3. Seasonal fluctuations in water levels on Hanson Lake, Saskatchewan. Water levels are shown in relation to a constant reference point, zero (RP:0).



was only 10.5 cm (in 1974).

### 3. VEGETATION

The dominant forest cover surrounding Hanson Lake is White Spruce (*Picea glauca*); interspersed are White Birch (*Betula papyrifera*) and stands of aspen (*Populus tremuloides*). Low-lying areas and islands support stands of Black Spruce (*Picea mariana*), and Jackpine (*Pinus banksiana*) dominate a recent burn along the northeast shore of Hanson Lake. Most of the shoreline is rocky and well-drained with shallow soil development; marshy regions are few. Emergents, largely *Phragmites communis* or *Scirpus* sp., occur infrequently and in sparse stands. Submergent vegetation occurs in several sheltered shallow regions.

### 4. VERTEBRATES

The Common Loon was the most abundant non-passerine bird species on the study area. With the exception of predators and prey species, few vertebrates interact regularly with Common Loons. Potential interactions and their importance have been assessed here.

#### i. Food Supply

The diet of the Common Loon consists almost exclusively of fish (Olson and Marshall 1952, Palmer 1962). Barr (1973) found the loon opportunistic in prey selection, exploiting species in relation to their abundance and ease of capture. Fish taken as prey normally ranged from

8 to 20 cm fork-length (Barr 1973).

At least 12 species of fish inhabit Hanson Lake (Sawchyn 1967). Fish biomass in Hanson Lake (op. cit.) compared favourably with that found in other Saskatchewan shield lakes (Johnson 1967, Rawson 1960, Ryder 1965). Barr (1973) considered percids and coregonids to be most important in the diet of the loon. Together these two groups constituted more than half the standing crop of fish in Hanson Lake and the majority were within the size classes available for exploitation by loons (Sawchyn 1967).

An assessment of the adequacy of food supply for supporting the loon population on Hanson Lake was beyond the scope of this study. However food supply was not thought a limiting resource. As seen above, principal components in the diet were abundant. Furthermore the lake has been fished commercially in the past (Sawchyn 1967). Theoretically, commercial fishing should augment fish biomass available to loons. Removal of larger (older) age classes through commercial fisheries stimulates fish production (Healey 1975, Miller 1956) and leads to proliferation and increased biomass in the smaller, younger age classes (Christie 1968, Healey 1975, Nickolsky 1962). It is these younger size (age) classes which loons exploit (Barr 1973). Once commercial fisheries have stimulated fish production, sustained cropping by loons would serve to maintain fish production and delay reversion to the older more stable age distribution.

ii. Competition for Food

Many vertebrates which inhabit the lake environment are piscivorous and thus potentially compete for food with Common Loons. Four larids (*Larus argentatus*, *L. delawarensis*, *L. philadelphia* and *Sterna hirundo*) and two mergansers (*Mergus merganser* and *M. serrator*) frequented Hanson Lake commonly, but they forage mainly on cyprinids and other smaller fish which are not normally taken by loons. Mink (*Mustela vison*), Otter (*Lutra canadensis*), Osprey (*Pandion haliaetus*), Bald Eagle (*Haliaeetus leucocephalus*) and the White Pelican (*Pelecanus erythrorhynchos*) take fish within the size range taken by loons; although these species were observed regularly on Hanson Lake, their numbers were probably too low to have a significant competitive influence. Predatory fish, mainly Walleye (*Stizostedion vitreum*) and Northern Pike (*Esox lucius*), formed more than 25% of fish biomass in the lake (Sawchyn 1967), and were undoubtedly the loon's major natural competitors for food.

iii. Competition for Space and Nesting Sites

Other than the Common Loon, no bird species which breeds in the Hanson Lake region occupies large areas of open water as territories; thus loons were never excluded from Hanson Lake through interspecific competition for territory. The loon has been reported to be intolerant and aggressive towards other aquatic bird species within its territory (Munro 1939, Witherby et al. 1940). Loons and waterfowl (which were not abundant on Hanson Lake) have marked differences in habitat requirements (Sowls 1955).

The Common Loon typically nests on island shorelines (Olson and Marshall 1952), unlike other species inhabiting the lake.

Thus loons encounter no competition for nesting sites. The closest competitors for nest sites were pairs of Herring Gulls which nested on the tops of small islands and, while never using actual sites available to loons, they potentially deterred loons from nesting on certain islands.

#### iv. Predators

Adult Common Loons were virtually predator-free on Hanson Lake. Potential contact with mammalian predators existed only when on land during incubation and briefly during copulation. These activities were confined mainly to small islands which were generally not inhabited by mammalian predators. Although mink were abundant both on the mainland and islands, they would be incapable of taking adult loons under most circumstances. Among the local avian predators, only the Bald Eagle is known to feed opportunistically on diving birds (Munro 1938, Murie 1940). The only documented account of a Bald Eagle taking a gaviid involved an unhealthy Arctic Loon (see Hatler 1974). During this study unsuccessful attempts on adult loons by Bald Eagles were observed twice.

Mink, Herring Gulls and Common Ravens (*Corvus corax*) were common potential predators of eggs and newly hatched young. On occasion adult loons were observed successfully defending uncovered clutches against

both ravens and gulls. Northern Pike are known to take the young of aquatic birds (Solman 1945).

v. Interactions with Man

Frequent reference has been made to conflict between loons and commercial fishing interests, but Barr (1973) found that the economic impact of the loon was trivial. However loons are frequently drowned in commercial nets (Bartonek 1965, Parmelee et al. 1967) and setlines (Anthony 1921).

Commercial fishing on Hanson Lake has been largely discontinued. During the present study the lake was fished for two weeks in June, 1974, and two adult loons drowned in nets.

Although accessible by road, there has been little recreational development on Hanson Lake. The number of boats seldom exceeded 15 at any one time. A primitive outfitting camp offers 10 small boats for hire, but they were generally inadequate for travel other than in the shelter of Bertrum Bay. Local people occasionally visited the lake for weekend angling.

#### IV. THE BREEDING CYCLE

##### 1. SPRING ARRIVAL

Spring arrival of Common Loons at Hanson lake commenced early in relation to the seasonal phenology. Most territories were established before ice had completely disappeared.

All birds arrived on Hanson Lake in adult breeding plumage (as described by Palmer 1962). Subadults have been reported as far north as Cold Lake, Alberta (K. Vermeer, pers. comm.), but normally remain on wintering grounds (McIntyre 1975). No subadults were observed on Hanson Lake.

##### i. Pair Formation

Most authors report that loons arrive paired (Sjolander and Agren 1972, Yeates 1950). In Minnesota, McIntyre (1975) found 50 to 70% arrived unpaired and remained unpaired up to two weeks, and that the proportion of unpaired arrivals was lowest in phenologically late years.

Although it was seldom possible at Hanson Lake to establish precisely the times at which particular birds arrived, daily surveys of Bertrum Bay provided this information to within 24 hours. Considering 1973 and 1974 jointly, and deriving territorial limits in retrospect, 17 territories which were included in surveys on the day of initial breakup contained

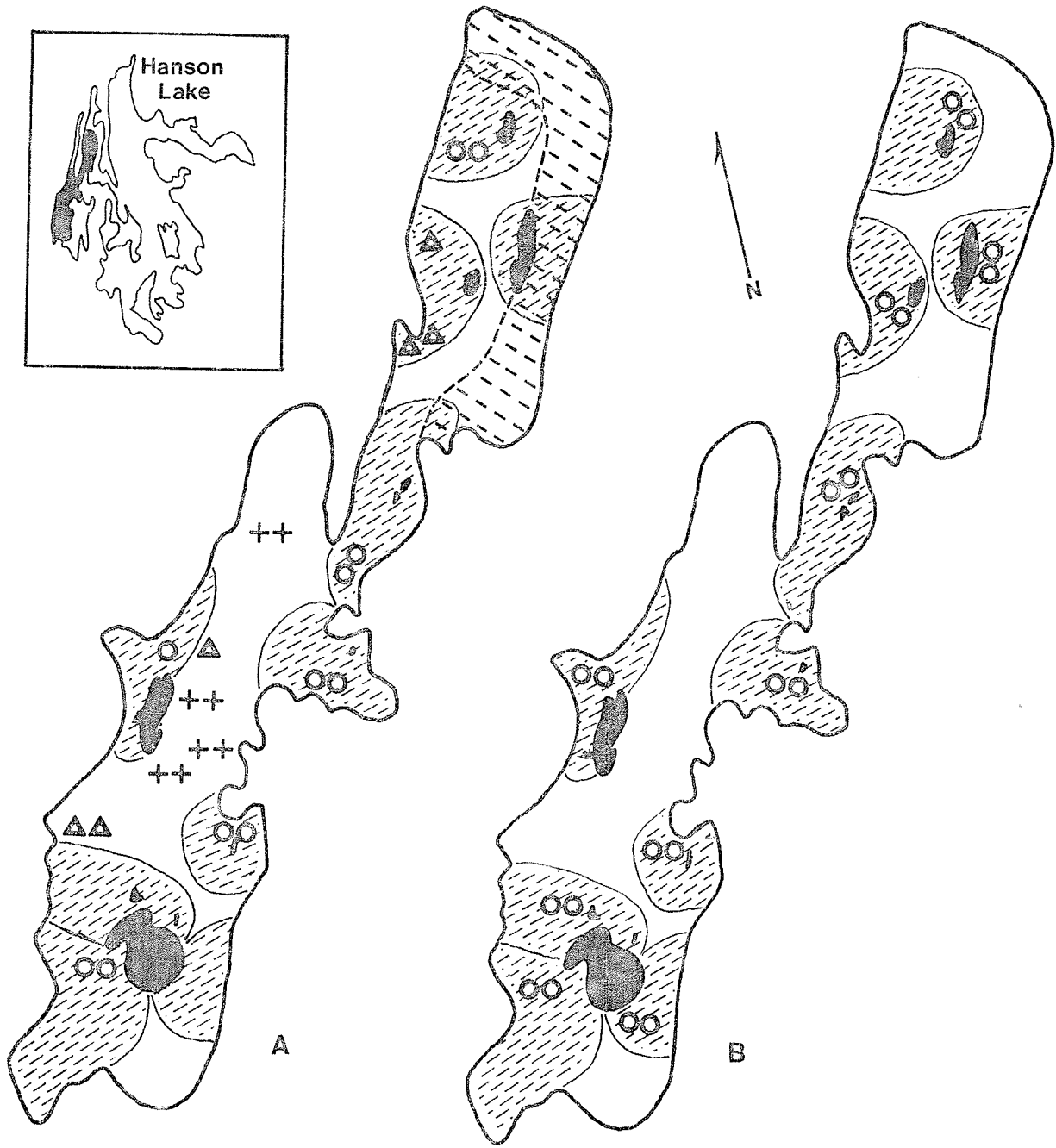
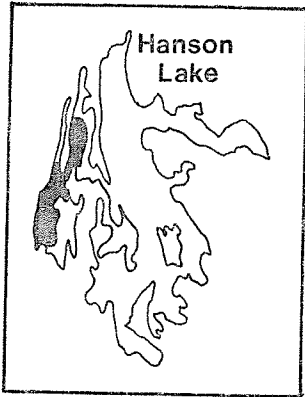
loons at that time. Sixteen of these observations were of pairs and one was of a single bird. Similarly, one day following initial breakup, 24 of 25 occupied territories contained paired birds. Excluding individuals which remained single during summer, all secured mates within four days of arrival. Most birds, including those presumed transients on areas ultimately not parts of territories, were paired when observed on arrival. It was evident that pairing took place prior to arrival on the territory.

ii. Chronology

Common Loons arrived as soon as there was open water sufficient to permit take-off and landing. Each year loons arrived first at the mouth of the Bad Carrot River, an area which opened one to two weeks before ice receded from lakeshores. In 1973 this location opened late in April and a pair of loons arrived on 1 May (F. Garrett, pers. comm.). A pair was observed there each day until ice-off at which time surveys were discontinued. A second pair was not observed that year until a small bay, which opened on the evening of 11 May, was occupied on 12 May. Subsequently, newly opened patches of water were occupied immediately by loons. Areas which were to become territories contained pairs of loons when still largely ice-covered.

Mass arrival occurred within hours of the first disintegration of ice cover. For example, initial breakup in 1973 commenced on the morning of 15 May, and an evening survey of Bertrum Bay revealed 25 birds on an area encompassing 10 territories (Fig. 4A). At that time loons were

Figure 4. Pattern of spring arrival by Common Loons on Bertrum Bay in 1973. The distribution of birds on the area surveyed is shown on A. May 15 (day of initial breakup), and B. May 18. Areas shown as territories were determined in retrospect. Inset shows area surveyed.



- resident adult
- + transient adult
- △ uncertain status
- territory
- ice
- island

present on 7 areas which ultimately became territories; many additional birds occupied open water non-territory areas and were presumably transients enroute elsewhere or awaiting icebound territories to open (Fig. 4A). During breakup, pairs were observed frequently at the edge of icepacks covering unopened areas of the lake, apparently awaiting access to territories. On a survey of this area three days later, no transients were observed and the 10 territories were each occupied by one pair of loons (Fig. 4B).

In 1973, Bertrum Bay became ice-free on 18 May. Although ice still remained on much of the lake, the distribution of birds on Bertrum Bay closely resembled that established for the duration of the breeding season. Twenty-one of 23 territories were occupied by pairs and two were vacant; five transients were observed. Birds thought to be transient were seldom observed once ice had entirely disappeared.

In summary, most birds were paired on arrival, and their arrival coincided precisely with the breakup of ice. A stable territorial structure was established as soon as birds arrived (established first on those areas which opened first). The exact co-ordination between arrival and breakup required that the birds be nearby prior to breakup, probably staging on open rivers adjacent to the study area. Although spring aggregations of Common Loons have not been reported at this latitude, they have been observed at Centerville Lake, Minnesota, where 200 to 300

loons staged but did not breed (Olson and Marshall 1952). Prior to breakup of inland breeding habitat, Arctic and Red-throated Loons aggregate on nearby coastal waters (Davis 1972). Such aggregations would permit the co-ordination of arrival with breakup, and would permit pair formation to occur prior to arrival, as observed.

Arrival at Hanson Lake was more precise than that reported at southern latitudes. In British Columbia, where breakup occurred some three weeks earlier, arrival was earlier in relation to date but later in relation to breakup (Munro 1945). In Minnesota arrivals peaked three to eight days following breakup and continued for two weeks (McIntyre 1975), whereas at Hanson Lake arrival peaked the first day and ended within four days; pairing was also accelerated at Hanson Lake. Increased precision in pre-breeding chronology has been well documented as a function of latitude (Barry 1962, Sealy 1975).

## 2. THE TERRITORY

Territories were established immediately following arrival in spring, some probably by pairs which held them the preceding year. The distribution of territories and their boundaries varied little from one year to the next (Appendix I). Common Loons maintain a Type A breeding territory (Hinde 1956) within which all activities associated with summer residence normally occur. Their territory consists largely of lake surface area and is defended from the open water. By defending areas of water as territories, other individuals are not permitted access to shoreline within or adjacent to the territory, and consequently nest-sites are de-

fended indirectly. Small bays, channels and areas surrounding one to eight islands were occupied as territories. Boundaries usually coincided with conspicuous topographical features of the lake such as mainland points and islands (Appendix I).

Territorial behaviour and intraspecific aggression in the Common Loon have been described by Rummel and Goetzinger (1975). Vocalizations are the primary means used in defense of territory, and this role has been ascribed to males (op. cit.). The "Yodel", the territorial call exclusive to males, was given most frequently in response to conspecifics flying over the territory, but also in response to a neighbour's "yodel" or spontaneously. The frequency of "yodels", and hence territorial aggressiveness, peaked during the prenesting period and declined steadily after nesting began. By mid-August "choruses" which were audible most of the night in spring became brief and infrequent. Throughout the summer daily peaks in calling coincided with peak flight activity at dusk, a pattern which continued throughout the summer.

Territorial distribution on the lake was established rapidly following arrival, and remained unchanged until fall departure commenced. Wing-tagged birds always remained on the same territory, thus territories were occupied by the same individuals throughout a season. During the prenesting and nesting periods, territories were at no time left unoccupied, and both adults were usually present. Broods were reared entirely within the territory, in the presence of one or both adults.

Although unpaired adults moved through undefended areas on

Minnesota lakes (Olson and Marshall 1952), singles on Hanson Lake appeared to hold territories like paired adults; singles restricted their activities to specific areas during the nesting period. Once the nesting effort ended in early July, single birds and pairs which lacked young often left their territories daily to aggregate for several hours on undefended areas of open water. This occurred with increasing frequency toward the time of fall departure, but pairs remained intact and birds always returned to territories before nightfall. The mid-summer aggregations of adults reported by Nero (1972), Rand (1948) and Wade and Wade (1963) illustrate this behaviour. The movement of birds returning to territories coincided with evening peaks in calling.

### 3. POPULATION SIZE AND STRUCTURE

The Common Loon population on Hanson Lake was large and apparently stable over three years (Appendix I). Each year an average of 200 adults (or one bird per 19 ha of lake surface), maintained territories on the lake (Table 2). The density of birds was greater by more than six times that found in other studies in Ontario (Barr, pers. comm.), British Columbia (Munro 1945), and Minnesota (McIntyre 1975, Olson 1951). However this was not an unusually high density, but characteristic of that found on other lakes adjacent the study area (G. Anweiler and K. Yonge, unpubl.).

The density was due to three factors. Most importantly, the many islands provided both an abundance of preferred locations for nesting (McIntyre 1977), and points about which territories are usually centered (Munro 1945). Although not a territorial requirement in the strict

Table 2. Status of adult Common Loons on Hanson Lake.

Status <sup>1</sup>	Numbers			Mean Percent of Population
	1973	1974	1975	
Breeding pairs	74	81	84	80.1
Probable-breeding pairs	5	4	0	3.0
Undetermined pairs	13	12	7	10.7
Non-breeding pairs	4	5	7	5.4
Paired birds	192	204	196	99.2
Unmated birds	1	0	4	0.8
Total birds	193	204	200	100.0

<sup>1</sup> Defined in methods.

sense, islands no doubt enhance the potential of an area as a territory. Secondly, the irregular configuration of the mainland shore divided the lake into numerous pockets and bays, thus providing territories which were naturally well delimited and probably defended easily. Thirdly, although accessible by road, Hanson Lake had little recreational or commercial pressure, conditions to which loons show limited tolerance (McIntyre 1975).

The population consisted almost entirely of paired birds (Table 2). Unmated adults occupied only 5 of 301 territories on Hanson Lake from 1973 to 1975. There were many fewer single adults in the Hanson Lake population than reported in populations in Ontario (J. Barr, pers. comm.) and Minnesota (McIntyre 1975, Olson and Marshall 1952). Barr (1973) collected paired and unmated adult Common Loons and found that unmated birds were smaller, and possibly younger. The apparent absence of unmated birds on Hanson Lake suggests they filter out of migratory populations early, and few reach northern breeding areas. On lakes such as Hanson on which loon populations are large, intense competition for territories among pairs may also deter unmated individuals.

Each year about 80% of the population were known to nest (Table 2). Although non-breeding pairs formed 18% of Olson's (1951) population, only five percent of the Hanson Lake population could be confidently classed as non-breeding. Eleven percent of the population were of undetermined status and three percent were of probable-breeding status (Table 2). As most of these probably nested unsuccessfully, breeding pairs formed more than 90% of the population on Hanson Lake.

#### 4. NEST-SITE VEGETATION AND NEST COMPOSITION

Common Loon nests varied from crude depressions to elaborate mats of vegetation. Although nests were often surrounded by water, they were always constructed on a firm substrate. No floating or semifloating nests were observed.

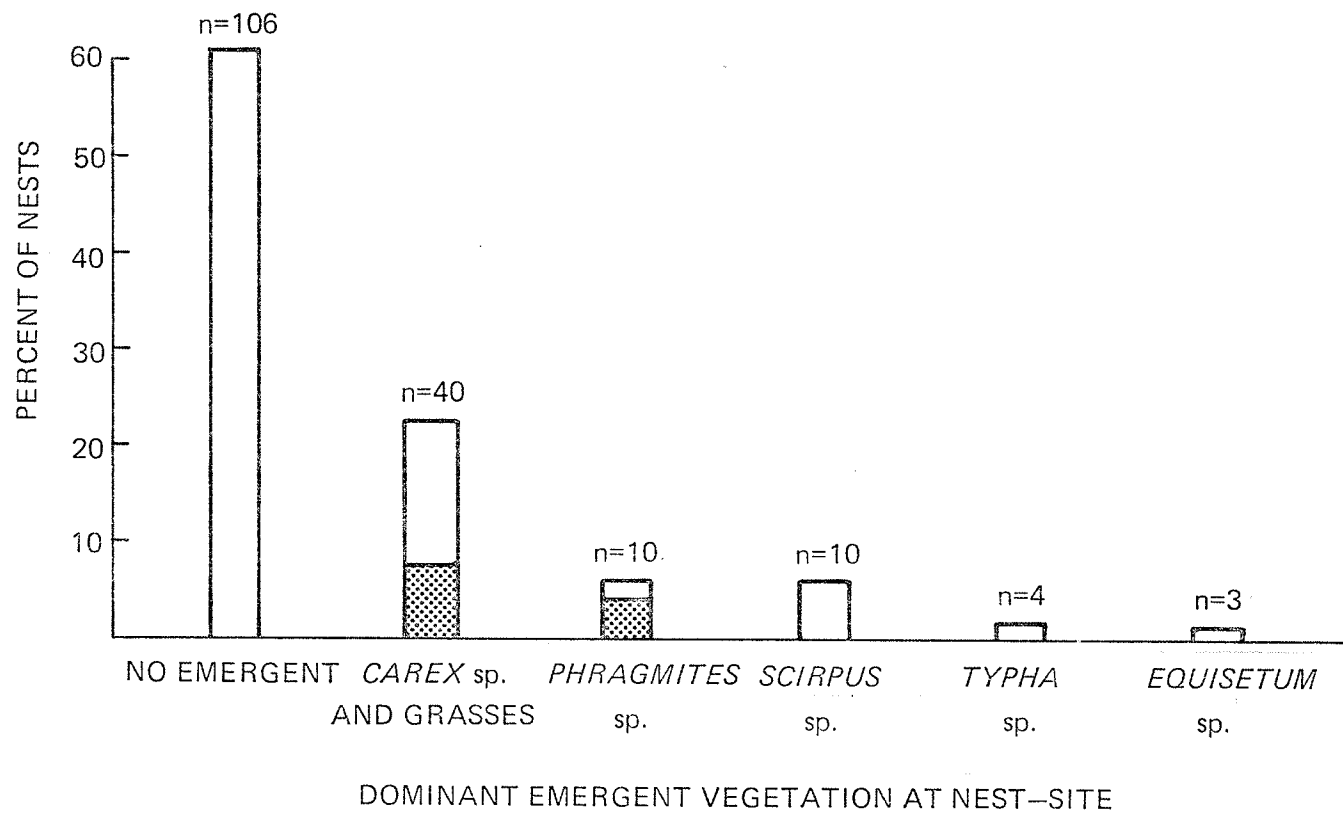
Nest building was seldom complete prior to laying. Usually, the first egg was deposited in a crude nest cup, and the remaining nest materials were added during early incubation. Material was rarely added to the completed nest unless it was threatened by rising water or wave action.

