BIOLOGY AND BEHAVIOR OF THE COMMON LOON (*Gavia immer*) WITH REFERENCE TO ITS ADAPTABILITY IN A MAN-ALTERED ENVIRONMENT

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ABSTRACT

BIOLOGY AND BEHAVIOR OF THE COMMON LOON (Gavia immer) WITH REFERENCE TO ITS ADAPTABILITY IN A MAN-ALTERED ENVIRONMENT

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Life history of the Common Loon includes a small clutch size, long period of parental care, onset of first breeding after the second year, iteroparity, and a long life span. Loons are subject to the potential hazards of a wide range of toxic chemicals and increased human recreational lake use because of their aquatic habits and conflict with man for prime habitat. Their annual biology was studied to assess their ability to adapt to these environmental changes.

Summer studies in north central Minnesota were conducted to look at possible behavioral modifications at the southern limit of a breeding range that has moved northward during the past century and to compare these with behavior described for more northerly populations. Migration maps and behavior are presented from observations and banding records, and spatial requirements and intraspecific associations are described from part of the wintering grounds at Chincoteague, Virginia.

Their potential for maintaining the stable Minnesota population density indicated from survey results of the past 15 to 20 years is discussed with the assumption that increased mortality or delay in onset of breeding would cause a greater population decline than would decreased annual productivity.

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INTRODUCTION

Loons, Gaviiformes, family Gaviidae, although a small order comprising but four species, and with a limited, holarctic, aquatic distribution, are nevertheless familiar to many people today, have been the subject of myths and legends of the past, and have achieved honored status from some governmental bodies.

We in North America refer to them as loons, the derivative of an old English word, "lumme" meaning clumsy, as in lummox, but in Europe they are called Divers, a reference to their superior diving ability. Their generic name, Gavia, may be from a term formerly used for gulls and sea mews, gavia, or it may be a derivative of gaudio, the Latin for rejoicing, and refer to their laughing call. The Common Loon, Gavia immer, receives its trivial name from another Latin word, immersio, to submerge (Jaeger, 1966).

The name Tullik, Too-lik, and similar Eskimo names, (Appendix I) derive from the word "took" meaning tusk, and "lik" meaning "having", an obvious reference to the long bill. Loons are eaten by the Eskimos and are considered delicacies. Their skins have been used to ornament pouches, bags, and articles of clothing by Eskimos, Laplanders, and the Barabinzians (Wilson and Bonaparte, 1831).

American Indian history relates that one of the original five clans of the Ojibway Nation was the Loon ("Mang" in Ojibway). A unique quality was ascribed to each clan, such as being very clever or extremely swift. "Mang" was proud (~~Carl~~ Robert Gawboy, pers. comm.). Other interpretations indicate "Mang" was considered the most handsome of birds. Cooke (1884) mentioned that the term "loon-hearted" was given to an individual who was thought to be extremely brave, much as we use the term "lion-hearted".

Seton (1911) indicated that Indians included loons in their list of "good food". Little is known of its relevance to early European man, although remains have been found in middens in the British Isles indicating that it was used as food in the 9th century (Ticehurst, 1908).

Accounts from early Canadian history note that one name, "spotted loo", was perhaps derived from the British term "Tommy loo". Its cries were thought to announce a coming storm (McAtee, 1957). In Quebec "huard", a French word meaning "crier" is also used.

- Fishermen off the Eastern Shores of the United States use loons to aid in finding fertile fishing areas. The Loons feed on smaller fish and so do the large fish, so when fishermen find a location where loons are feeding, they set their nets. Arctic and Red-throated Loons were authorized as National Monuments in Japan in 1931 because of their importance to Japanese fishermen of the Inland Sea near Seto who use loons to lead them to lance, a small fish which they circle, and then net for bait (Austin and Kuroda, 1953). If a loon is killed, it is put in the bottom of the boat so as not to disturb other loons, and later is taken to shore and laid at a shrine.

In 1961 the Common Loon became Minnesota's State Bird after lengthy legislative debate (summary, Strnad, 1961). Loons exemplify the essence of lake and wilderness country in northern Minnesota. Breckenridge (1949) said, "... it puts the stamp of genuineness on a North Country setting like Sterling does on silver." And Olson and Marshall (1952) wrote,... "Its freedom, independence, and simplicity characterize the true spirit of the wilderness."

Such adulation and respect has not always been accorded to loons. In the early history of the United States, loons were used for shooting sport because they were thought to dive faster than a bullet could be fired, and great skill was ascribed to the man who could successfully shoot a swimming or flying loon. After 1900, improved rifles and improved shooting skills took their toll (Brewster, 1924). Shooting of ducks and loons by passengers on the decks of Lake Umbagog steamers made such a noise that it announced the arrival of the boat. Spring shooting occurred in Massachusetts from mid-April to the first of June (Forbush, 1912). Loons flew low up Buzzards Bay if the wind was from the southwest, and the islands on either side of the channel between Buzzards Bay and Manomet Bay provided access for gunners. As recently as the 1950's loons and cormorants were shot as moving targets by groups of gunners practising in the spring migration period (Anoka County, Minnesota, Warner, pers. comm.).