##### i. Cover from Emergent Vegetation

Nests were seldom in the cover of emergent vegetation. Sixty-one percent were devoid of emergent cover within one meter (Fig. 5); 23 percent were located near sparse *Carex* sp. and unidentified grasses which grew intermittently along most shorelines. Four genera of larger emergents were found on the lake, but only 16 percent of the nests were near or among them (Fig. 5).

The fact that few nests were in the cover of emergent vegetation reflected in part its sparse distribution on the lake, but in part a preference for nest-sites which lacked emergent cover. Although emergent

Figure 5. Dominant emergent vegetation at Common Loon nests.  
Stippled portions show proportion of nests in which  
dominant vegetation formed the primary nest material.



vegetation was available on most territories, nests were seldom placed there. Nests located within emergent vegetation were usually placed peripheral to the main growth and with unobstructed visibility toward open water. Unobstructed visibility from the nest-site was considered a nesting requirement by Munro (1945). A preference for emergent cover has been suggested in loon populations studied south of the Shield (Henderson 1924, Olson and Marshall 1952), but emergent growth in those habitats was widespread and well developed. Even in those more productive southern habitats where most shorelines support emergent cover unprotected nests were not common. Sharp and Richardson (1976) found a negative correlation between the presence of emergent vegetation and the distribution of loons near shorelines.

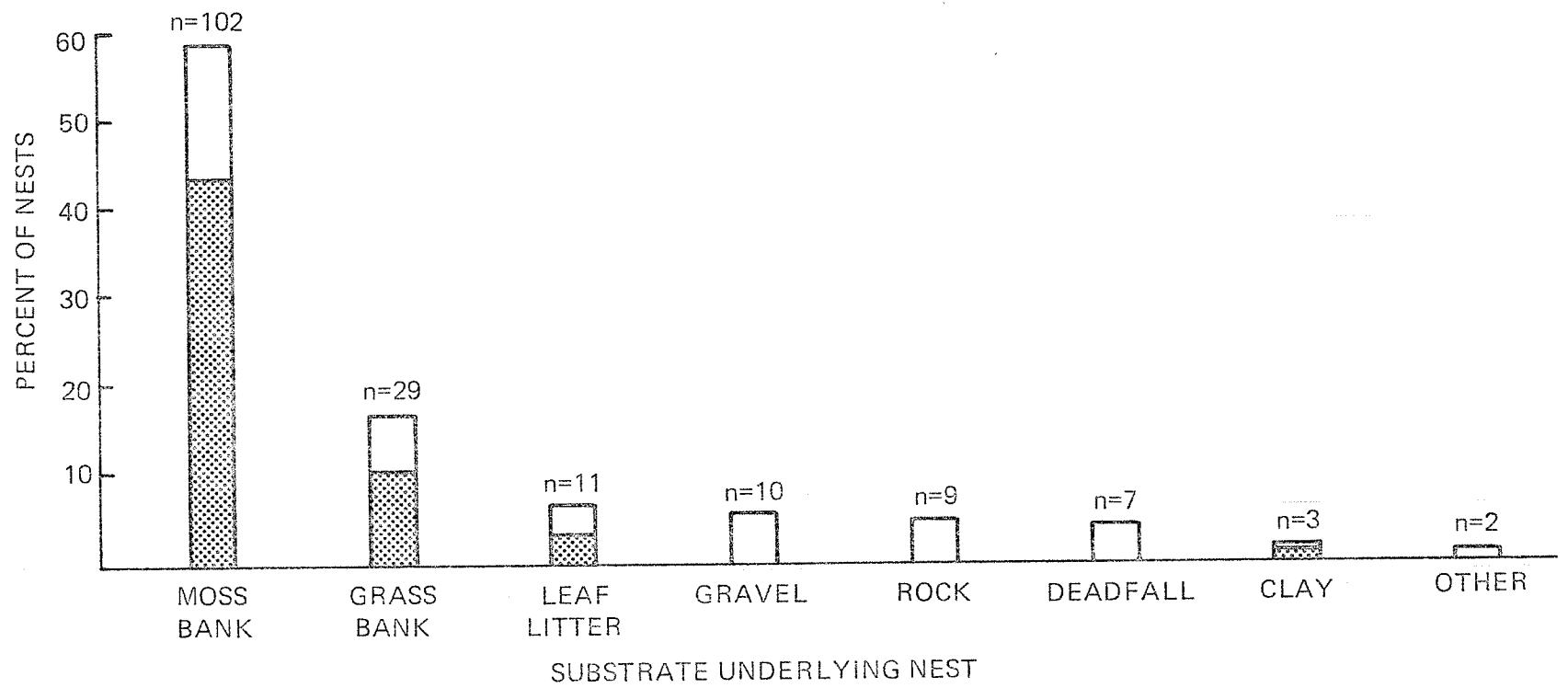
ii. Substrates Under Nests

Nests were always placed on solid substrates (Fig. 6). Fifty-nine percent were on banks of moss, the most common component of the shoreline herb layer. Grassy banks were also common substrates. Those used less frequently included leaf-litter, pebbles, rock, deadfall and clay.

iii. Nest Composition

Nests are usually constructed from materials gathered unselectively from the immediate vicinity of the nest (McIntyre 1975, Olson and Marshall 1952). This was evident at many nests on Hanson Lake where ground vegetation within one half meter of the clutch had been scraped into the nest.

Figure 6. Substrates under Common Loon nests. Stippled portions show occurrence of substrates as primary nest material.



Selectivity in nest composition was evaluated by noting whether the primary material corresponded to either the dominant emergent vegetation (where present) or the substrate on which the nest had been placed. Nest materials included the range of vegetation types available (Table 3). Chunks of moss pulled from the vicinity of the nest were found in 75% of nests and formed about 41% (by volume) of all materials used. Moss chunks compacted well and provided the most rigid and permanent nest structures. *Carex* sp. and unidentified aquatic grasses were also major components of nests (Table 3). Twigs were identified in 23% of nests and leaf litter in 13%, but contributed little to the overall volume of nests (Table 3). Apparently these components were selected inadvertently during nest building. Larger emergents and detrital vegetation from the lake bottom were added to several nests in negligible amounts. Twenty-eight percent of nests consisted of little more than a depressed cup in the soil substrate of the bank with little or no vegetation added.

Where emergent vegetation was available it was invariably included in the nest structure, but was incorporated as the primary material in only 30%. The type of emergent available was a factor in whether it was used. At 40 nests where *Carex* sp. and aquatic grasses were available, these formed the primary material in only 33% (Fig. 5). However, where *Phragmites* sp. was available ( $n = 10$ ), it was the primary material in 70% (Fig. 5). Nests of *Phragmites* occurred where sheaves of dead stems washed ashore and had been rearranged to form the bulk of the nest. Therefore the use of *Phragmites* involved no selective accumulation by the

Table 3. Composition of 173 Common Loon Nests.

Material	Percent Occurrence <sup>1</sup>	Percent by Volume <sup>2</sup>
Moss chunks	75	41
<u>Carex</u> spp. and unidentified aquatic grasses	73	20
Twigs	40	2
Leaf litter	23	4
Detrital vegetation from lake bottom	12	3
<u>Phragmites</u> sp.	9	3
<u>Scirpus</u> sp.	9	1
<u>Typha</u> sp.	2	trace
Soil substrate (little vegetation added)	48	25
Other	2	trace

<sup>1</sup> Percent of nests.

<sup>2</sup> All nests pooled.

birds. No other large emergents formed the primary material of any nests, and generally the use of emergent vegetation in nest building was avoided.

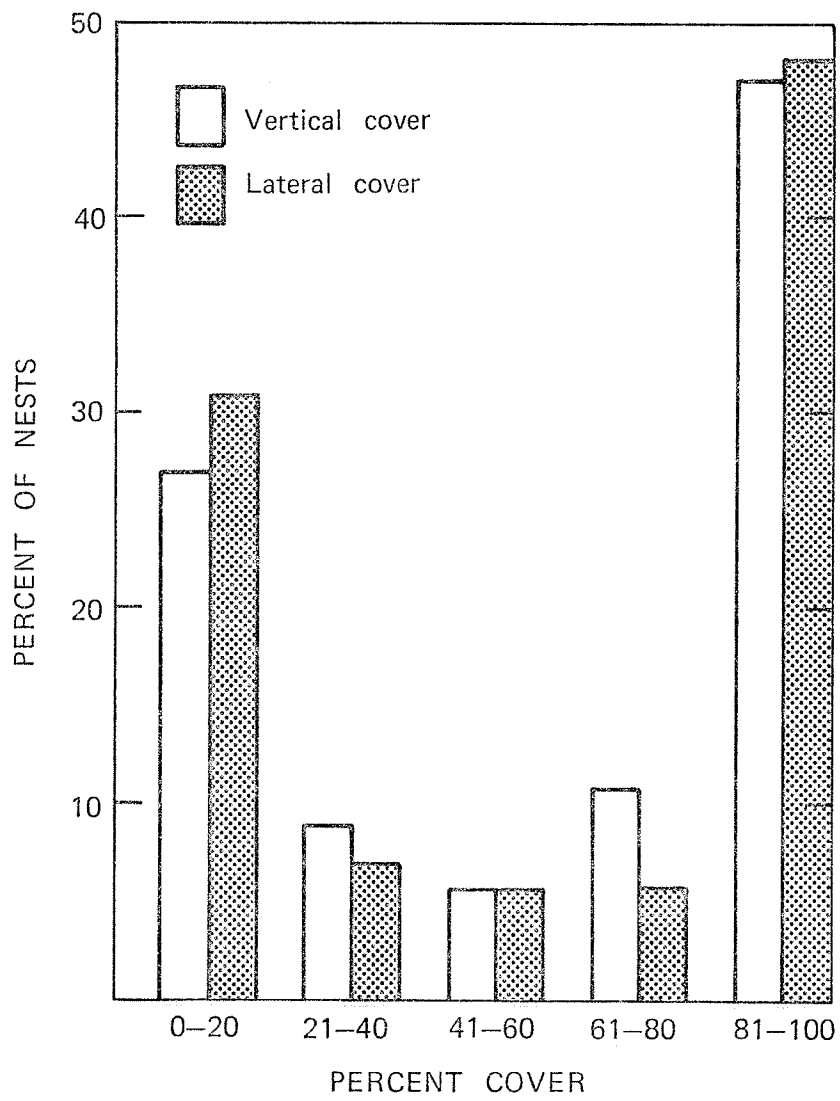
Where nests were placed on vegetative substrates, those substrates were usually the primary nest material also (Fig. 6). Where nests were placed on soil or rocky substrates, vegetation was gathered to form the nest structure. The majority of nests were built on vegetative substrates and consequently the substrates underlying nests usually formed the primary nest material.

#### iv. Clutch Concealment

Olson and Marshall (1952) found Common Loons selected nest-sites concealed from visually hunting predators by terrestrial rather than aquatic vegetation. Similarly nests on Hanson Lake were within small openings in dense shoreline foliage so that the nest was concealed but movements of a bird were not hindered.

Vertical and lateral cover estimates at each nest usually fell within the same percent class as both estimates measured mainly the density of the overhanging terrestrial shrub layer. Only about 30% of nests had 20% cover or less (Fig. 7), and for the most part these lacked cover entirely. Most nests were obscured by some (21-100%) covering vegetation (Fig. 7). Long (1970) found that even a sparse growth of foliage provided sufficient cover to reduce detection of duck nests by visual predators through disruption of the outline of the clutch; 70% of loon nests were in this way somewhat protected and half were concealed almost entirely by vegetation

Figure 7. Vegetation cover at 173 Common Loon nests.



(Fig. 7). Apparently this was not due to a preference by the loons, but because most shorelines were densely foliated. Generally foliage on Hanson Lake shorelines was either well developed and overhanging water or absent within one to two metres of the lakeshore.

#### 5. NEST PLACEMENT

Lack (1968) viewed island nesting by birds as an adaptation to reduce clutch loss to mainland-inhabiting mammalian predators. Common Loons, which nest mainly on islands (84% of nests on Hanson Lake), illustrate this adaptation well. Loons lay large eggs which are both conspicuous and attractive to predators. The nest itself is a conspicuous structure due to its size. The size and awkwardness of the adult on land also serves to draw attention to the nest. As young were produced on several territories which lacked islands (Henderson 1924, McIntyre 1975, Olson and Marshall 1952, present study), the presence of an island is not an essential component of a territory. However, islands undoubtedly enhance the suitability of an area for occupation as a territory by loons.

Common Loons usually nest so that the rim of the nest is in contact with water and as a result their nests are vulnerable to wave action. On larger lakes, such as Hanson Lake, the potential for nest washout is high as large waves arise from winds which cross unsheltered expanses of water. Since the surfaces of such lakes are seldom calm, the choice of a well sheltered nest-site is an important prerequisite to nesting success in this bird.

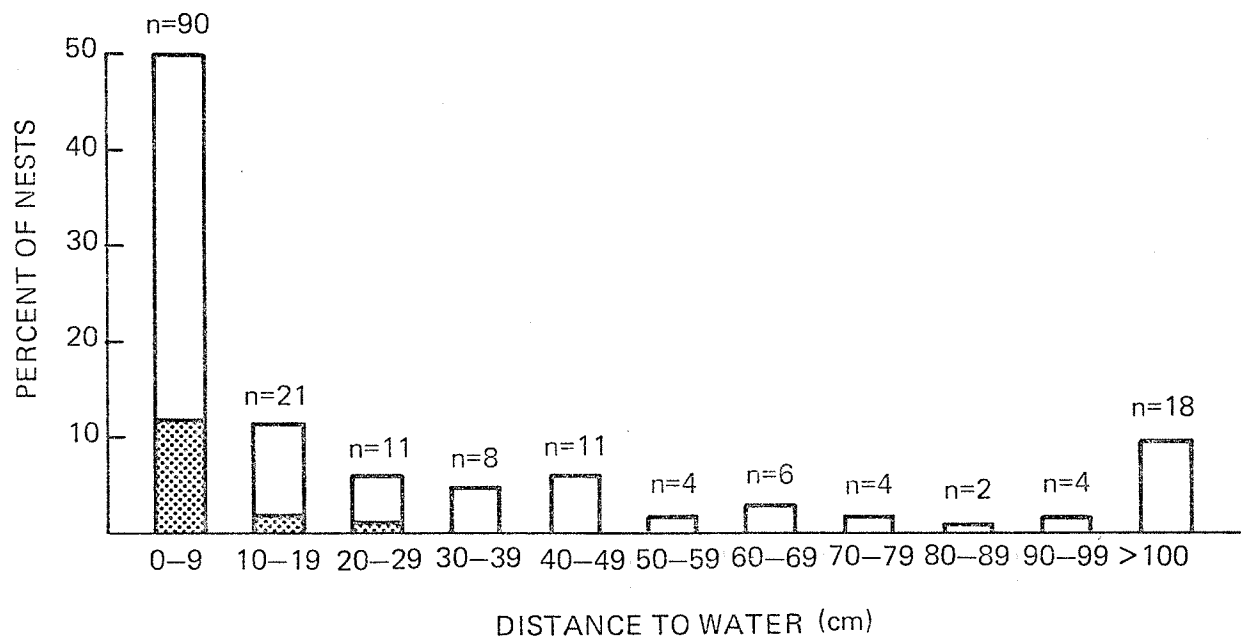
Theoretically there are at least three ways in which the potential for clutch failure due to washout could be reduced through the process of selecting a nest-site: 1) displacement, where the nest is placed upshore, further from water; 2) positioning, whereby nests are protected from wave action by irregularities in local shoreline topography; and, 3) directional orientation, where nests are placed on those shores least exposed to wind and wave action. Natural selection could favor any or a combination of such mechanisms. The importance of each was examined.

i. Displacement From Water

At 177 nests the distance between water and the leading edge of the nest was 1.5 m or less, 122 of these (69%) were within 0.3 m (Fig. 8). Two nests were on steeply inclined shores and were 2.2 and 4.0 m from water. About half the nests (50%) touched water, whether placed on shore or directly in the water. Those located in the water either touched the shoreline behind the nest or were entirely surrounded by water. Nests surrounded by water did not float, but were supported by submerged solid substrates such as logs, gravel bars or, most frequently, mats of aquatic vegetation.

Within the narrow range of nest-to-water distances, the distribution of nests was heavily clustered in those classes close to water. The distribution (Fig. 8) suggested no tendency for displacement, but rather a preference to minimize the nest-to-water distance. As all instances of clutch failure due to washout occurred at nests less than 0.3 m from water (23% of nests within this range), and as no washout occurred at

Figure 8. Distance to water from leading edge of Common Loon nests. Shaded portions represent proportions of nests in each category which were washed out during incubation (n = 28).



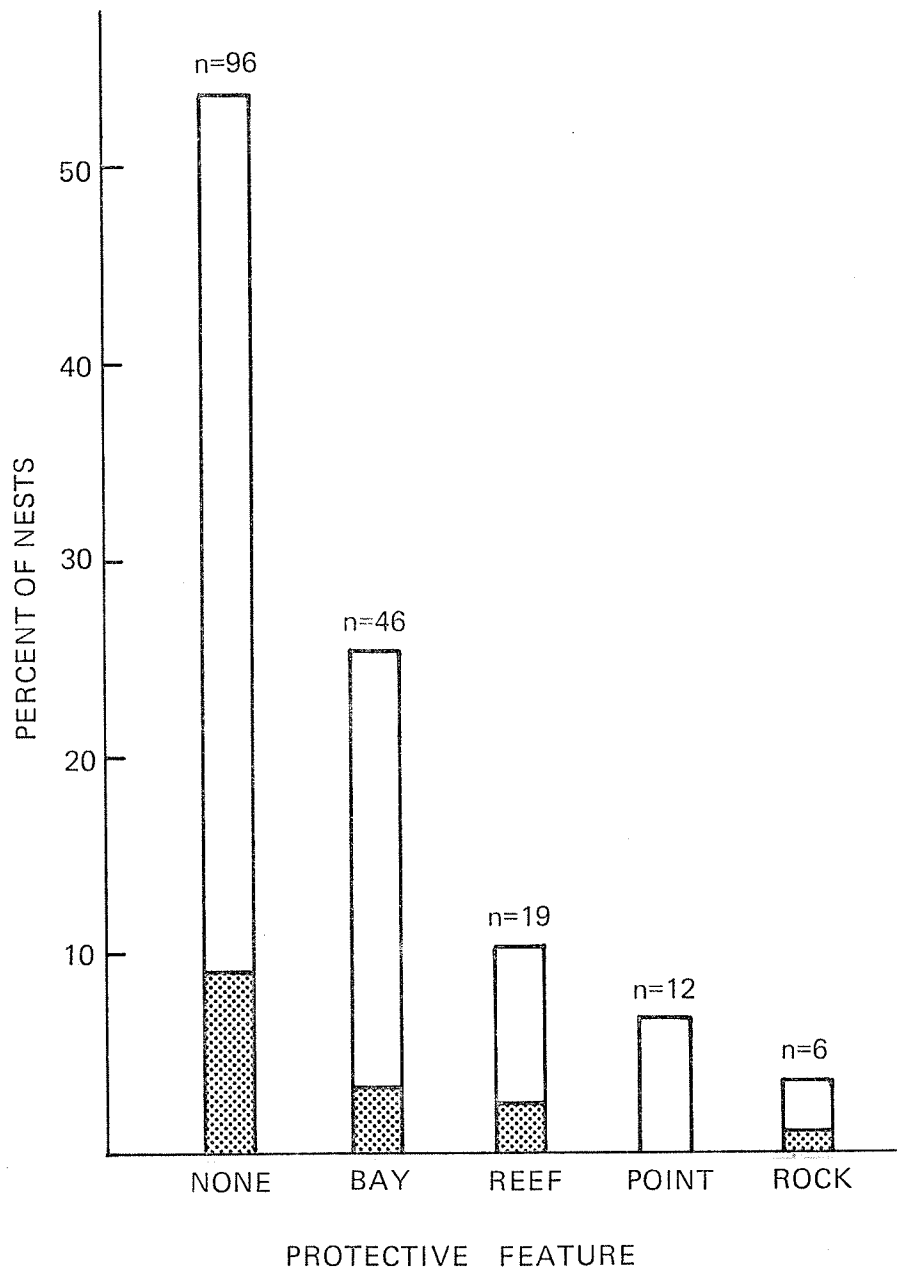
nests beyond this range (Fig. 8), it was apparent that clutch loss from washout could virtually have been eliminated by selection favouring pairs which nested beyond this limit. That this has not occurred suggests that protection of the clutch through nest displacement has been an impractical avenue for natural selection. Although nest displacement of less than one meter would be sufficient to avoid washout, it may be that a resulting minimal increase in adult activity at the nest may in fact make the nest more conspicuous to predators, and negate the benefits of reduced clutch loss to waves.

ii. Positioning

Features of nest-site microhabitat provided some clutches with protection from wave action (Fig. 9). Other studies have shown that loons often nest in bays or other concavities of shores which reduce direct exposure of nests to waves (McIntyre 1975, Olson and Marshall 1952). In this study the importance of such positioning was assessed by noting the presence of shoreline features which protected the nest from wave action. Bays, points, reefs, and rocks protruding from waters were among protective features which sheltered some nests on the study area. Although the nests of several grebes (Podicipedidae) derive protection from emergent vegetation (Simmons 1974, Nuechterlein 1975), emergents were of little consequence to loons on Hanson Lake.

Since most nests received no protection through positioning (Fig. 9), it appeared that shoreline irregularities were not important criteria in the selection of nest sites. Only 26 percent of nests were in

Figure 9. Features of the shoreline which provided protection from wave action at Common Loon nest-sites (n = 179). Shaded portions represent proportions of nests in each category which were washed out during incubation.



bays, with fewer yet in the shelter of reefs, points and rocks (Fig. 9). Although almost half the nests had some protective features, the 17% rate of washout at protected nests was the same as at unprotected nests ( $\chi^2 = 0.14$ , NS).

Protective features were equally common at nests 0.3 m or farther from water (nests not vulnerable to wave action) as at those within the vulnerable range ( $\chi^2 = 0.51$ , NS). When only nests within the range vulnerable to washout were considered, waves destroyed equal proportions of nests with and without protective features ( $\chi^2 = 0.03$ , NS). Overall it appeared that clutches derived little protection against washout from shoreline irregularities, and no preference was shown for protected sites.

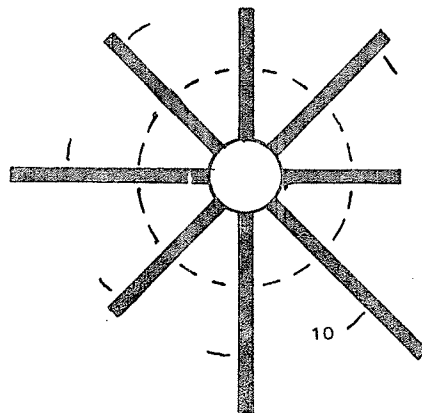
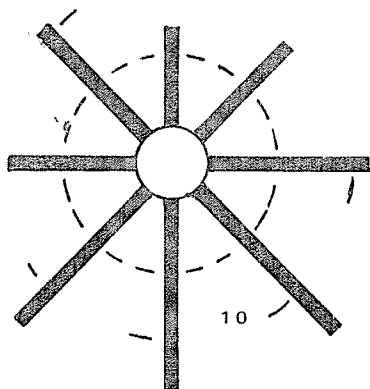
### iii. Directional Orientation

Direction has been noted as a factor which influenced nest-site selection in loons. In Finland, where winds prevail from the south, Lehtonen (1970) found 90% of Arctic Loons nesting on sheltered northern shores of islands. In Minnesota, Common Loon nests were concentrated on northwestern shores of lakes due to wind-induced vegetational differences (McIntyre 1975).

Nests on Hanson Lake were classified (in 8 categories) according to the direction faced by the shore on which the nest was situated. No preference was evident when all nests were considered collectively (Fig. 10A), nor were nests positioned in relation to mean wind patterns (Fig. 10B). Spearman's coefficient of rank correlation (0.14 in 1973; -0.31 in 1974)

Figure 10. Directional orientation of nests on Hanson Lake in 1973 and 1974 in relation to wind. A. numbers of nests per direction, and B. amount of wind per direction (percent of total mileage).

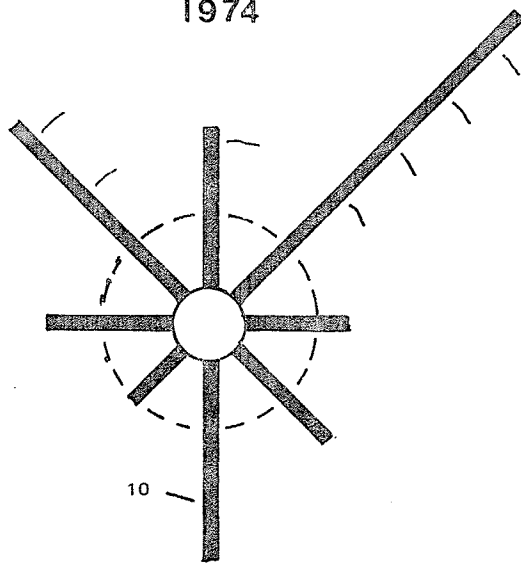
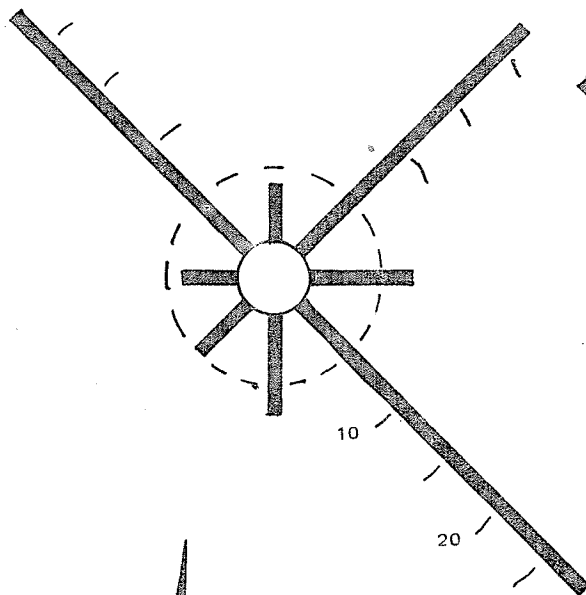
A



1973

1974

B

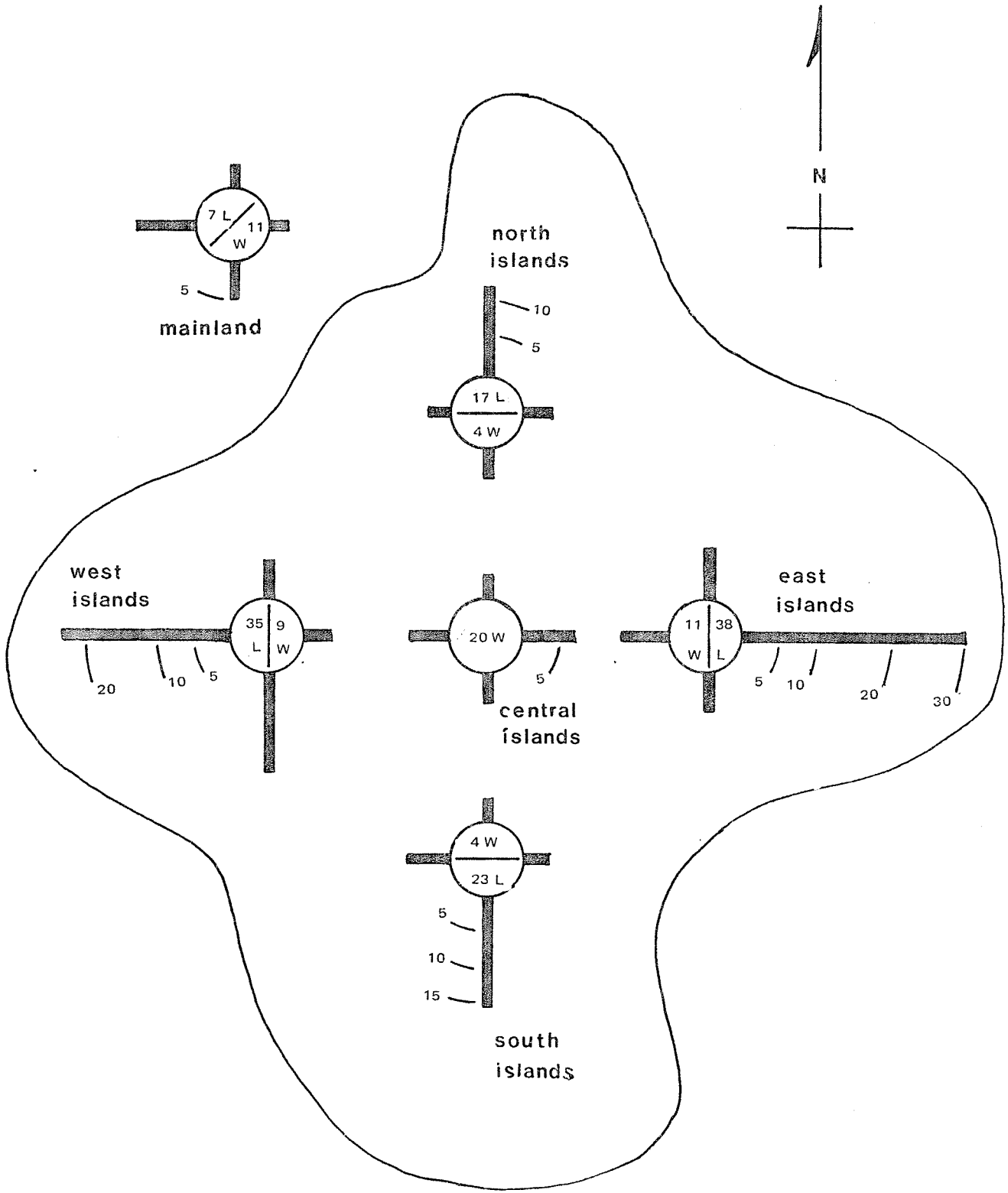


showed independence between eight wind directions and corresponding directions of nest placement. Wind direction alone was not a factor governing nest placement. Since both wind speed and direction were highly variable (Canada D. of T. 1973-1975), and since incubation is lengthy, no directional preference in itself would ensure protection from wave action.

Despite independence between nest direction and wind direction overall, directional orientation proved to be an important component of the nest-site selection process. Based on the position of nest on the lake as a whole, six categories of nest locations were considered. North Islands, East Islands, South Islands and West Islands, collectively termed "Peripheral Islands", were situated within the shelter (<250 m) of the north, east, south and west shores, respectively. Central Islands were those more than 250 m from the nearest shore (thereby unprotected), and Mainland locations were all those not on islands. In addition, nests on islands with proximate mainland shore were judged as "Water-facing" or "Land-facing", depending on which side of the island they were positioned (according to an imaginary bisecting line running parallel to adjacent shore). All nests on Central Islands were Water-facing; mainland nests, except those on the protected sides of mainland points, were also classed as Water-facing.

Nests located on peripheral islands were generally oriented toward the adjacent land mass, thereby deriving some shelter against the potential buildup of waves (Fig. 11). Of 141 nests on peripheral islands, 80% (113) were Land-facing. Nests on North Islands were concentrated on the sheltered northern shores of those islands ( $\chi^2 = 11.57$ ,  $df = 3$ ,

Figure 11. Directional orientation of nests shown in relation to island positions on the lake. Numbers of Land-facing (L) and Water-facing (W) nests are given for each class.



$p < 0.01$ ). Similarly, nests were placed predominantly on east shores of East Islands ( $\chi^2 = 34.51$ ,  $df = 3$ ,  $P < 0.01$ ), south shores of South Islands ( $\chi^2 = 14.33$ ,  $df = 3$ ,  $P < 0.01$ ), and west shores of West Islands ( $\chi^2 = 22.55$ ,  $df = 3$ ,  $P < 0.01$ ). Nests on Central Islands were uniformly distributed and showed no directional trends (Fig. 11).

Facing an adjacent shoreline, the nest is less vulnerable to destruction from waves. Wave buildup is less as winds cross only short expanses of water. The potential for increased nesting success is greater than would be the case where nests were oriented to direction only.

Not only would this behaviour of orienting toward land reduce wave action at the nest-site, but would allow more flexibility than either Displacement or Positioning in selecting sites from the range of sites available. Contrary to both Displacement and Positioning, a Land-facing orientation does not require any sacrifice of other site requirements such as direct access to open water and unobstructed visibility. It is also clear that land orientation could be maintained genetically and could be advantageous for nesting loons in all localities.

#### iv. Flexibility in Nest Placement

Further comparison of features of Land-facing and Water-facing sites revealed behavioural trends. Nests placed on Central Islands (which lacked Land-facing shores) were located farther from water: 40% were placed 1.0 m or more, whereas only 7% of Peripheral Island nests were placed within this range. Nest protection afforded by positioning in relation to shoreline habitat features was more frequent at Central

Island nests (70%) than Peripheral Island nests (46%), although this difference was not significant statistically. Similarly, shelter from features of the immediate shore topography was more frequent at vulnerable Water-facing sites (63%) than at vulnerable Land-facing sites (44%). It was evident that nest protection from Displacement and from Positioning was more prominent in nest-site choice where protection from Directional Orientation was less prominent.

As nest-site selection occurs over several days (Sjolander and Agren 1972) choice of protected sites may be explained as a response to proximate factors prior to laying. Natural selection could act by favouring birds which selected sites that were calm or provided some degree of security prior to laying. Conditions prior to laying generally would indicate the range of wave conditions to which a given site would be subjected. Land-facing shores with less vigorous wave action would be selected more frequently. Where protected shores are absent, an increase in other protective features would be required at a site to provide a pre-nesting bird with the same level of security.

Previous experience is also important in nest-site choice. Loons are long-lived (Dement'ev *et al.* 1968) and show territory affinity (McIntyre 1974). The role of experience is supported by the behaviour of nest-site tenacity characteristic of Common Loons.

## 6. EGG-LAYING

Each year laying occurred in a six week period from late May to the

end of June (Fig. 12). Laying commenced consistently on either 21 or 22 May, and peaked within the first ten days. No clutches were attempted past 1 July.

i. Synchrony

Although the duration of laying of both initial clutches and replacement clutches was the same each year, peak laying varied (Fig. 12) in relation to seasonal phenology. Variations in phenology are reflected by differences in the annual pattern of breakup. Although the date for onset of laying was the same each year ( $\pm$  one day), peak laying (50% of clutches started) varied from nine, six and four days after onset, during late, medium and early years, respectively (Fig. 13). Similarly during the early year (1975), the first 25% of clutches commenced within two days, whereas in the late year (1973) the 25% point was not reached until day seven of laying (Fig. 13). Annual differences had largely evened out by the time 75% of clutches had commenced.

Peak laying was more closely related to initial breakup than to ice-off (Fig. 13). Twenty-five percent of clutches commenced 13, 14 and 14 days following initial breakup in 1973, 1974 and 1975, respectively. The period from initial breakup to peak laying was similarly constant, showing just two days variation: 15, 17 and 17 days in successive years (Fig. 13). As most of the birds arrived on the day of initial breakup, onset of laying was more likely governed by arrival than by actual breakup. Territorial aggressiveness associated with the occupation of territories in spring is regarded as one of the releasers of gonadal

Figure 12. Dates of clutch commencement (1973 to 1975) showing initial clutches (n = 149) and replacement clutches (n = 48).

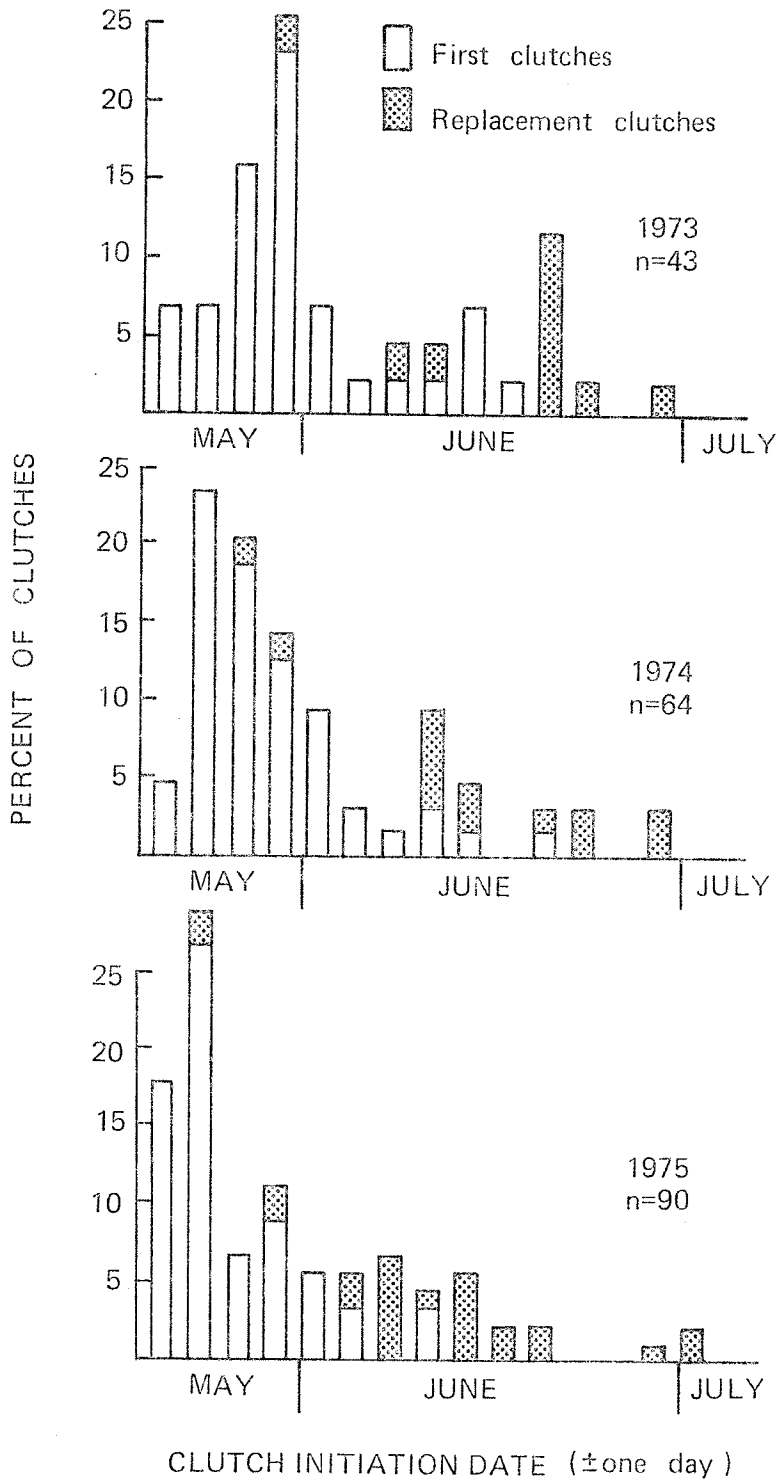
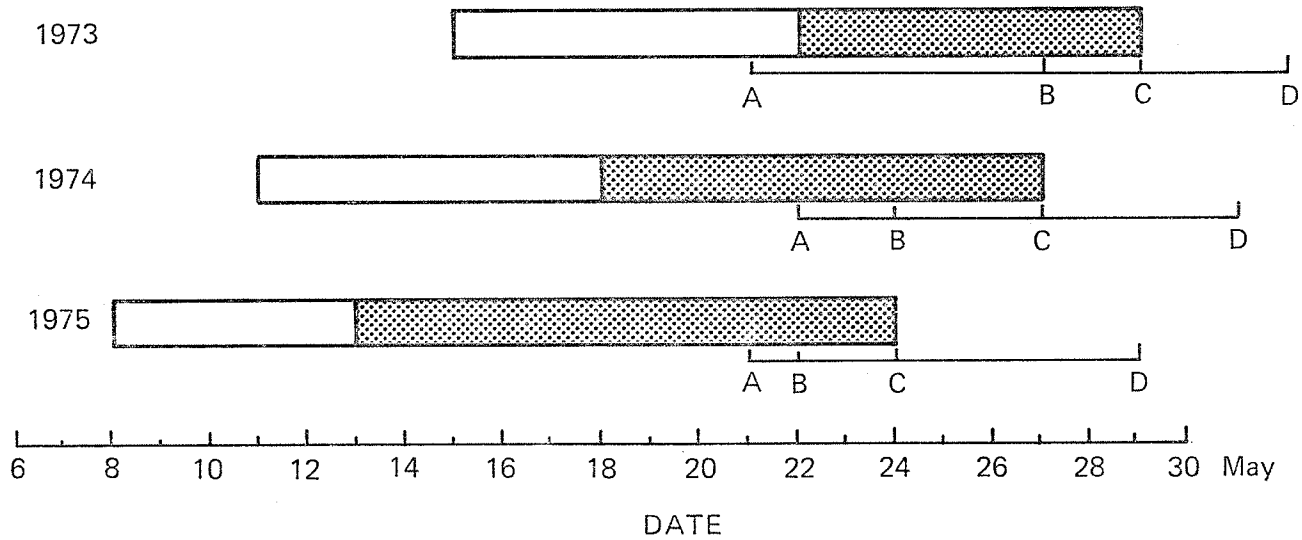




Figure 13. The pattern of clutch commencement (Initial Clutches) in relation to spring breakup on Hanson Lake. A. onset of laying; B. 25% of clutches commenced; C. 50% of clutches commenced (peak laying); and D. 75% of clutches commenced.



-  Period of breakup ( date of initial breakup to date of ice off )
-  Period from date of ice off to date of peak laying

cycles in birds (Lofts and Murton 1973, Marshall 1961). On average this cycle in loons appears to take two weeks to proceed to egg laying.

The interval between return in spring and egg-laying was brief on Hanson Lake. In Minnesota peak laying occurred four weeks following ice-off, with two weeks being the shortest interval between arrival and laying by an individual (Olson and Marshall 1952). However on Hanson Lake peak laying occurred seven, nine and eleven days after ice-off (Fig. 13), and one female laid a first egg four days after arriving on territory.

Reproductive expediency is favoured in populations occupying habitats in which favourable conditions are limited or reduced by climate. Such is the case on northern Precambrian Shield lakes. In species with extensive breeding ranges, delicate timing of breeding is common in those populations which nest at higher latitudes (Holmes 1966, Immelmann 1971, Lack 1968). Compared with Common Loons at lower latitudes (McIntyre 1975, Munro 1939), Hanson Lake birds arrive later where a shorter ice-free period prevails, yet compensate by laying earlier and compressing the nesting period. A similar laying chronology was found in the Common Loon in Iceland (Sjolander and Agren 1972) and in the Arctic Loon in Finland (Lehtonen 1970). The incubation and fledging periods in loons are lengthy, thus acceleration of the laying cycle and contraction of the breeding period in northern populations is necessary for successful reproduction.

In the Slender-billed Shearwater (*Puffinus tenuirostris*), the classical example of laying synchrony, 85% of the population starts lay-

ing in a seven-day period (Marshall and Serventy 1956, Serventy 1963). Loons at Hanson Lake were not greatly different in synchrony, as 75% nested within nine days (1975) to twelve days (1973). This synchrony was more remarkable considering loon pairs are solitary and lack the unifying influence of intra-colonial stimulation (Darling 1938) which operates in shearwaters. In spite of solitary nesting and large inter-pair distances, social interaction (largely vocal) is frequent. Vocalizations, important components of territorial behaviour (Rummel and Goetzinger 1975) and courtship (Tate and Tate 1970), may function to co-ordinate reproductive events in Common Loon populations.

In some species, laying synchrony increases in late seasons (Cooch 1961, Barry 1962). The reverse was true in loons on Hanson Lake. This was apparently due to a limit on the onset of nesting, prior to which birds did not nest. This limit probably reflects endogenous control of the gonadal cycle. Since a preparatory pre-nesting period is required by loons (Olson and Marshall 1952), early seasons allow more flexibility in the length of pre-nesting activities, and therefore allow greater laying synchrony.

#### ii. Clutch Size

Audubon (1838) originally reported three eggs to be the usual clutch size of the Common Loon. Two eggs are now regarded as the norm, with frequent records of only a single egg. The three-egg clutch has proven anomalous (Boyer 1961, England 1955, England 1957). Among 548 active clutches examined in this and other studies, only five contained three eggs (Table 4). Only one of 252 clutches during the present study con-

Table 4. Clutch sizes of Common Loons in North America.

Region (Source)	N	1 Egg	2 Eggs	3 Eggs	Mean
North America, Entire Range (Anderson et al. 1970)	183				1.84
Alberta (Henderson 1924)	19	1	16	2	2.05
Alberta (Vermeer 1973a)	24	5	18	1	1.83
Minnesota (McIntyre 1975)	51	18	32	1	1.67
Minnesota (Olson & Marshall 1952)	47	21	26	0	1.55
Ontario (Royal Ontario Museum <sup>1</sup> )	155	42	113	0	1.73
Saskatchewan (present study)	252	54	197	1	1.79
All sources pooled	731	141	402	5	1.77

1 Ontario Nest Records Scheme (1887 to 1974).

tained three eggs: this was a replacement clutch of a pair which, having lost the initial clutch before the second egg was laid, probably represents the completion of two laying cycles.

Mean clutch size reported by other workers has varied from 1.55 to 2.05 eggs, with an overall mean of 1.76 eggs (Table 4). With the exception of Henderson's (1924) sample (Table 4), the contribution to these means by three egg clutches was trivial; variability was due entirely to the frequency of one-egg clutches. Anderson et al., (1970) reported a slight geographic variation in clutch size and suggested it may follow clines described for egg size and body size (Rand 1947).

The mean clutch size of 1.79 eggs, based on 252 active clutches found on Hanson Lake, was the same as the mean of 1.76 eggs based on all the reports summarized in Table 4 ( $\chi^2 = 0.05$ , 1 df, NS). However, 109 of those clutches were discovered after the onset of laying and possibly lost an egg prior to discovery; 39 additional clutches which were not incubated may have been incomplete. The remaining 104 clutches were observed daily during, and for at least three days following laying, and all but seven contained two eggs. All initial clutches followed through laying contained two eggs (Table 5). The seven one-egg clutches were all replacement clutches and were all initiated during the latest part of laying. The tendency for reduced clutch size in late clutches has been found in Horned Grebes (*Podiceps auritus*) (Ferguson 1977) and several other northern nesting species (Klomp 1970).

The most important finding here was the precision with which the

Table 5. Mean Clutch Size in Common Loons  
on Hanson Lake, Saskatchewan.

	<u>Total Active Nests</u>		<u>Adjusted<sup>1</sup> Total Nests</u>	
	N	X	N	X
Initial Clutches	189	1.84	74	2.00
Replacement Clutches	63	1.63	30	1.77
All Clutches	252	1.79	104	1.93

<sup>1</sup> Total Active Nests, excluding those not observed during laying nor incubated at least 3 days after laying.

Common Loon laid a two-egg clutch. When those clutches which could have provided erroneous data were excluded, there was no apparent departure from a two-egg laying cycle in initial clutches, and no evident flexibility in clutch size. This points to the importance of not assuming the number of eggs in a nest represents the number laid. Clutch size variation previously reported in loons is perhaps only an artifact of observation technique and, at best, possibly reflects different rates of egg loss in different areas.

Kendeigh (1952) pointed out that a precise distinction between determinate and indeterminate laying patterns is seldom possible. This is true in Common Loons. In 1975, Egg I was removed from 22 nests immediately after Egg II had been laid, for toxicological studies, reported elsewhere. No third eggs were laid, indicating clutch size is predetermined. Contrary evidence emerged where Egg I was lost to natural causes prior to Egg II: only Egg II appeared in 5 cases, Egg II and Egg III appeared in seven cases, and no further egg appeared in seven cases. Overall, the Common Loon appears to be a determinate layer with a margin of flexibility.

### iii. Laying Interval

Of 21 nests visited prior to and during laying, Egg II appeared two and three days after Egg I in 12 and 9 cases, respectively. On this basis, the laying interval somewhat exceeded two days. There was no trend for the longer, three day interval to occur either early or late in the season ( $T = 82.5$ , NS; Mann-Whitney test, Snedecor and Cochran 1967).

iv. Egg Dimensions

Analysis of egg dimensions was confined to 1975 data because measurements were made with greater accuracy that year. Lengths, breadth, weight and volume of eggs are summarized in Table 6.

Comparing eggs within a clutch, Egg II averaged 2.0 g lighter ( $n = 30$ ) and  $2.6 \text{ cm}^3$  smaller ( $n = 32$ ) than Egg I, but statistically the dimensions did not differ ( $P > 0.85$ ). However a statistical difference did exist ( $P < 0.05$ ) between eggs of the first and second laying cycles which occurred on a territory. Cycle I eggs averaged 6.7 g (5%) heavier and  $4.9 \text{ cm}^3$  (4%) larger than Cycle II eggs.

Hatchability was apparently not linked to egg volume, and weights could not be compared due to insufficient data. Examining initial and replacement clutches separately, mean volumes of 13 and 7 eggs, respectively, which failed to hatch when incubated full term were not significantly smaller.

Table 6. Dimensions of Common Loon Eggs from Hanson Lake in 1975.

Maximum length (L) - mm	77 - 96	87.1 (148)
Maximum breadth (B) - mm	48 - 61	54.7 (148)
Weight (W) - g	108 - 175	146.1 (128)
Calculated volume <sup>1</sup> (V) - cm <sup>3</sup>	95 - 161	129.5 (147)

$$^1 V = 0.63 \left[ \pi \left( \frac{B}{2} \right)^2 L \right] \text{ from Anderson et al. 1970.}$$

## 7. INCUBATION

In all loon species both sexes incubate (Palmer 1962). McIntyre (1975) found male Common Loons did about 60% of the incubation. Observations of 3 wing-tagged pairs on Hanson Lake indicated role-sharing during incubation and hatching.

Although Palmer (1962) reports the presence of a brood patch, 10 individuals, including at least three females, captured from nests on Hanson Lake showed no brood patch. McIntyre (pers. comm.) who also found no brood patch on Minnesota birds in the hand, suggests the feet may be used to incubate. Use of feet has been documented in the Gannet (*Sula bassana*) which undergoes a vascularization of foot tissue during nesting (Nelson 1966). In loons, the feet are located well back on the abdomen, and the eggs are positioned between them. As the feet generally feel warm to touch, it is likely they are used to incubate the eggs.

### i. Incubation Period

Incubation period is the interval between laying and hatching of the last egg in a clutch (Swanberg 1950). Incubation period for the Common Loon has always been given as 29 days (Bent 1919, Olson and Marshall 1952, Palmer 1962). However, where methods for determining incubation period have been given, the reported 29 day "incubation period" refers more appropriately to "egg stage" (laying of first egg to hatching of last egg).

The average incubation period in Common Loons on Hanson Lake was 26 days (Table 7). The egg stage averaged, as found for Common Loons

Table 7. Duration (days) of Incubation in Common Loons on Hanson Lake.

	Range	Mean (n)
Duration of Egg Stage (one or more eggs in nest)	27.4 - 30.6	28.6 (17)
Duration of Egg I in nest	26.6 - 30.4	27.7 (6)
Duration of Egg II in nest (Incubation period)	24.6 - 30.1	26.2 (17)

elsewhere, approximately 29 days, but varied by as much as 2 days (Table 7). The duration of Egg II in the nest was always less than for Egg I, shorter by as little as 3 hours and as long as 2 days. The 26 day incubation period shown by Common Loons is the same as in other species of loons. Arctic Loons incubate for 26 (Davis 1972) to 27 days (Sjolander 1968) and Red-throated Loons do so for 25 (Davis 1972) to 26 days (Johnson and Johnson 1935).

ii. Onset of Incubation

Clutch attentiveness during incubation exceeds 99% (McIntyre 1975), and sitting commences with the first egg (*op. cit.*, Palmer 1962). Although this was generally true at Hanson Lake, clutches started late in the nesting season were often unattended when incomplete.

Egg I was in the nest an average of 1.5 days longer than Egg II (Table 7), indicating either a delay in the onset of incubation until arrival of Egg II or differential developmental rates within a clutch. On the one hand, Swanberg (1950) noted a clutch may be covered yet not incubated, and gave numerous examples where incubation of covered clutches was postponed until deposition of the last egg. In other species, on the other hand, differential development has been found to occur during late stages of incubation (Vince 1969). Paludan (1951) found that, with only partial covering during the laying cycle, embryo development in gull eggs proceeded at about half the normal rate.

Of 50 clutches on Hanson Lake tested subjectively as "warm" or "cool" both during and following the laying cycle, only 31 were "warm" prior to

completion whereas 48 were warm following completion. Although not a rigid test, this showed the relative level of nest attentiveness to be lower during laying, and suggests a lower rate of embryo development in Egg I at that time.

Reduced nest attentiveness during laying is thought to result from an increasing but sub-threshold impulse to incubate early in nesting (Drent 1970, Kendeigh 1952). The physiological basis for this behavior was evident in the Black-headed Gull (*Larus ridibundus*) in which early attentiveness levels were correlated with incomplete brood patch development, a direct reflection of the ovarian cycle (Beer 1963).

The advantage to loons of covering the clutch before incubation is speculative. Attentiveness during incubation is known to protect eggs both from predators and from overheating (Drent 1970). It is less important to provide protection from cooling or moisture, at least for undeveloped eggs; complete clutches of some arctic-nesting shorebirds may be left up to a week without covering (Lind 1961). Some Charadriiformes leave the nest unattended during laying, which promotes hatching synchrony (Kendeigh 1952, Sealy 1976).

In loons the unnecessary presence of a bird on a nest could also be detrimental to nesting success. Structural specialization for aquatic mobility has rendered gaviids, particularly the Common Loon, almost immobile on land (Gier 1952, Schorger 1947, Storer 1960). Ungainly movements associated with covering an incomplete clutch might draw unnecessary attention of predators. This disadvantage must be

offset by two apparent benefits of covering prior to clutch completion. First, a sitting bird protects against egg loss from washout (see Section IV.8). Second, partial development of Egg I at the time of laying of Egg II served to maintain a degree of asynchrony in hatching which led to increased fledging rates (see Section IV.10).

iii. Extended Incubation

Several eggs failed to hatch within the normal incubation period due to infertility or embryonic death. In three cases, incubation time was extended to 36, 44 and 53 days ( $\pm$  one day). Clutch attentiveness for both viable and inviable clutches appeared to decline in late June, and 17 July was the latest recorded date for incubation.

8. FATES OF EGGS

The outcome of 424 eggs was determined (Table 8). Mean annual hatching rate was 38% and ranged from 29% in 1975 to 47% in 1974. Hatching success on Hanson Lake was similar ( $\chi^2 = 0.28$ , NS) to Minnesota rates of 43% (Olson and Marshall 1952) and 40% (McIntyre 1975). Low success on Hanson Lake in 1975 was due mainly to higher losses to predators which in turn may have been related to more observer activity at nest-sites that year.

Predators and washout caused most of the clutch failures (Table 8). Eggs which disappeared with no evidence of cause formed the largest category of failed eggs (Table 8), but undoubtedly several factors contributed to disappearance.

Table 8. Fates of marked Common Loon eggs.

Fate	Number of Eggs			Total (%)
	1973	1974	1975	
Hatched	49	66	48	163 (38.4)
Depredated	12	21	38	71 (16.8)
Washed out	21	15	23	59 (13.9)
Failed to hatch	13	6	4	23 (5.4)
Deserted	6	6	6	18 (4.3)
Knocked from nest	5	6	4	15 (3.5)
Disappeared <sup>1</sup>	15	20	40	75 (17.7)
Total	121	140	163 <sup>2</sup>	424

<sup>1</sup> No eggs in this category hatched or were washed out; most were probably lost to predators.

<sup>2</sup> In addition, one egg was removed from 22 clutches for pesticide analysis.

i. Predators

Predators took almost 17% of all eggs, which was 38% of losses of known cause (Table 8). Avian predators were responsible for 82% (and mammals for the remaining 18%) of 33 losses where the predator could be identified. Common Ravens and Herring Gulls were both observed taking loon eggs during this study. The Raccoon (*Procyon lotor*) and the Striped Skunk (*Mephitis mephitis*), which were the prominent egg predators in Minnesota (McIntyre 1975), did not occur at Hanson Lake. All losses to mammalian predators at Hanson Lake were attributed to mink which commonly forage shorelines and travel between islands (Errington 1961).

ii. Washout

Washout accounted for almost 14% of eggs laid and 32% of losses of known cause (Table 8). Natural wave action, particularly at unsheltered nest-sites or during storms, accounted for 61% (n = 36) of the washout. About 17% of washout occurred from rising lake levels, and 22% resulted from the recreational use of power boats.

iii. Other causes

As clutches were seldom abandoned, desertion had little effect on the overall production of young (Table 8). Abandoned eggs were either pushed into the water or left unattended in the nest, but reasons for abandonment were seldom evident. Predator loss of one egg occasionally led to

the abandonment of the remaining egg (4 instances), but more often incubation resumed normally. Four cases of observer activity and one case of Beaver (*Castor canadensis*) activity were thought to have led to clutch abandonment.

Eggs were occasionally found in water beside the nest (Table 8). All fifteen eggs found in the water were viable, indicating that loss was accidental rather than intentional. Some accidental egg loss was likely since some nests were flat and surrounded by water.

About 5 percent of eggs failed to hatch following a full term of incubation. Of 9 failed eggs examined, 4 were addled, 4 contained dead embryos (23 to 25 days development), and one showed no development. Adult infertility, which was suspected on one territory where eggs in the same nest failed to hatch for three years in succession, was evidently not widespread, since the other egg hatched in 11 of 20 clutches in which an egg failed to hatch.

#### 9. REPLACEMENT CLUTCHES

Eggs were lost frequently during incubation (see Section IV.8). Where only one egg was lost, incubation of the remaining egg usually continued without interruption, but where both eggs were lost the clutch was often replaced. Clutch replacement never occurred following the loss of a brood, even when the brood was lost at the time of hatching. Pairs rarely attempted more than one replacement clutch in a season, thus females rarely underwent more than two laying cycles. Two females each completed

three laying cycles (also documented by McIntyre 1975 and Olson and Marshall 1952), but in both cases the last cycle yielded only one egg.

i. Replacement interval

The time between clutch failure and laying of Replacement Egg I (Replacement Interval) varied. Following the loss of an incomplete clutch, the next egg, if laid at all, was always deposited within three days (Fig. 14). This was within the limits of a normal laying interval. When completed clutches were lost, the replacement interval averaged 13 days, and ranged from 8 to 19 days (Fig. 14). This replacement interval was similar but more variable than recorded by Barr (pers. comm.) and McIntyre (1975).

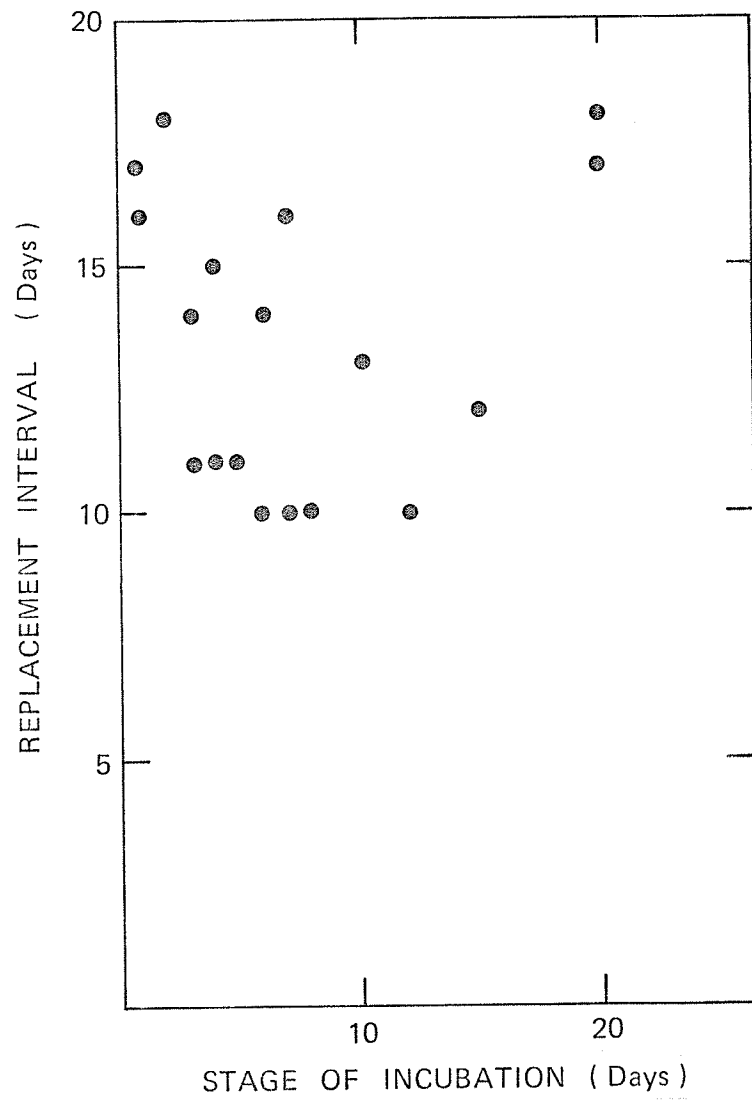
As the nesting season progressed, the replacement interval increased. This is demonstrated by the simple linear regression of replacement interval on date (Fig. 14). Although stage of incubation at the time of clutch failure influences the clutch replacement interval in anatids (Sowls 1955), there was no such relationship evident in loons on Hanson Lake (Fig. 15). Clutches which had been incubated for up to 20 days took no longer to be replaced than those lost shortly after laying (Fig. 15).

Most studies of avian reproductive physiology have documented changes in gonadal cycles only to the point of laying (Immelmann 1973, van Tienhoven 1968), and most have not examined the mechanism of clutch replacement in detail. Erpino (1968) suggested that interrelations between mated magpies (*Pica pica*) during nest-building stimulated gonad development, and that remodelling nests for renesting provided sufficient physiological priming for a second clutch.

Figure 14. Relationship between the time required to replace a clutch and the date on which clutch failure occurred.



Figure 15. Relationship between the time required to replace a clutch and the stage of incubation at which clutch loss occurred.



After laying the female gonads regress rapidly (Barry 1962, Bullough 1942, Payne 1966) to a level slightly above refractivity. Incomplete ovarian regression is correlated with endocrine regulation of brooding behavior (Lehrman and Wortis 1960, Saeki and Tanabe 1955), but indirectly facilitates renesting (Payne 1969, Phillips and van Tienhoven 1962). Phillips and van Tienhoven (1962) observed that "renesting behavior" in the Pintail (*Anas acuta*) increased progressively during incubation in the absence of clutch failure as a stimulus.

For loons on Hanson Lake, the capacity for additional laying cycles was retained well into incubation (Fig. 15). The seasonally progressive increase in replacement interval was consistent with our fragmentary knowledge of mechanisms controlling clutch replacement.

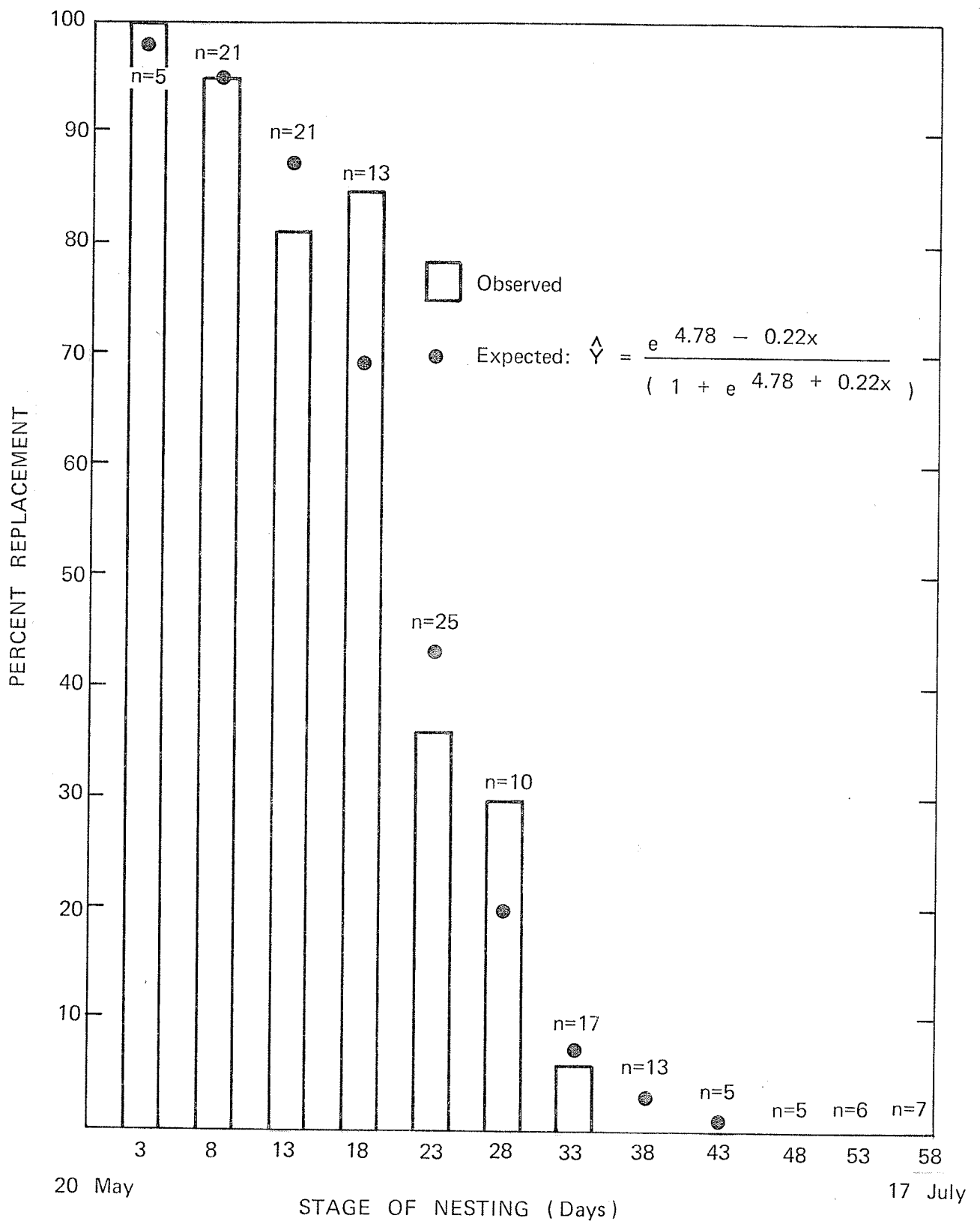
ii. Likelihood of replacement

Of 148 clutches for which the date of failure was determined ( $\pm$  one day), 66 were subsequently replaced. On the basis of shoreline searches and pair behavior, the rest probably were not replaced. Therefore the likelihood of a failed clutch being replaced was about 45%.

The probability of replacement was not the same for all failed clutches, but was related to date of failure. The likelihood of replacement was highest early in the nesting season and declined markedly thereafter (Fig. 16).

Several factors probably influenced whether a clutch was replaced. Since

Figure 16. The likelihood of clutch replacement in relation to date (stage of nesting season) on which failure occurred. Actual and theoretical (modelled on the actual data) probabilities are given.



photoperiod exerts endogenous control over breeding in most temperate species (Immelmann 1973, Payne 1969), the date of failure may influence re-nesting. Similarly, as the ovaries regress following laying (Lofts and Murton 1973), the ability to undergo an additional laying cycle may be influenced by the time elapsed since the last cycle. Finally, as the loon appears to be a determinate layer (Section IV.6.ii) the egg production capacity of the female may be limited, giving rise to more difficulty replacing a replacement clutch than an initial clutch. With these factors in mind, the likelihood of clutch replacement was examined in relation to date of failure, stage of incubation at time of failure (early  $\leq 13$  days, late  $> 13$  days), and clutch type (initial vs. replacement). Effects due to age and male variability were uncontrolled, but the latter at least was assumed to be negligible in view of the prolonged testicular recrudescence typical of territorial species at this latitude (Immelmann 1973, Lack 1968).

Observations following failure of 121 clutches are summarized in Table 9. There was no replacement of nests which failed later than Day 31 although 40% of failures occurred after this. Date of failure (X) was the most important factor influencing the probability of clutch replacement (Y). This relationship fitted the linear logistic model  $\hat{Y} = e^{\lambda} / (1 + e^{\lambda})$  where  $\lambda = a + bX$  (Cox 1970). Estimates of the model are shown for comparison in Fig. 16. The likelihood of replacement was almost 100% during the first week of nesting and diminished logistically as the nesting period progressed (Fig. 16).

Table 9. Number of clutches replaced (r) shown in relation to number which failed (n), classed according to 3 temporal characteristics of the clutch which failed<sup>1</sup>.

Clutch Type	Stage of Incubation	Stage of Nesting (days)							Total
		1-6	7-11	12-16	17-21	22-26	27-31	≥ 32	
Initial	Early	4,4	15,16	16,17	3,6	2,5	0,1	0,0	40,49
	Late	0,0	0,0	0,0	2,2	3,8	1,3	0,18	6,31
Replacement	Early	0,0	1,1	1,2	0,0	1,5	0,2	0,16	3,26
	Late	0,0	0,0	0,0	0,0	0,0	0,0	0,15	0,15
Total		4,4	16,17	17,19	5,8	6,18	1,6	0,49	49,121

<sup>1</sup> Values in each cell are r, n.

Removal of the effect of date of failure permitted the residual variation to be examined for effects due to the other factors (Cox 1970: 59). No effect of either with clutch type or stage of incubation were detected statistically, although clutch type residuals showed a slight separation. As supporting evidence, examination of Table 9 reveals no effect by stage of incubation, but indicates that failed initial clutches were more frequently replaced than were failed replacement clutches for any given time period. There was therefore a reasonable basis to conclude that, removed from seasonal constraints of available time, some physiological upper capacity for egg production would remain.

Therefore it was evident that date of clutch failure was the key determinant of whether a replacement clutch was attempted, and this was probably a manifestation of the photoperiodic control of reproduction in Common Loons. It was also evident that there was a limit to the number of eggs which could be laid in one season, irrespective of photoperiod.

### iii. Termination of renesting

Although latest laying occurred on 1 July at Hanson Lake, Barr (pers. comm.) observed loons laying during late July in Algonquin Park, Ontario. This suggests that some capability to nest extends well beyond the latest laying observed on Hanson Lake.

In the Magpie (*Pica pica*), Erpino (1969) found irreversible testicular

regression during incubation correlated with the fact that males did not incubate, and he concluded the ability to reneest was ultimately limited by the male. Since in loons both sexes incubate, the reproductive capabilities of males are probably extended. In view of the clutch size reduction in late nesting attempts, reneesting in Common Loons is probably limited by the female. Certainly the inability of loons to lay eggs once a brood is lost can be tied to ovarian regression associated with broodiness, as documented in Magpies by Erpino (1969).

#### 10. HATCHING

Common Loon eggs on Hanson Lake hatched asynchronously and always in the order of laying. Egg I hatched first in all 16 clutches where both laying sequence and hatching interval were known. Hatching intervals (determined to  $\pm$  3 hr.) ranged from 6 to 42 hr., and averaged 17.3 hr. ( $n = 39$ ). Hatching intervals were the same for initial clutches and replacement clutches ( $t = 0.588$ ,  $df = 37$ , NS).

Where the hatch was relatively synchronous (both eggs within 12 hr.), the young left the nest at the same time. When the hatch was prolonged, the first hatchling left the nest in the care of one parent, while the other parent remained to hatch the second egg. Within 6 hours of Chick II hatching, the nest was abandoned for the duration of the summer and was not used for brooding.

i. Hatching chronology

The hatching period in the Hanson Lake population spanned 24, 29 and 19 days in 1973, 1974 and 1975, respectively. The hatching period was always shorter than the laying period, as late clutches seldom hatched. The annual constancy in the onset of laying was reflected in the commencement of the hatch which varied by only two days among the 3 years (Fig. 17). Although some hatching continued well into mid-July, most eggs hatched by the end of June (Fig. 17). Annual variation in egg-laying, due to differences in the break-up of ice as described in Section IV.6, were reflected in both the peak and the duration of hatching (Fig. 17).

ii. Weight of eggs and young at hatching

Eggs weighed on the day of laying and again on the day prior to hatching ( $n = 10$ ) lost a mean of 15.6 g (10.6% of initial weight) during incubation. Upon hatching, chicks weighed 77 to 99 g ( $\bar{X} = 88.5$  g,  $n = 29$ ); this represented 60 percent of the weight of their eggs at laying. Larger eggs lost proportionately more weight than smaller eggs (Fig. 18).

In 5 clutches of known laying and hatching sequence and known laying and hatching weights, the chick from Egg II always weighed proportionately more of the initial egg weight than the chick from Egg I. Lewin (1963) attributed differential weight loss within eggs of a clutch to differences in the quantity of unassimilated yolk resulting from the varying residence times of eggs in the nest. Although mean initial weights of eggs I and II did not differ, Chick II was usually heavier at hatching ( $\bar{X} = 3.2$  g)

Figure 17. Hatching chronology of Common Loon eggs on Hanson Lake during three nesting seasons.

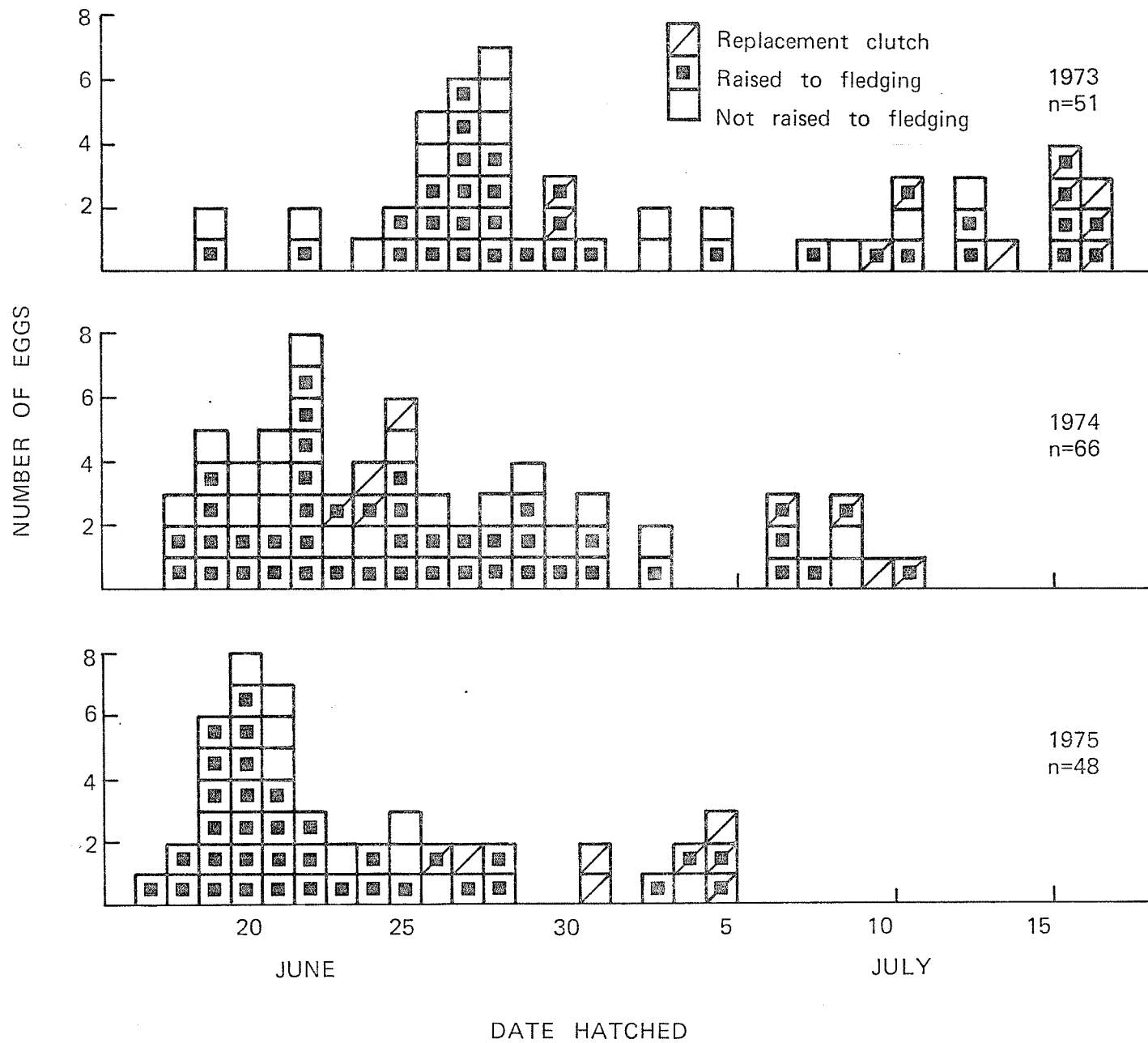


Figure 18. Percentage weight loss by Common Loon eggs during incubation. All eggs were weighed on the day of laying and again at hatching.



than its sibling.

Although Chick II generally weighed more at hatching than Chick I, Chick I always maintained a weight advantage. By virtue of hatching first, Chick I had been fed and gained weight by the time Chick II received its first feeding. In 5 broods weighed at the time Chick II emerged, Chick I already averaged 6.4 g heavier. In four broods weighed in the first 12 days of age, Chick I weighed more. Davis (1972) found first hatched chicks in broods of Arctic Loons and Red-throated Loons maintained this weight advantage throughout the brood-rearing period.

iii. Asynchrony

The mean hatching interval of 17.3 hr. (0.7 days) was considerably shorter than the mean laying interval (2 to 3 days). Relative to the laying interval, the hatching interval showed a gain in synchrony within the clutch which likely reflected an acceleration in hatching of Egg II.

Pre-incubative covering may retard the development of Egg I somewhat (Section IV.7.ii). On the other hand, vocal communication within a clutch prior to hatching is known to accelerate growth of younger embryos, which in turn serves to synchronize hatching (Vince 1969, Vince 1973). Embryos of Common Loons on Hanson Lake were audible as early as 4 days before hatching commenced, and Chick II generally was less developed upon hatching than its sibling upon hatching (see Section IV.10.ii for description of body weights and extent of yolk absorption at

hatching). Vocal communication late in the egg stage was probably the main factor in reducing the hatching interval, relative to the laying interval.

The benefits of asynchronous hatch have been widely debated (Klomp 1970, Lack 1954, Lack 1966). Asynchronous hatch generally serves to ensure survival of elder, stronger young in environments where food supply fluctuates (Ingram 1959). Elder brood members often maintain a competitive advantage throughout rearing (established initially by hatching earlier than siblings) by dominating in intra-brood hierarchies (Kear 1970). Davis (1972) studied the importance of asynchronous hatching in Arctic and Red-throated Loons, and found that asynchrony ensured the survival of the first-hatched young in environments with limited food resources.

In species which hatch asynchronously, it is logical to explain the hatching interval as a compromise between two opposite processes. One encourages asynchrony, selecting ultimately for production of fewer more vigorous young, and thus favors survival of the elder brood members. The opposite process encourages synchrony, selecting for the maximum production of individuals, and thus favors the survival of younger brood members.

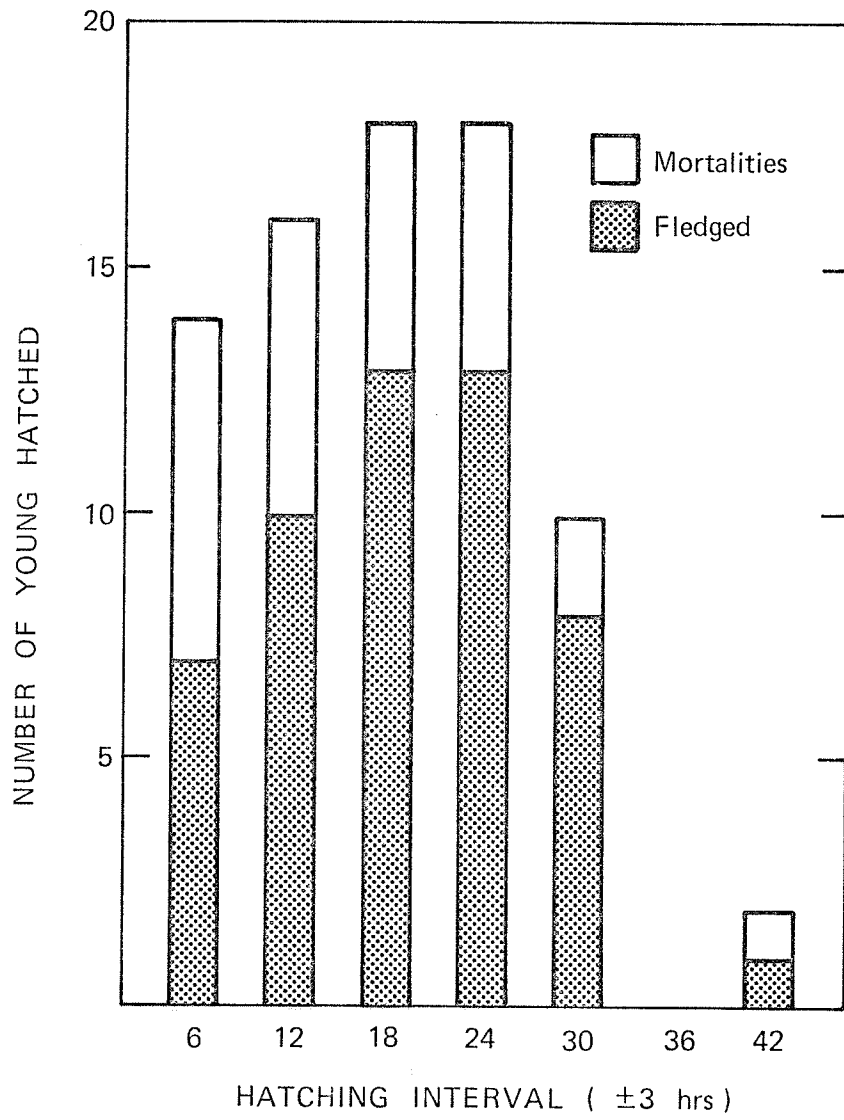
The selective force favoring synchrony in loons is clear. The longer the egg stage, the longer is the period during which the incubating adult and the potential offspring are most vulnerable. Furthermore, too long a hatching interval could create an excessive imbalance in the sibling

rivalry, and thereby place the younger chick at an unnecessary disadvantage at times when resources would permit survival (Kear 1970, Kluyver 1951, Owen 1960).

The selective force favoring asynchrony in loons, the one which ultimately compromises the former to an "optimum" hatching interval, is not so apparent. Theoretically it ensures survival of the first-hatched young through the brood stage, and results in a balance in the competitive ability (relative fitness) of each young in a brood which is controlled by the hatching interval.

Because the hatching intervals of Hanson Lake Loons were variable, it was possible to evaluate the optimum hatching in two ways. First, by comparing the proportion of broods which hatched at various different intervals, it was evident that a hatching interval of within 24 hr. was favored (Fig. 19), even though a longer interval was certainly possible due to the lengthy laying interval. The number of clutches with hatching intervals of 6, 12, 18 and 24 hours were similar and there was statistically no peak hatching interval (Fig. 19). Second, by comparing chick survival to fledging in broods with different hatching intervals, it was possible to measure any reproductive advantage of various hatching intervals. Admittedly there was no means to assess variation in the number of young which ultimately reached breeding age. Figure 19 shows the proportion of young fledged in relation to the hatching interval. Although there were no statistical differences, a trend for higher survival was evident in broods which hatch farther apart. The rate of chick survival increased directly as the hatching interval increased. This differential

Figure 19. Intervals between the hatching of eggs in two-egg clutches (n = 39), showing survival to fledging of young from those eggs.



in survival was apparently due to the occasional loss of both young in broods which hatched close together (6 to 12 hr.), and the fact that no more than one young was ever lost in broods which hatched farther apart. It was significant that in all cases in which a color-marked chick was lost (see Section IV.11), it was invariably the younger bird.

If no specific interval offered any survival advantage in production, and if the interval was only a manifestation of pre-incubative covering behavior, no differences in survival among hatching interval classes should be evident. If, on the other hand, chick mortality rates were sufficiently different to give statistical separation between hatching intervals, then strong selection should have reduced the variability in hatching interval. Such selection should then be evident as an unequal proportion of clutches hatching at different intervals: one would expect most clutches to hatch at the apparent "optimum" interval, and few at the shorter "suboptimal" intervals. There appears to be a reproductive advantage to a hatching interval of 18 to 30 hr. (as opposed to 6 or 12 hrs.), but this is probably offset by the risk of additional incubation time.

iv. Hatching success in relation to clutch type.

Hatching success in replacement clutches was significantly lower than in initial clutches ( $X^2_{(adj)} = 4.55, P < 0.05, df = 1$ ). Forty-two percent of eggs hatched from initial clutches, whereas only 26% hatched from replacement clutches (Table 10). No single factor accounted for this difference; washout, disappearance (probably depredation) and failure to hatch were all higher in replacement clutches (Table 10).

Table 10. Fates of marked eggs in relation to clutch type.

Fate	No. Initial Clutches (%)		No. Replacement Clutches (%)	
Hatched	138	(42.1)	25	(26.0)
Washed from nest	41	(12.5)	18	(18.2)
Depredation	55	(16.8)	16	(16.7)
Failed to hatch	15	(4.6)	8	(8.3)
Desertion	15	(4.6)	3	(3.1)
Knocked from nest	11	(3.3)	4	(4.2)
Disappeared	53	(16.1)	22	(22.9)
Total	328	(100.0)	96	(100.0)

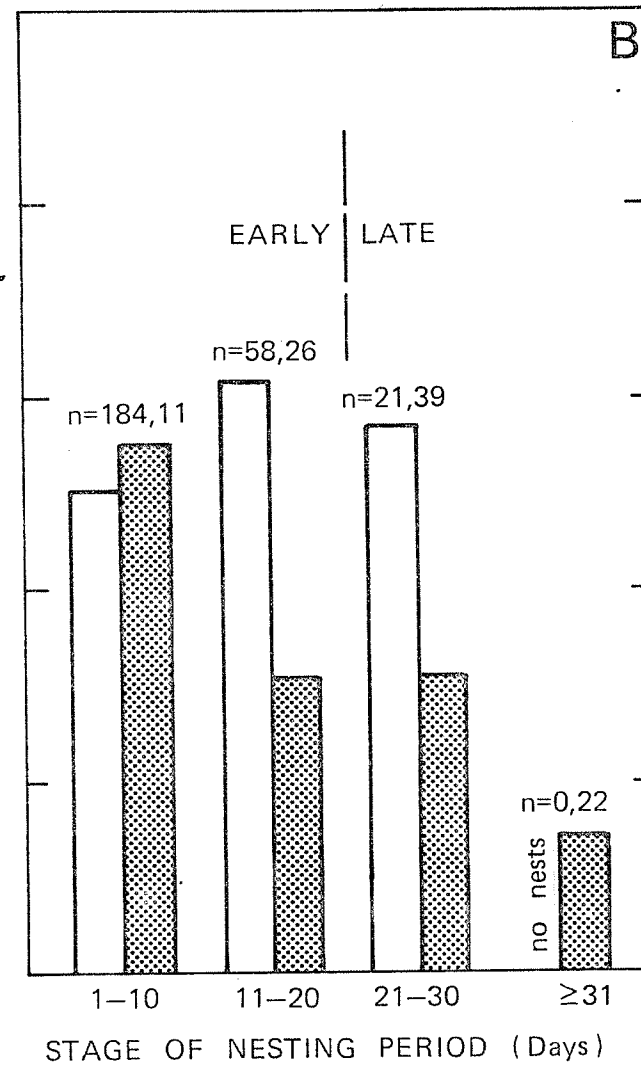
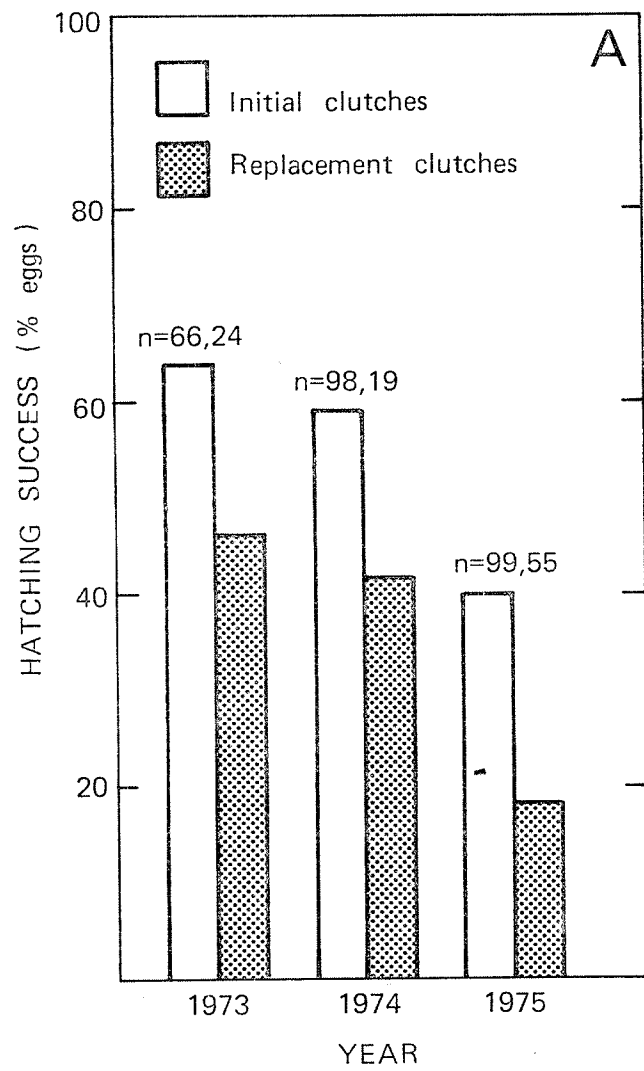
Because most replacement clutches commenced later in the nesting season, it was unclear whether the reduced hatchability was due to clutch type (laying cycle I vs. cycle II) or stage of nesting (to time of laying). Annual variation may also have been a factor influencing the measurement of hatchability.

Fienberg's (1970) procedures were used to analyze the correlates of hatching success because they can be applied to discrete (or binary) data and they take into account interactions between factors. Details of this analysis are provided in Appendix II. Applying this analysis revealed that hatching success was not dependent on stage of nesting: eggs of initial clutches were equally likely to hatch whether they were laid early or late in the season; similarly early replacement clutches were as successful as late replacement clutches. However replacement clutches as a whole were much less likely to hatch ( $P < 0.01$ ) than initial clutches (Appendix II).

Not only were success differences between clutch types significant, but the direction and degree of differences were consistent (Fig. 20). Although annual hatching success varied overall, about 20% fewer eggs hatched from replacement clutches than initial clutches each year (Fig. 20A).

Since differences were not due to laying dates (Fig. 20B), and since inviability of eggs was not a major factor, an alternate explanation is offered. Hatching success was related in part to the outcome of previous nesting attempts. The probability of success was low following any nesting failure. Hatching success was lower if a pair had failed the year

Figure 20. Comparison of hatching success in initial and replacement clutches. Graph A shows hatching success in relation to annual variation. Graph B shows hatching success in relation to stage of nesting season (with May 21 as day 1).



before; moreover the low likelihood of success from a replacement clutch, following failure within a season, was the same as for an initial clutch which followed a failure the previous year (Yonge and Sealy, unpubl. data). A pattern of repetitive failure exhibited by many pairs was attributed to age-related inexperience (Yonge and Sealy, unpubl.) as has been demonstrated in other long-lived territorial species (Coulson and White 1958, Richdale 1957).

The fact that initial clutches were more successful than replacement clutches has a mathematical, rather than physiological, explanation. Given that low success follows failure and high success follows success, all replacement clutches follow failure and thus have a low likelihood of success. However, with initial clutches, some follow failure and some follow success in the previous year, and overall the mean chance of success is higher. Therefore it follows that birds which failed and chose to reneest were generally younger, less experienced birds.

Although laying date did not affect hatching success, early nesting was advantageous. Pairs which nested early and failed had more time to reneest. Thus production per pair increased by nesting early, although the hatching probability per egg was the same. This advantage to early nesting probably explains the skew toward early laying (Fig. 12).

#### 11. BROOD REARING

As in other gaviids, the period of parental investment following hatching is long. McIntyre (1975) reported a brood stage of 11 weeks, and Barr

(1973) observed parental feeding until young attained full juvenal plumage at about 8 weeks of age. Common Loon family units on Hanson Lake remained intact for 10 to 13 weeks, but no effort was made to study feeding behavior during this period.

i. Parental behavior

From the outset the young are closely guarded by the parents. Back-riding is common during the first week, and swimming young were generally positioned between the parents. If one chick, in swimming, failed to keep up with the family group, in spite of vocal encouragement, one and often both parents dropped back to accompany it. Young were seldom allowed to stray from the parents until 2 to 3 weeks of age.

Adults behaved differently when brood safety was threatened. The adults and young separated. The young swam to shore and remained inconspicuous. The adults moved conspicuously to open water, performing the exaggerated and vocal displays for which the loon is known (Munro 1945, Olson and Marshall 1952). Once alarm subsided, the young were recalled to open water and the intact family departed for another region of the territory. If the intruder remained nearby and the young did not rejoin the parents at the same time, the parents often swam away with the chick which arrived first and ignored the other chick. Although the remaining chick was always vocal, the adults generally did not respond and left it to its own resources to rejoin the family.

It appeared that the chick with the parents was not to be jeopardized

for the protection of the other. This behavior favored the survival of at least one brood member, and suggested the other may be expendable. There was no apparent discrimination for either the first or second hatched chick, but merely for the one which reached the adults first. Although there were insufficient observations of individually marked broods to show whether Chick I or Chick II more often reached the adults first, this behavior probably favored the more vigorous Chick I, as found in Red-throated Loons by Davis (1972).

ii. Survival of young to fledging

Of the Common Loon chicks which hatched during studies on Hanson Lake, 69, 67 and 73 percent survived to fledging in 1973, 1974 and 1975, respectively (Fig. 21). The slight annual variation was insignificant ( $\chi^2 = 0.16$ , NS,  $df = 2$ ), although survival in 1975 was nominally inflated due to a higher proportion of one chick broods because an egg was removed from several clutches for toxicological studies (the effect of brood size on fledging rate is discussed in Section IV.11.v). Mean chick survival to fledging (excluding 1975) was 68 percent (Fig. 21).

Fledging success at Hanson Lake was the same as Olson and Marshall (1952) found in northeastern Minnesota, but less than McIntyre (1975) found in central Minnesota (Table 11). McIntyre (1975) recorded only two mortalities in young loons, significantly fewer than at Hanson Lake and northeastern Minnesota (Olson and Marshall 1952) combined ( $\chi^2 = 7.70$ ,  $P < 0.01$ ,  $df = 1$ ). In other gaviids, a limited food supply was the main factor

Figure 21. Survival of young Common Loons to fledging.

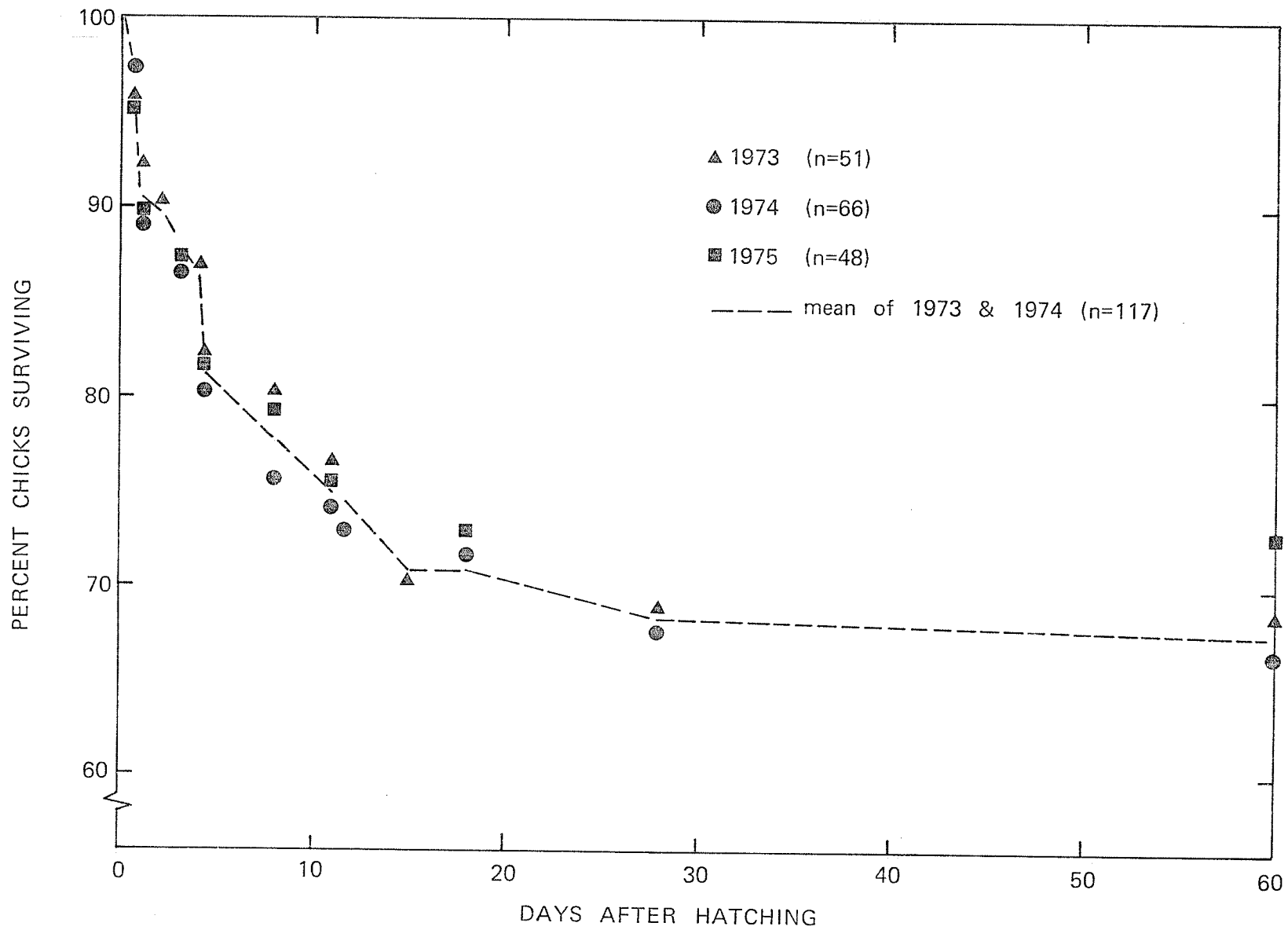


Table 11. Comparison of fledging success in the Gaviidae.

Species	Source	Locality	No. Hatched	No. Fledged	Fledging Success (%)
<i>G. immer</i>	McIntyre (1975)	Minnesota	36	34	94
	Olson and Marshall (1952)	Minnesota	31	21	68
	Present Study <sup>1</sup>	Saskatchewan	117	79	68
<i>G. artica</i>	Davis (1972)	Northwest Territories	84	54	64
	Lehtonen (1970)	Finland	72	34	47
<i>G. stellata</i>	Davis (1972)	Northwest Territories	100	38	38

<sup>1</sup> Excludes 1975 data.

causing mortality of young (Davis 1972). Extrapolating from Davis' (1972) work to Common Loons, it is not surprising McIntyre (1975) found high chick survival. Her study population consisted mainly of pairs isolated on small eutrophic lakes with abundant food. In contrast, both Hanson Lake and Olson and Marshall's (1952) Knife Lake study area were large, unproductive waters inhabited by numerous loons.

The Common Loon has the highest fledging success of the three species of loons for which this is known (Table 11). Davis (1972) studied sympatric populations of Arctic and Red-throated Loons and found significantly higher fledging in Arctic Loons due to differences in habitat selection and foraging behavior. Red-throated Loons nested on tundra ponds devoid of prey for loons, and adults spent much of the brood-rearing period flying between their nesting pond and the ocean where all food was obtained (Davis 1972). Arctic Loons nested on lakes and larger ponds which provided food for the young; only the adults fed coastally which permitted more time for feeding the brood. Thus, in the Common Loons, which forage entirely within their territories, the importance of foraging time in limiting chick production would be further reduced. The feeding pattern of the Common Loon probably accounts for this species having the highest fledging success.

Most mortality occurred on the first day; 10 percent of hatchlings failed to survive the first day (Fig. 21). This initial loss constituted 31% of the overall mortality. Sixteen of 165 young were lost during this period, and six of these died before leaving the nest. By 4 days of age, 61% of the total mortality had occurred. Eighty-one percent of young

survived Day 4, at which point the mortality rate declined (Fig. 21). Ninety percent of mortality occurred in the first two weeks following hatching, and only incidental mortality occurred once young achieved age 3 weeks (Fig. 21). With the exception of one 6 week old juvenile which disappeared, no mortality was evident past 4 weeks of age.

Date of hatching did not influence fledging success. Survival rates were the same for early hatching and late hatching chicks (Table 12). Pooling years, there were no differences in mortality rates among five groups of young divided equally by both date ( $\chi^2 = 1.51$ , NS) and proportion of young which hatched ( $\chi^2 = 1.96$ , NS).

The energy demands of young loons are highest immediately following hatch (McIntyre 1975), thus mortality was highest in the first 4 days. The period crucial for survival was about 18 days (Fig. 21), beyond which survival was almost assured. This period corresponds closely to that required for the outgrowth of Stage B down (Palmer 1962).

### iii. Sources of chick mortality

The cause of chick mortality was seldom determined; generally it was detected only because young had disappeared. Of 13 losses of known cause, 6 occurred in the nest, within 3 to 4 hours of hatching, and 7 occurred within 2 days of leaving the nest. Of those in the nest, one young was abandoned, 2 died upon hatching, 2 were taken by an unidentified mammalian predator, and one was taken by a Herring Gull drawn to the nest by my presence. Of those chicks which had left the nest,

Table 12. Comparison of chick survival among years shown in relation to time of hatching. In any given year, the first half of chicks which hatched were classed as early; the other half were classed as late.

Year	Percent Surviving (n)		Late	$\chi^2$ (1df)
	Early			
1973	68 (17)	69 (18)		0.00 (NS)
1974	66 (21)	68 (23)		0.01 (NS)
1975	83 (20)	63 (15)		0.71 (NS)
Total	72 (58)	67 (56)		0.14 (NS)

Herring Gulls took 2 (in separate incidents in which observer disturbance may have contributed), a brood of 2 disappeared within an hour of leaving the nest (presumably to an unidentified predator), a brood of 2 disappeared during a severe storm, and one was killed by an adult loon which intruded from an adjacent territory.

Initially young loon chicks are vulnerable to depredation through several sources. Avian predators, particularly gulls, are quick to take chicks from the water; the 3 observed cases of depredation by gulls occurred because adults protected one chick and allowed the sibling to separate. Mammalian predators would be a threat briefly at hatching, but would not be a major factor once the nest has been abandoned. Solman (1945) found the Northern Pike (*Esox lucius*) was a major predator on young waterfowl in the prairies. Loon chicks were frequently found in stomachs of Northern Pike at commercial fish plants in the Hanson Lake area, and as large pike were numerous in Hanson Lake (Sawchyn 1967), they were likely responsible for much of the chick loss. The back-riding behavior of young loons is an adaptation which reduces chick loss to underwater predators (McIntyre 1975). McIntyre (1975) found back-riding was frequent until chicks reached 7 to 10 days of age, and ceased by age 3 weeks. At that age the young are probably immune to most predators.

The extent of mortality caused by other adult loons was unknown. The fact that Barr (pers. comm.) and McIntyre (pers. comm.) also observed it during their studies, suggests it may occur frequently. Protection of the young from other loons is perhaps one reason why territoriality is maintained throughout the rearing period, and why the young remain on the

natal territory until the adults depart (see section IV.12).

iv. Differential survival between siblings

Starvation was the main factor contributing to chick mortality in Arctic and Red-throated Loons (Davis 1972). In both species, differential fitness through both intra-brood competition and parental discrimination insured survival of the first young, often at the expense of the second. Davis (1972) also found that first chicks in two chick broods grew and survived as well as chicks in one chick broods, but that second chicks grew more slowly and accounted for most of the mortality.

On Hanson Lake, 5 of 13 marked broods lost one chick and two lost both. In broods which lost one chick it was consistently the second chick. Where both were lost, chick II disappeared first in one brood, and the order of mortality was not determined in the other. The marking procedure was not a mortality factor, as loss of marked chicks (9 of 26) was the same ( $\chi^2 = 0.00$ , NS) as in unmarked two chick broods (36 of 104) during 1973 and 1974. In 5 cases prior to 1975 in which one young of known sequence had been lost, it was the second chick in each case. As there was no evidence during this study that any second hatched young survived its older sibling, it appears that differential mortality within broods insures the survival of the older young. The second hatched young is at a disadvantage, and may be expendible.

Several factors suggest that intra-brood competition is the main cause of mortality in young Common Loons. First, this has been documented as the

main mortality factor in other species of loons (Davis 1972). Second, the lower survival of second young was not related to the viability of second-laid eggs; survival of one chick broods from first eggs (n = 7 of 7) was the same ( $\chi^2 = 0.12$ , NS) as those from second eggs (n = 11 of 13). Third, although factors such as exposure or predators may have resulted in mortality, only competition between brood members could explain why it was invariably the second hatched young which was lost. When threatened, parents protect the closest chick which, in most cases, will be the stronger first chick. Predators are likely to take chicks which lag behind, again favoring the stronger young. Resistance to exposure would also be a function of relative fitness. Finally, the low mortality rate in single chick broods demonstrates the high potential survival in the absence of intra-brood competition. Thus competitiveness between brood members for food and parental protection emerges as the main mortality factor. From hatching, the second chick is at a competitive disadvantage and its chance of survival is lower.

v. Influence of brood size on chick survival

Initial brood size was important in determining the fledging success of young loons on Hanson Lake. Forty-seven of 132 young in two chick broods were lost, whereas only 5 of 46 young in one chick broods were lost ( $\chi^2 = 7.15$ ,  $P < 0.01$ ,  $df = 1$ ). As there were no annual differences in the fledging success from either two chick broods or one chick broods, the data for the 3 years were pooled for the following comparisons.

The probability of raising at least one young was the same for one-

and two-chick broods ( $\chi^2 = 0.01$ , NS): at least one chick fledged from 60 of 66 two-chick broods and 41 of 46 one-chick broods (Table 13). Therefore brood size did not affect whether a pair successfully raised a single offspring. However, the probability of losing a chick was significantly higher in two-chick broods than one-chick broods ( $\chi^2 = 17.3$ ,  $P < 0.01$ ,  $df = 1$ ). Forty-one of 66 two-chick broods lost one or more young, whereas only 5 of 46 one-chick broods lost young (Table 13).

Most pairs which were successful in hatching young were also successful in raising at least one to fledging stage (Fig. 13). Only 10% (11 of 112) failed to do so, and initial brood size was of no importance ( $\chi^2 = 0.09$ , NS). Therefore it was evident that brood size had no effect on the capabilities of adult Common Loons to raise one offspring and no effect on the survival of a single brood member. As the majority of chick mortalities occurred through the loss of one chick from two chick broods, it was obvious that the presence of a sibling places one chick, but not both, at a disadvantage. The survival of one was almost ensured.

Fledging success in relation to brood size is shown in Table 14 for 3 loon species. Mortality rates differed significantly among the species ( $\chi^2 = 22.751$ ,  $P < 0.01$ ,  $df = 2$ ), being highest in the Red-throated Loon and lowest in the Common Loon. Most of this difference arose from species differences in mortality which occurred in two chick broods ( $\chi^2 = 10.530$ ,  $P < 0.01$ ,  $df = 2$ ); although this trend was also evident in one chick broods, differences were not significant ( $\chi^2 = 1.632$ , NS). When the 3 species were compared further, there were no differences in

Table 13. Fledging success of Common Loons in relation to brood size at hatching.

No. Hatched	No. Fledged	No. of Broods			Total
		1973	1974	1975	
1	1	10	13	18	41
	0	3	1	1	5
2	2	11	8	6	25
	1	12	18	5	35
	0	1	2	3	6

Table 14. Fledging success among the Gaviidae in relation to initial brood size.

Species	Brood Size At Hatching	No. Broods	No. Fledged			Success Rate
			2	1	0	
Red-throated Loon (Davis 1972)	2	42	3	23	16	0.35
	1	16	-	9	7	0.56
	Total	58	3	32	23	0.38
Arctic Loon (Davis 1972)	2	31	8	21	2	0.60
	1	22	-	17	5	0.77
	Total	53	8	38	7	0.64
Common Loon (Present study)	2	66	25	35	6	0.64
	1	46	-	41	5	0.89
	Total	112	25	76	11	0.71

their ability to raise at least one young from a two chick brood ( $\chi^2 = 3.175$ , NS), but differences existed in their ability to raise both young from two-chick broods ( $\chi^2 = 9.368$ ,  $P < 0.01$ ,  $df = 2$ ). Both chicks fledged from only 7% of Red-throated Loon broods, and from 38% of Common Loon broods. Thus the species do not differ in their ability to raise a single young, regardless of initial brood size, but do differ in their ability to raise two young. These differences probably reflect variations in feeding strategies (see Davis 1972).

#### vi. Fledging

Little information is available on the time of first flight by juvenile Common Loons. The fledging period is an estimated 10 weeks (McIntyre 1975, Olson and Marshall 1952, Wilson 1929), based on suspected first flights. Common Loons are probably capable of flight at 7 to 8 weeks of age, as are Yellow-billed Loons (Sage 1971), but loons of any age rarely fly on the breeding areas and flights are seldom observed.

In 1974, family break-up coincided with fall departure by adults. Adults vacated their territories separately and abandoned the young. When abandoned the chicks were as young as 10 weeks of age, but usually ranged from 11 to 13 weeks. The young did not remain on their territories, but moved freely about the lake, associating often with other young. McIntyre (1975) observed that some juveniles moved to other lakes and established feeding territories, but this was not apparent on Hanson Lake. Juveniles had not left Hanson Lake by the time observations ended (October 3), but flights by juveniles were observed

frequently during the last week in September. Four juveniles which were recorded daily in a small bay beginning on 24 September were present on 3 October when observations ceased.

## 12. FALL DEPARTURE

Adults began to leave Hanson Lake in late August, but little decline was evident until the second week of September. Birds departed singly, rather than in pairs, and one bird usually remained 2 or 3 days longer than its mate. This suggests that pair bonds are not maintained over winter, an observation supported by McIntyre (1975) who observed mainly unpaired birds on Atlantic wintering areas.

### i. Flocking behavior

Prior to departure, small groups of loons (3 to 22 birds) assembled on neutral central areas of Hanson Lake. Mid-summer aggregating by Common Loons is thought to be pre-migratory behavior involving birds which failed to produce young (Nero 1972, Rand 1948), but the breeding status of flocking birds has not been confirmed. On Hanson Lake, broodless adults were less commonly on their territories during late summer surveys than were adults which raised young (Table 15). Broodless adults also left the lake earlier, and by mid-September only adults with chicks remained (Table 15). In August, older juveniles were often not accompanied by their parents, but at least one adult (usually both) was present within the territory until young were abandoned. Therefore most individuals in late summer aggregations could only have been those unsuccessful in

Table 15. Changes in the distribution of adult Common Loons on Hanson Lake during fall departure in 1974.

Survey (Date)	Territories Surveyed	<u>Territories with Broods</u>			<u>Territories without Broods</u>			Adults Per Territory
		Both Adults	One Adult	No Adults	Both Adults	One Adult	No Adults	
I (27 Aug.)	35	15	5	0	6	5	4	1.49
II (6 Sept.)	24	6	4	1	6	3	4	1.29
III (13-14 Sept.)	32	3	4	11	0	0	14	0.31

the breeding effort.

ii. Pattern of departure

Observations from 3 late-summer surveys in 1974 have been summarized in Table 15. On 27 August (Survey I) 25% of the summer resident population was absent from the surveyed area (Table 15). The proportion of absent birds which had actually left the lake was uncertain, as some were likely among open water flocks and returned to their territories at dusk.

Aggregations of as many as 22 birds were dispersed throughout the lake during Survey I. Survey II (6 September) showed little change in adult distribution (Table 15). However, as no aggregations of more than 4 adults were observed during Survey II, it was evident that many had left the lake by that time. Thirty-five percent of the surveyed population was absent. Survey III (13 and 14 September) showed most adults were gone (Table 15), having departed during the second week of September. The last day of departure was not determined as further surveys were not conducted until 24 September, but during 10 days of observation from 24 September to 3 October, no adult loons were observed on Hanson Lake.

Common Loons breeding in the northeastern United States started to depart in late August and early September (McIntyre 1975, Palmer 1949), similar to Hanson Lake. However McIntyre (1975) observed a more gradual departure than seen at Hanson Lake, as some adults remained until November when lakes started to freeze. Thus the period of departure by adults on Hanson Lake was much compressed.

## V. ANNUAL PRODUCTION AND HABITAT REQUIREMENTS

Hanson Lake served as breeding habitat for a stable, dense population of Common Loons. Characteristic of Boreal Forest lakes, Hanson Lake provided a relatively stable habitat. The Common Loon is a terminal consumer in an aquatic food chain, and is morphologically specialized as an underwater predator of fish (Barr 1973, Gier 1952, Schorger 1947, Wilcox 1952).

Because the loon occupies a specialized feeding niche, stability of the breeding population is dependent partly upon a relatively uniform annual food supply. Although lakes in the Precambrian Shield have low limnetic productivity (Wetzel 1975), they provide a stable prey population for loons. As the species shows territorial affinity from year to year (McIntyre 1974, Yonge and Sealy unpubl. data) and is incapable of effective locomotion on land, population stability also depends in part on an unchanging nesting habitat. Precambrian Shield lakes generally have convoluted shorelines and relatively uniform water levels, thus offering a diversity of stable potential nest sites on shore.

### 1. Breeding Performance

An average of 49 young loons fledged from Hanson Lake each year (Table 16). A mean of 0.54 young per pair successfully reached fledging stage (Table 16). This estimate was biased low by 1975 in which reduced production resulted from the removal of several eggs for pesticide studies (Section IV.10). Production of 0.61

Table 16. Annual production to fledging of Common Loons in the Hanson Lake population.

<u>Comparison</u>	<u>Number Fledged Young</u>			<u>Mean</u>
	<u>1973</u>	<u>1974</u>	<u>1975</u>	
By population per year	48	58	40	48.7
Per nesting pair (observed nests only)	0.61	0.64	0.39	0.54
Per individual in population	0.25	0.28	0.20	0.24

to 0.64 young per nesting pair observed in 1973 and 1974, respectively (Table 16), is probably more typical of Common Loon breeding performance in the Boreal Forest.

An average of 0.24 young fledged for each adult in the Hanson Lake population (Table 16). Production per adult was higher on McIntyre's (1975) Minnesota study area, where chick mortality was low. Adjusting McIntyre's (1975) production statistic with the chick mortality rate observed on Hanson Lake yielded a value of 0.25 young per adult. Thus excluding habitat-related differences in fledging success, production would have been the same in the two populations. A mean of 0.25 fledged young per adult loon per year appears to be normal for this species.

i. Production and nesting chronology

Although the duration of the nesting period was lengthy, not all stages of nesting contributed equally to chick production. Clutches commenced during a period of about 40 days, but 58% of the young which fledged were from clutches initiated during the first 10 days of laying. The contribution from the first 10 days reflected seasonal variation in break-up, being most important (70% of young) in 1975 when spring was early (Table 17). The last 10 days of laying contributed little to annual production.

Seventeen percent of the chick population hatched from replacement clutches (Table 17). Renesting, which contributed less than 10% to

Table 17. Contribution to chick production (at hatching) from nesting stages and clutch types<sup>1</sup>. May 21 was Day 1 of nesting.

Year	Clutch Type	Day of Clutch Commencement				Total
		1-10	11-20	21-30	≥ 31	
1973	Initial	0.38	0.24	0.17	0.00	0.79
	Replacement	0.00	0.04	0.11	0.06	0.21
	All	0.38	0.28	0.28	0.06	1.00
1974	Initial	0.56	0.27	0.05	0.00	0.88
	Replacement	0.06	0.00	0.06	0.00	0.12
	All	0.62	0.27	0.11	0.00	1.00
1975	Initial	0.70	0.10	0.00	0.00	0.80
	Replacement	0.04	0.12	0.04	0.00	0.20
	All	0.74	0.22	0.04	0.00	1.00
Total	Initial	0.55	0.21	0.07	0.00	0.83
	Replacement	0.03	0.05	0.07	0.02	0.17
	All	0.58	0.26	0.14	0.02	1.00

<sup>1</sup> Values represent proportions of annual chick production.

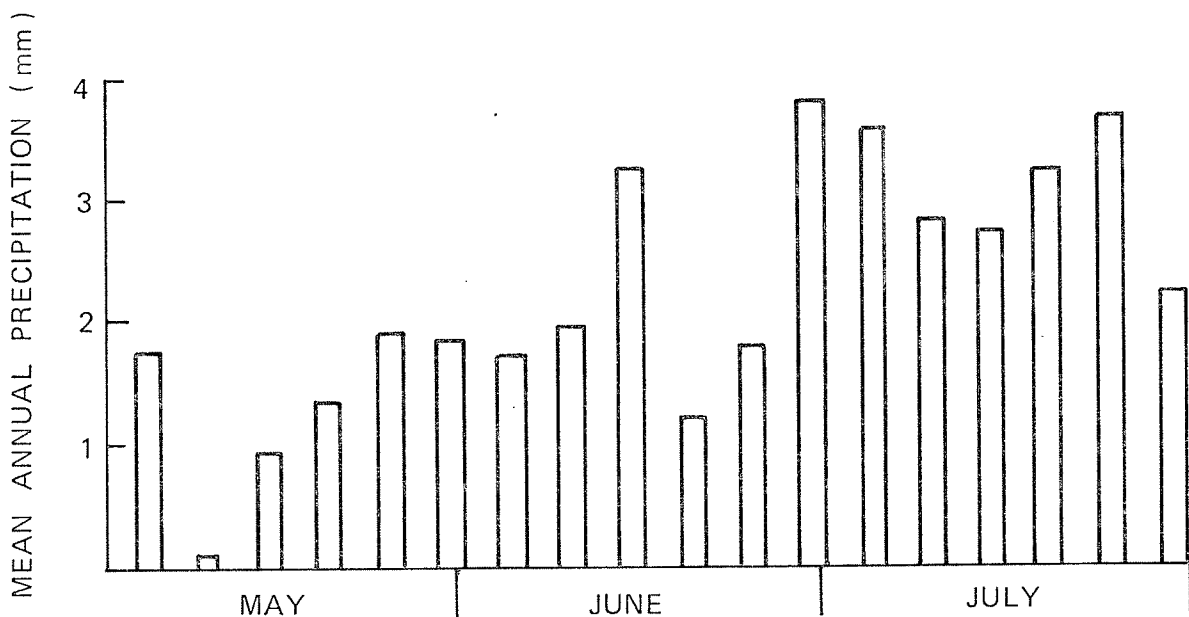
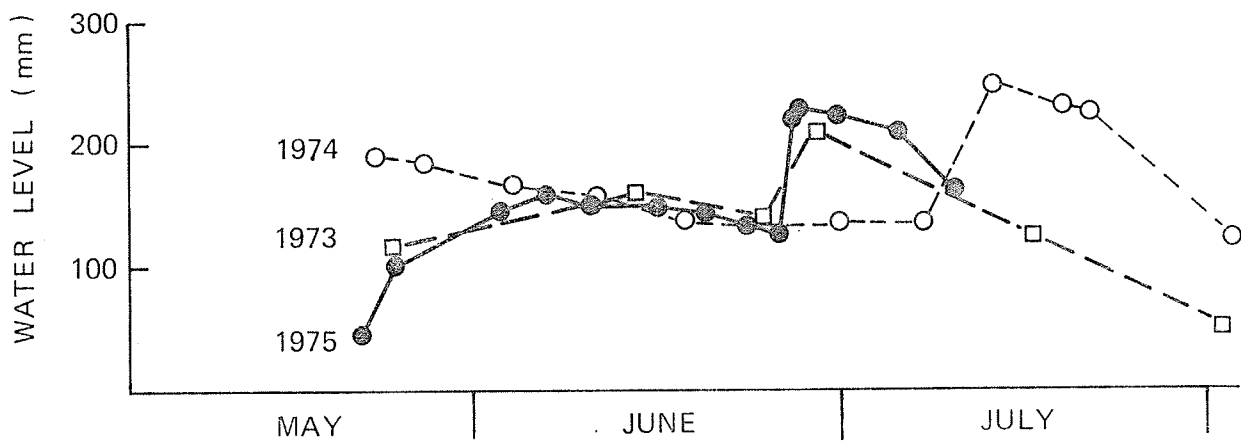
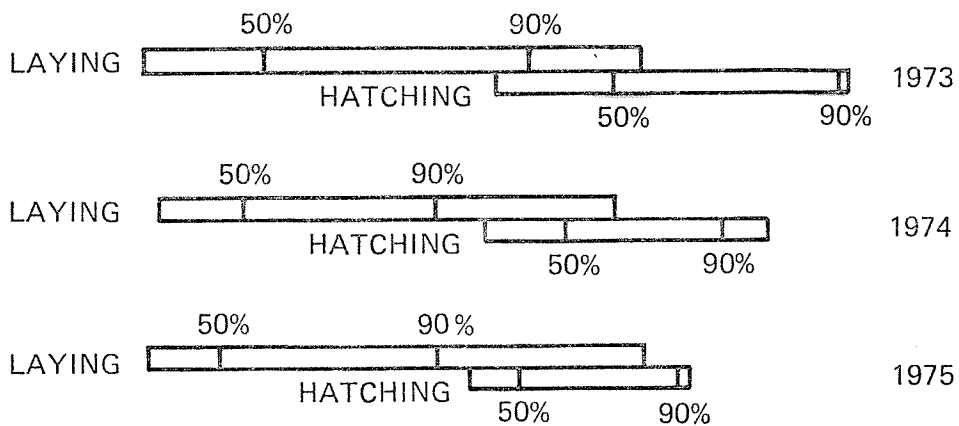
annual production in the Black Duck (*Anas rubripes*) was considered important in maintaining population levels in that species (Stotts and Davis 1960). Considering that the contribution from replacement clutches was much higher in Common Loons (a less fecund species), renesting probably plays a major role in maintaining population levels in loons, even though the hatching success from replacement clutches was relatively low.

ii. Lake levels

Although the level of Hanson Lake was relatively constant (Section II.2), even small fluctuations created marked changes in shoreline. For example, a 10 cm rise in water along a shoreline with a  $20^{\circ}$  slope would flood 29 cm upshore. Thus a loon nest originally touching the water would then be largely surrounded by water and have the eggs partly flooded. Although minor flooding alone would seldom damage the eggs (Tullett and Board 1977), flooding reduces the effectiveness of the shoreline and the nest rim as a buffer to wave action. As the majority of nests were within 30 cm of water, a 10 cm rise in lake levels would eliminate the washout protection of most nests.

Although the influence of lake levels on breeding activity was unclear, nesting events on Hanson Lake coincided closely with the period of maximum water level stability. The level of the lake stabilized rapidly following ice-off each spring, and remained constant until late June (Fig. 22). Levels then rose abruptly from late June to early July each year due to increased rainfall. Increased rainfall occurred annually during this period as shown by mean daily precipitation during the 10

Figure 22. Duration of nesting activities relative to lake levels and mean daily precipitation. Precipitation levels shown are means of 5 day intervals for 10 years preceding this study (Canada D. of T. 1963 to 1973).



years prior to this study (Fig. 22). Therefore the early summer rise in lake levels was a regular event, one to which birds could adapt.

All nesting, and most importantly all nest-site selection, occurred within the period of greatest lake level stability (Fig. 22). Furthermore, each year more than 50% of chicks hatched prior to the annual rise (Fig. 22). It appeared that nesting was synchronized with the annual lake level cycle, and that the reproductive effort was concentrated within the optimum period for nesting. Fluctuating water levels possibly contributed to the end of nesting. The fact that lake levels fluctuated briefly following break-up may also have retarded the onset of laying in early years (Fig. 22). The effects of varying phenology, which were still evident at the end of the hatching period (Fig. 22), apparently exerted more influence on nesting chronology than did the water level cycle.

## 2. Common Loon Demography

The Common Loon is best adapted to a predictable habitat. Nesting was synchronous and regular from year to year. Clutch size was fixed and annual production was constant. There was considerable parental investment in brood-rearing resulting in slow uniform recruitment. These attributes are characteristic of K-selected species (MacArthur and Wilson 1967, Pianka 1972).

Ricklefs (1972) defined the parameters necessary for constructing a life table. Our present knowledge of Common Loon demography contains many gaps, particularly with respect to annual recruitment and age-

specific fecundity (McIntyre 1975). As present techniques do not permit clearer definition of these parameters, formulation of a life table for loons must be based in part on inferences. The following discussion of clutch size and recruitment may reduce some of these gaps.

i. Clutch size

It was apparent in the Hanson Lake population that there was no variation in clutch size, yet it has been shown (Table 13) that fledging success from one-chick broods (89%) was much higher than from two chick broods (64%). How then, do Common Loons benefit by producing a two-egg clutch? As all initial clutches had two eggs, and as all one-chick broods originated from two-egg clutches, there appears to be no mechanism for variability or change. In spite of a reduced fledging rate, pairs with two-chick broods produced more young by virtue of a larger initial brood size. Pairs which hatched two young raised 1.28 young per pair, whereas those which hatched one young raised 0.89 per pair, thus the larger clutch size would retain a selective advantage. There is no record of Common Loons raising more than two young, but as rearing two chicks apparently taxes the capabilities of the parents (Davis 1972), it is unlikely that three young could be reared.

ii. Recruitment and fitness

Fledging success is the only recruitment statistic available for loons. Assuming no post-fledging mortality, the population on Hanson Lake would replace itself every four years (Table 16). On the other hand,

it is assumed that the adult mortality rate is low and the recruitment rate is slow. At least one summer (and possibly more) is spent as a subadult on wintering areas (Palmer 1962), and delayed maturity is evidence of low recruitment (Lack 1966). Adult Common Loons encountered no regular depredation on any breeding areas studied to date, and McIntyre (1975) found no evidence of natural mortality on coastal wintering areas.

Gaviids are considered to be long-lived. Arctic Loons banded as adults have been recovered 16 and 22 years later (Schüz 1957). Nilsson (1977) extrapolated from banding records to estimate a lifespan of over 30 years in Arctic Loons. McIntyre (1975) suggested conservatively a lifespan of 15 to 30 years in Common Loons. Regardless of the longevity, production to fledging on Hanson Lake far exceeded the capacity for recruitment into the breeding population. Thus post-fledging mortality in the juvenile and perhaps subadult stages must be high.

Recoveries of birds banded as pre-fledged juveniles support this: three of nine juveniles banded on their natal territories in 1974 were recovered as mortalities during their first winter (McIntyre 1975). In spite of the small sample, this suggests that mortality in juvenile loons must be very high, considering that generally few banded birds are recovered at death.

Davis (1972) has shown the constraints placed on production by food supply, and demonstrated how specialized parental and chick behaviors insured survival of at least one young when food was limited. Feeding in loons is a specialized behavior for which efficiency improves with

learning; lengthy parental investment is required to allow young loons to become proficient feeders (Barr 1973). Food supply may limit Common Loon density; presumably the large breeding territory is a spacing mechanism which ensures adequate resources both for raising a brood and for sustaining the adults. Thus food availability, partly a reflection of foraging efficiency, could be a major selective force through all stages of the life cycle. This selective pressure would act most strongly on younger individuals with less foraging experience.

Given a high post-fledging mortality rate, and a major role to feeding efficiency in balancing recruitment to mortality, the relative fitness of young at fledging would be the most important factor in determining survival to maturity. Although fledging success was not affected either by hatching date or, after 3 weeks of age, by brood size (Section IV.11), those factors may have influenced survival to breeding age. In other species, late hatched young have higher mortality rates (Lack 1966, Perrins 1965). In the Manx Shearwater (*Puffinus puffinus*) a greater proportion of early hatched and early fledged young returned to the colony to breed (Perrins 1966). This pattern was also evident in the Pied Flycatcher (*Ficedula hypoleuca*) (von Haartman 1967). Late-hatching Herring Gulls experienced excessive post-fledging mortality as juveniles (Nisbet and Drury 1972).

In juvenile loons, age and body weight may provide a rough measure of relative fitness. At any given time, late-hatched juveniles are younger; younger individuals are relatively inexperienced and therefore less likely selected. Within a brood the younger chick

encounters a weight disadvantage which is probably maintained through fledging (Davis 1972), and as such is less fit and less likely selected. In terms of fitness, late-hatched young face a competitive disadvantage within their age class.

In terms of energetics, it is unlikely that incubation imposes a major stress on adults. Otherwise the prolonged incubation of inviable eggs (Section IV.7) would have been reduced. Therefore, although late clutches are less likely to produce individuals which will be recruited into the breeding population, the small investment into late clutches is outweighed by the potential gain.

### 3. Recreational and Commercial Effects on Loons

Loons and human activities are usually regarded as incompatible (Vermeer 1973b), and recent concern has arisen following apparent declines in Common Loon abundance on recreational and commercial waterways. Such declines are difficult to verify as past records are seldom available for comparison. Indeed population declines have occurred in some regions, particularly in southern Ontario (Barr, pers. comm.), but as yet these do not appear widespread. Where islands for nesting were numerous, densities on other northern Saskatchewan lakes were comparable to Hanson Lake (G. Anweiler, unpubl.) and gave no cause for concern about loons in that region.

Although Common Loon populations appear healthy across much of the northern breeding range, high density alone is insufficient grounds on

which to dismiss the species as endangered. As a terminal consumer in an aquatic food chain, and as a primarily K-selected species, the Common Loon is vulnerable to subtle changes in the quality of its environment.

i. Water quality

Piscivorous birds are first to suffer the toxic effects of industrial or agricultural chemicals in water systems (Fimreite 1974). The sublethal effects of waterborne contaminants can be equally as damaging as the direct inviability of eggs (Jeffries 1973). McIntyre (1975: 200) pointed out that in Common Loons the "insidious chemical effects that delay breeding or cause premature death will have a greater long range effect than thin eggshells and increased embryonic mortality".

All egg contents or tissue samples from Common Loons taken in Alberta (Vermeer 1973a), Saskatchewan (Fox *et al.*, 1980), Ontario (J. Barr, unpubl.), Minnesota (McIntyre 1975, Ream 1976) and New Hampshire (Sutcliffe 1978) contained significant organochlorine levels. However, as levels in Alberta and Saskatchewan samples were low, it is assumed that most northern populations are not seriously affected at present. As most northern habitats remain free from commercial developments, loons seldom encounter industrial contamination on their breeding areas, but there is potential for contacting toxic chemicals on wintering areas or during migration. Thus high quality breeding habitat does not ensure a healthy population.

ii. Lake level stability

The stability of water levels is an important criterion for nesting success (Desgranges and Laporte 1979, Merrie 1979). The observation that nesting on Hanson Lake coincided with the period of maximum stability supports this (Fig. 22). In the spring of 1975, high water in the English River system in Ontario covered nest sites used by loons in previous years and caused a 6 week delay in nesting (Barr, pers. comm.). In 1974, a small sudden rise in water levels terminated nesting on Hanson Lake that year. Heavy Common Loon mortality from botulism on Lake Michigan in 1963 was attributed to eutrophication arising from a sharp drop in lake level (Kaufmann and Fay 1964, Rosen 1971). Because of the loon's sensitivity to water levels, the impoundment or diversion of inland waters could severely reduce annual production by Common Loons.

iii. Water clarity

Land clearing operations may contribute indirectly to local declines in populations. Loons capture most prey under water, and locate prey visually. Therefore water clarity is essential for efficient foraging. Although loons established territories on shallow turbid waters in Minnesota, turbid waters deeper than 3 m were not occupied (McIntyre 1975); turbidity reduced light penetration which in turn restricted foraging efficiency. Uncontrolled clearing of watershed basins which increases surface drainage and increases the silt and organic load of the waterways, will affect the foraging efficiency of loons and make favorable breeding habitat uninhabitable.

iv. Recreational use of lakes

McIntyre (1975) examined some responses by Common Loons to habitat changes induced by man. She was concerned mainly with the behavioral adaptability of the bird in habitats subjected to recreational development. Loons on lakes with heavy recreational use occupied only the remote areas of those lakes, and seldom nested or foraged near developed shorelines (McIntyre 1975). She also found significantly fewer adults on her high-use study area, although production per pair was higher there than on adjacent lakes which had low recreational pressure.

The responses of loon populations to intense recreational use of lakes are unclear. Repeated nesting failure due to recreation may lead to the abandonment of territories. Recreation could cause nesting failures in several ways. Prolonged angling or camping activity, inadvertently near nests, may disrupt incubation and stress the embryo or allow discovery of the nest by predators. Although embryos of most aquatic birds are tolerant to cooling, overheating in sunlight may be a serious mortality factor; as eggs are incubated at temperatures close to the upper lethal limit, brief exposure to direct sunlight can raise the internal temperature above this limit (Drent 1973). As loons generally leave the nest when boats approach, a brief intrusion on a territory could result in clutch failure.

Power-boating presents the greatest recreation-based threat to loon reproduction on a local scale. Virtually all nests are vulnerable to washout, as loons are structurally maladapted for land and are

restricted to nesting adjacent to water. But given this limitation, selection has favoured birds which chose protected nest sites where the potential for washout was low (Section IV.5). Washout from wave action is minimized by nesting on shores which face proximate mainland, rather than open expanses (Fig. 11). Washout from rising water is minimized by nesting during the period of greatest water level stability (Fig. 22). Yet under the limitation of nesting at water, few nests could be protected from the wave action of passing boats. The wake from a boat may crest at 40 or 50 cm, a height sufficient to wash out most nests, and slow moving boats generate the largest wake. Thus nests on island shores protected from natural wave action by proximate mainland are still vulnerable to washout from boats. As boats have unrestricted mobility on water, their wakes can reach normally sheltered shores from any direction. Loons could avoid washout from boats by learning to nest farther from water, but this is unlikely due to their structural specialization. Therefore it is unlikely that the effects of washout from boats could be reduced by natural selection operating on choice of nest-sites.

Brood success, on the other hand, is probably little affected by recreational activities. The family unit is extremely mobile on the territory once the young have left the nest, and they avoid areas of human activity and interactions with man seldom occur. Interactions with family groups at close range may contribute slightly to chick mortality. When approached the adults and young separate and the young find refuge in weedbeds or along shorelines. While separated the young are more vulnerable to aerial and underwater predators, and gulls quickly cue to the

distraction behavior of loons under these circumstances.

Common Loons and the recreational use of lakes are by no means incompatible. Probably the largest lakes have few breeding loons as wind-induced seiches cause frequent water level fluctuations and make shorelines unstable as nesting sites. Such lakes are suitable for recreation without interfering with loon reproduction. Boaters and anglers can also be encouraged to minimize their impact on loon production by reducing activity near islands and channels during May and June. The wilderness that loons are traditionally thought to require is not so much a requisite of their habitat as a reflection of it.

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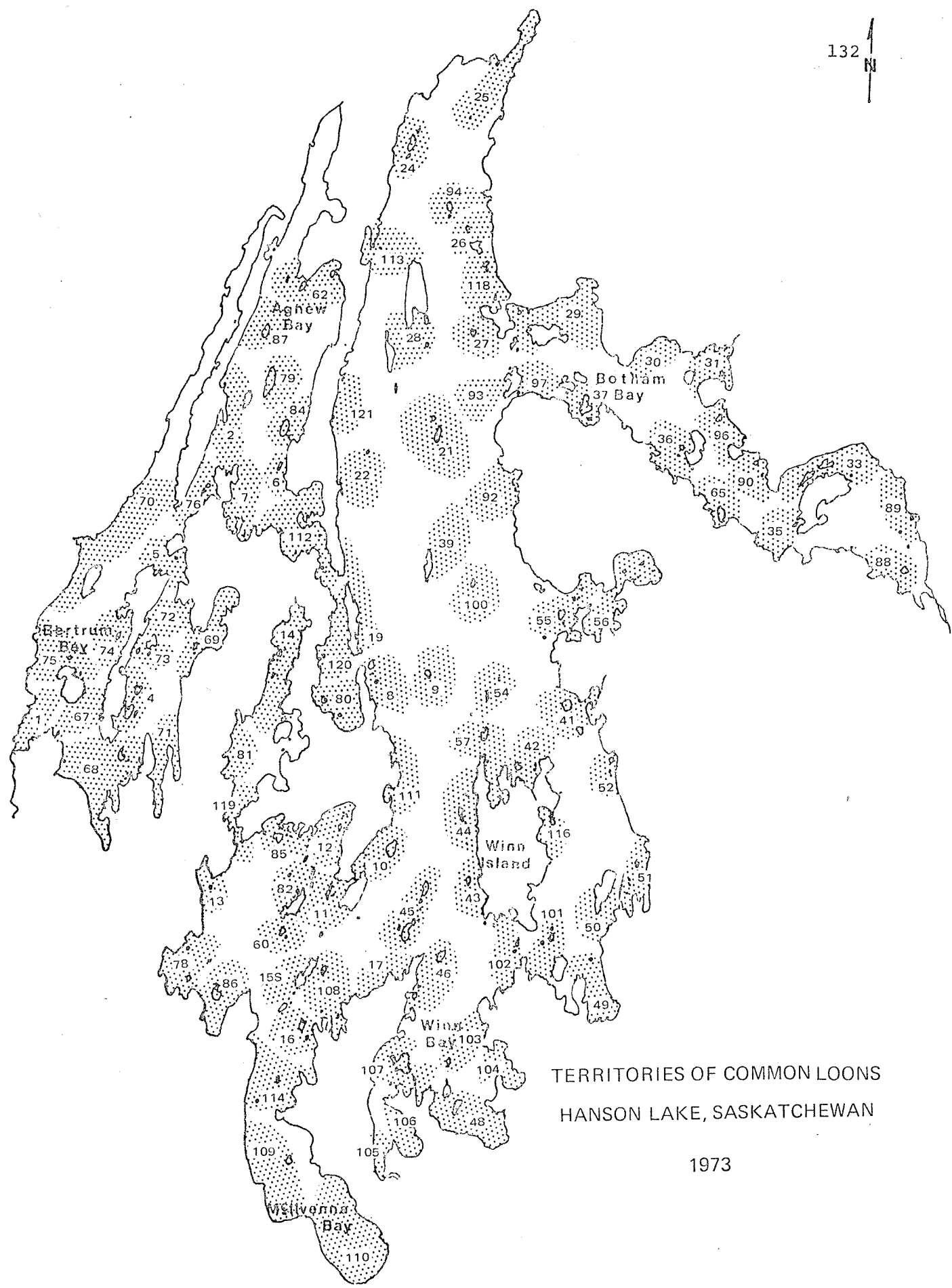
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Appendix I. The distribution of Common Loon territories on Hanson Lake.

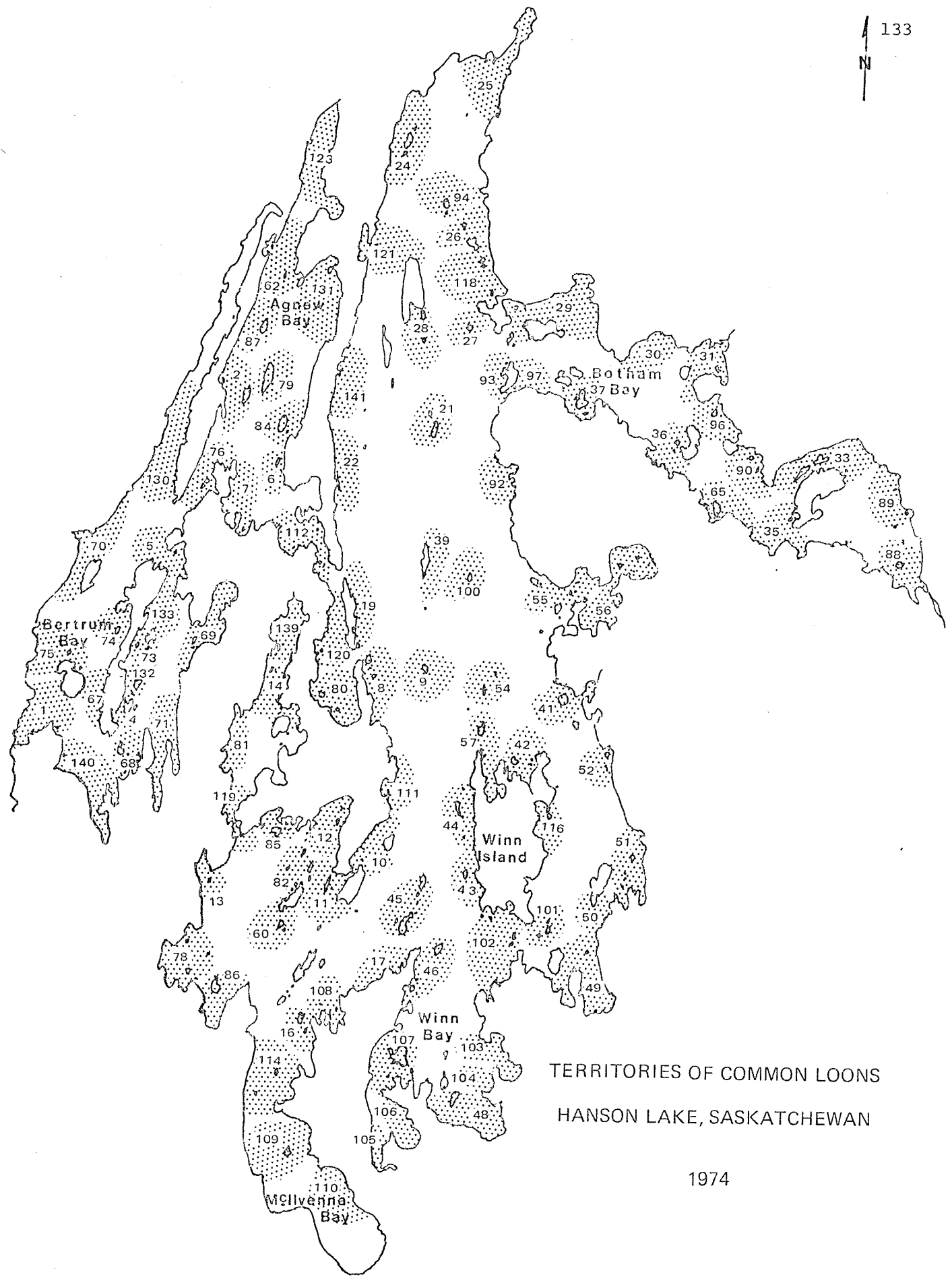
The distribution of territories is shown separately for each year. Territory limits were determined by charting the location of all birds observed on the lake during May and June each year. Each territory is numbered to correspond with the pair number occupying that territory.

The charted territories encompass the areas over which birds were positioned in the course of normal daily activities. In fact the territories of some pairs may have extended beyond the limits observed, thus some territories perhaps represent only minimum activity areas. On the other hand, conspecifics were not always excluded from peripheral activity areas, thus stringently defended areas may actually be somewhat smaller than shown. Observations during this study support Barr's (pers. comm.) opinion that defended areas vary with date, time of day, breeding status and stage of the reproductive cycle.



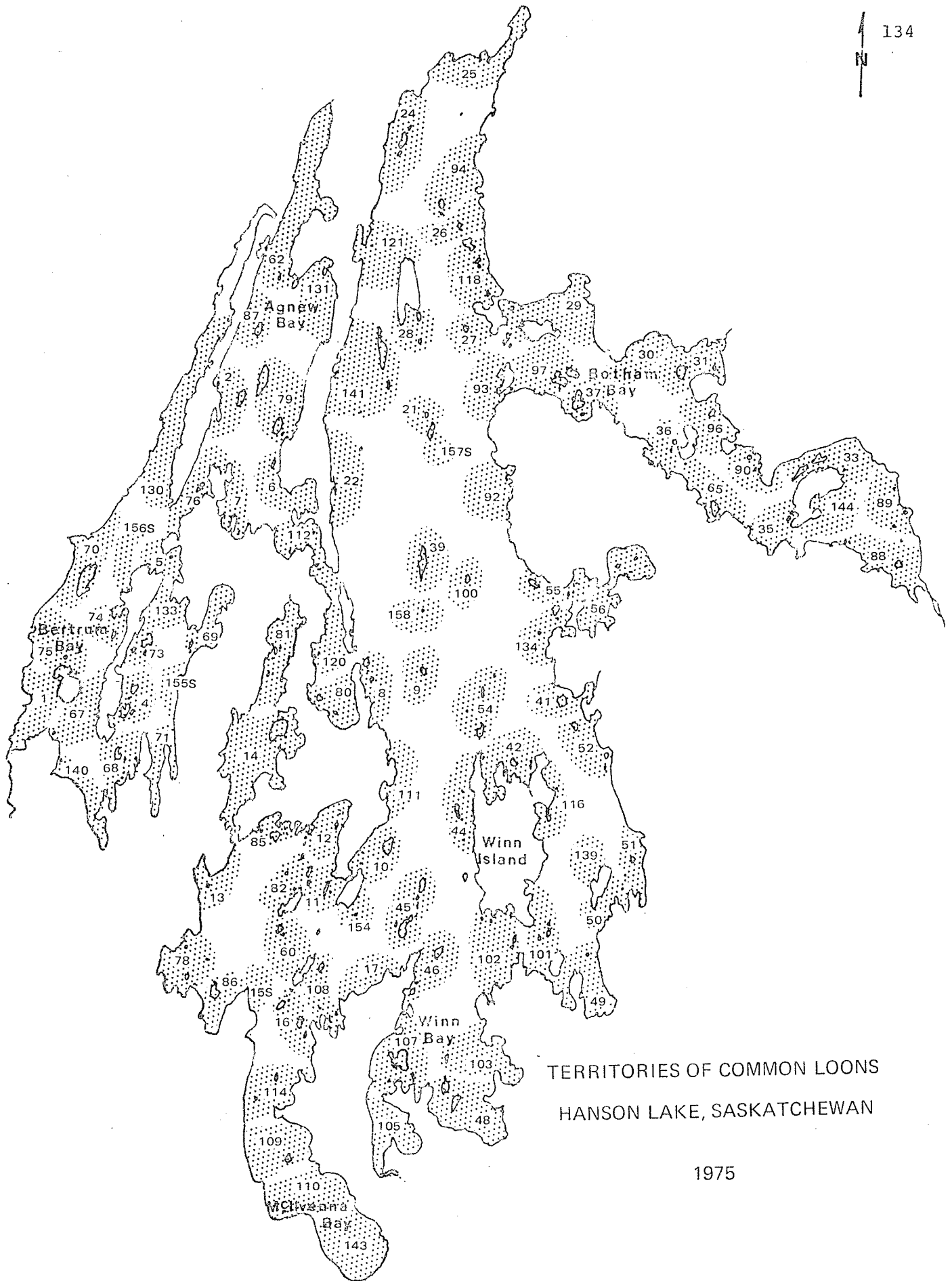
TERRITORIES OF COMMON LOONS  
HANSON LAKE, SASKATCHEWAN

1973



TERRITORIES OF COMMON LOONS  
HANSON LAKE, SASKATCHEWAN

1974



TERRITORIES OF COMMON LOONS  
HANSON LAKE, SASKATCHEWAN

1975

Appendix II. Multidimensional contingency table analyses of hatching success in relation to four variables.

Fienberg (1970) developed procedures for partitioning chi-square to assess simple and interactive effects in multidimensional contingency tables. His analysis and notation has been followed here.

Eggs of known fate ( $n = 361$ ) were classed according to four variables in a four-way contingency table (Table A-1). Variables  $A_r = 2$ ,  $B_s = 3$ ,  $C_t = 2$ , and  $D_u = 2$  were fate, year, stage of nesting and clutch type, respectively, where subscripts denote the number of levels assigned to each variable. Levels for variables A, B and D are self-evident (Table A-2). For variable C, early clutches ( $C_k = 1$ ) were those commenced on or before Day 20 of nesting (9 June); those commenced thereafter were considered late clutches ( $C_k = 2$ ).

A nested hierarchy of models was constructed around the four variables (Table A-2). Each successive model included all terms of the simpler one which preceded it. Model I implies a mutual independence among the four factors. Model II implies that, allowing for annual differences in hatching success, all factors were independent. Model III implies conditional independence of A, C and D, given the year. Model IV removes the year effect and in addition the effect of C on D, and implies that hatching success was independent both from stage of nesting and from clutch type. Model V implies independence of hatching success and stage of nesting given the year and clutch type. Model VI implies the presence of all two-factor interactions, but no three-factor inter-

Table A-1. Counts of eggs categorized by four variables (n=361).

Fate	Year	<u>Initial Clutch (D<sub>1</sub>=1)</u>		<u>Replacement Clutch (D<sub>1</sub>=2)</u>	
		Early (C <sub>k</sub> =1)	Late (C <sub>k</sub> =2)	Early (C <sub>k</sub> =1)	Late (C <sub>k</sub> =2)
Hatched (A <sub>i</sub> =1)	1973 (B <sub>j</sub> =1)	33	9	2	9
	1974 (B <sub>j</sub> =2)	55	3	4	4
	1975 (B <sub>j</sub> =3)	40	0	8	2
Failure (A <sub>i</sub> =2)	1973 (B <sub>j</sub> =1)	23	1	2	11
	1974 (B <sub>j</sub> =2)	37	3	0	11
	1975 (B <sub>j</sub> =3)	54	5	21	24

Table A-2. Nested hierarchy of models to describe hatching success of eggs.

Model	ln e <sub>ijkl</sub>
I	$(1) + (A)_i + (B)_j + (C)_k + (D)_l$
II	$(1) + (A)_i + (B)_j + (C)_k + (D)_l + (AB)_{ij}$
III	$(1) + (A)_i + (B)_j + (C)_k + (D)_l + (AB)_{ij} + (BC)_{jk} + (BD)_{jl}$
IV	$(1) + (A)_i + (B)_j + (C)_k + (D)_l + (AB)_{ij} + (BC)_{jk} + (BD)_{jl} + (CD)_{kl}$
V	$(1) + (A)_i + (B)_j + (C)_k + (D)_l + (AB)_{ij} + (BC)_{jk} + (BD)_{jl} + (CD)_{kl} + (AD)_{il}$
VI	$(1) + (A)_i + (B)_j + (C)_k + (D)_l + (AB)_{ij} + (BC)_{jk} + (BD)_{jl} + (CD)_{kl} + (AD)_{il} + (AC)_{ik}$

action.

Expected cell estimates based on each of the models are given in Table A-3. Kendall and Stuart (1973) recommend that disproportionate contribution to  $\chi^2$  from cells with low expected values be minimized by following Yarnold's (1970) limitation that no expected cell frequency be less than  $5p$ , where  $p$  is the proportion of cells with expectations less than 5. Fienberg (1970) however used no such limitation in his procedure as he was concerned less with fitting models than with the magnitude of differences between them. Thus in the present analysis models having cells with low expectations ( $<5p$ ) did not complicate selection of the best model, although in some cases goodness-of-fit had to be interpreted with caution (Table A-3). Therefore null hypotheses for goodness-of-fit were not rejected unless  $P < 0.01$ .

For each model Wilks' (1935) likelihood ratio chi-square statistic was calculated (Table A-4). Components of the chi-square statistic due to differences between successive models represented the variation explained by those factors added to the model at each step of the hierarchy.

Models I to IV were rejected as they fitted the data poorly and  $\chi^2$  well exceeded the significance level (Table A-4). Models V and VI on the other hand fitted adequately and were accepted (Table A-4). Were it not for an anomalous contribution to  $\chi^2$  from cells with the small expectations, the fit of Models V and VI would have been improved.

Table A-3. Observed cell frequencies (O) and expected frequency estimates (E) used in calculating LR  $\chi^2$  for six models (I to VI) which describe hatching success of eggs. Minimum acceptable cell estimate (5 p) is given for each model.

Cell (i, j, k, l)	0	EI	EII	EIII	EIV	EV	EVI
1111	33	23.7	29.8	25.9	33.0	35.6	37.2
1112	2	8.8	11.1	9.4	2.4	1.8*	2.3
1121	9	7.0	8.8	13.0	5.9	6.4	5.5
1122	9	2.6	3.3	4.7	11.8	9.2	7.8
1211	55	30.8	37.2	45.4	51.9	54.4	54.8
1212	4	11.5	13.8	8.8	2.3	1.7*	2.6
1221	3	9.1	10.9	9.9	3.4	3.6	3.9
1222	4	3.4	4.1	1.9	8.5	6.3	4.5
1311	40	40.6	28.2	25.7	30.5	38.0	37.6
1312	8	15.1	10.5	14.3	9.4	5.3	6.7
1321	0	11.9	8.3	6.5	1.6*	2.0*	1.2*
1322	2	4.4	3.1	3.6	8.4	4.7	4.9
2111	23	27.0	20.8	18.1	23.0	20.4	19.1
2112	2	10.0	7.8	6.6	1.6*	2.2*	2.3
2121	1	7.9	6.1	9.0	4.1	3.6	4.1
2122	11	3.0	2.3	3.3	8.2	10.8	11.8
2211	37	35.0	28.7	35.1	40.1	37.6	35.7
2212	0	13.1	10.7	6.8	1.7*	2.3	3.3
2221	3	10.3	8.4	7.7	2.6	2.4	3.6
2222	11	3.8	3.1	1.5	6.5	8.7	8.5
2311	54	46.1	58.6	53.3	63.5	56.0	57.7
2312	21	17.2	21.8	29.6	19.6	23.7	19.7
2321	5	13.6	17.2	13.4	3.4	3.0	2.7
2322	24	5.1	6.4	7.5	17.6	21.3	23.5
5p		1.0	1.0	1.0	1.9	2.3	2.3

\* Denote violations of 5p limitation through which anomalous departure from chi-square distribution may occur.

Table A-4. Partitioning of the likelihood ratio chi-square statistic for the data in Table A-1.

Component due to model	$\chi^2$	df	P
I	192.4	18	<<0.01
II	170.7	16	<<0.01
Difference between II and I	21.7	2	<<0.01
III	150.4	12	<<0.01
Difference between III and II	20.3	4	<0.01
IV	32.2	11	<0.01
Difference between IV and III	118.2	1	<<0.01
V	19.0	10	NS
Difference between V and IV	13.2	1	<<0.01
VI	19.3	9	NS
Difference between VI and V	Trivial	1	NS

With the exception of Model VI, each successive model in the hierarchy yielded a better fit to the data and the terms added at each step explained significant variation (Table A-4). Hatching success differed significantly among years (difference between II and I), due mainly to 1975 as shown in Section IV.8. Removal of the year effect on the other factors (difference between III and II) also explained significant variation. This difference was due to annual shifts in peak laying (Section IV.6). The majority of the total variation was due to the interaction between stage of nesting and clutch type (difference between IV and III), and was removed as a nuisance effect. Model IV left only two interactions not included: the effects of both clutch type and stage of nesting on hatching success; those were the effects with which the analysis was primarily concerned.

Model V was a significant improvement over Model IV (Table A-4) and the interaction between clutch type and hatching success was thus a real effect. Hatching success in replacement clutches was significantly lower than in initial clutches, irrespective of stage of nesting and of annual variation. There was however, no further improvement under Model VI, implying that stage of nesting did not influence hatching success. Given the clutch type, the probability of hatching for eggs laid early and late in nesting was the same. Therefore Model V was accepted as the best fit.