Sport fishermen sometimes complain that loons eat game fish and injure the fish supply. Before loons were protected, fishermen commonly shot them on the assumption they were competing for the same fish. Recent studies indicate the opposite (Barr, 1973);

in fact, loons may actually improve fishing by removing rough fish (Smorgarzhevsky, 1957).

Today, habitat alteration and toxic chemicals in the environment may be creating a secondary adverse effect to loons. This study was undertaken to investigate and compile an overview of the basic annual biology, migration, and current population status of Common Loons; to evaluate the potential biological flexibility of the species; and to assess the current effect of toxic chemicals, increased recreational lake use, and lakeshore development on Minnesota's State Bird.

CLASSIFICATION AND DISTRIBUTION OF LOONS

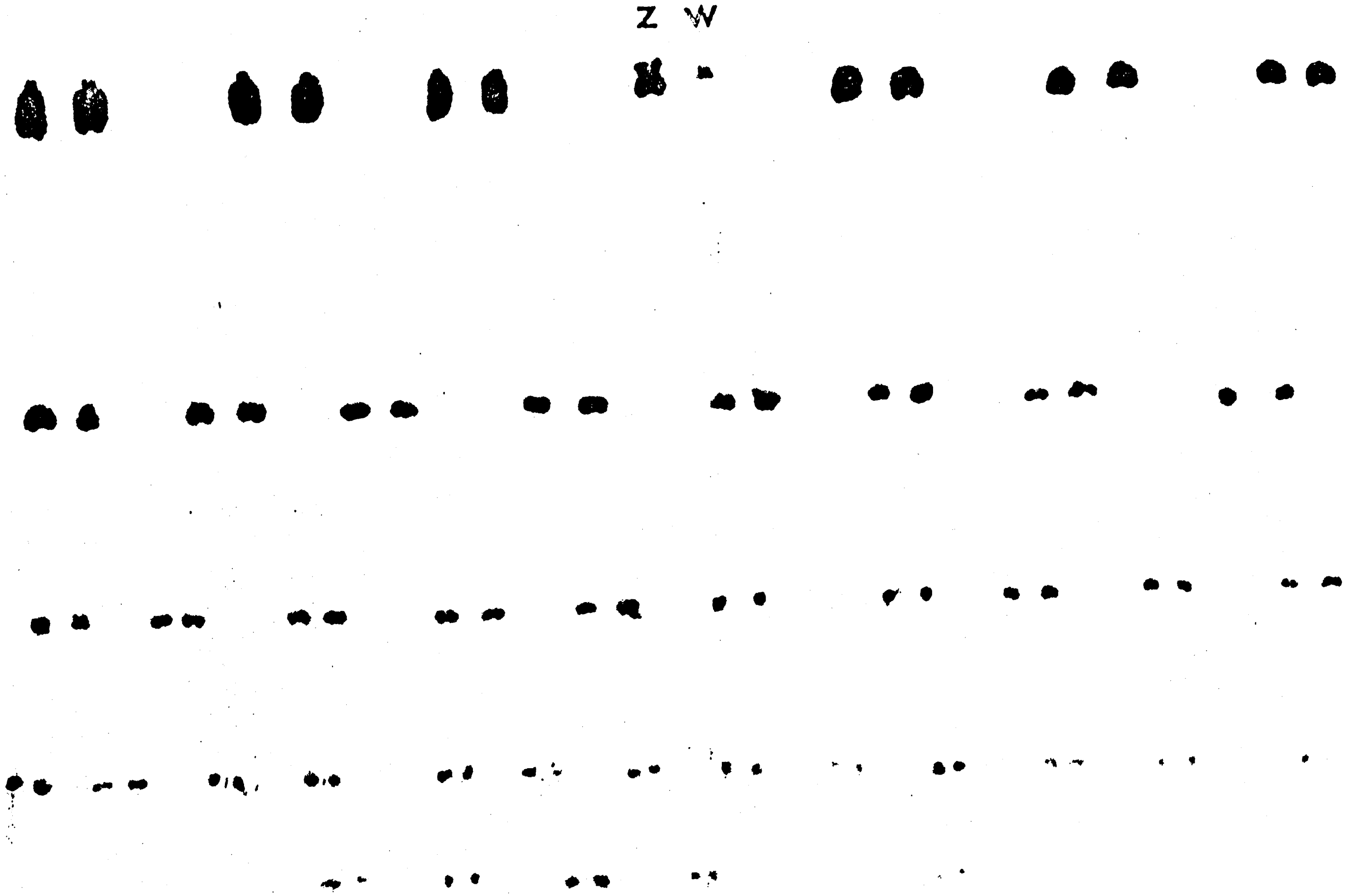
The family of loons (*Gaviidae*) is a holarctic, aquatic group of birds currently recognized as including four species, *Gavia immer*. the Common Loon or Great Northern Diver; *G. adamsii*, the Yellow-billed Loon or White-billed Diver; *G. arctica*, the Arctic Loon or Black-throated Diver; and *G. stellata*, the Red-throated Loon or Red-throated Diver (AOU check list, 1957). Mayr and Short (1970) place *G. immer* and *G. adamsii* in a superspecies.

Phylogenetic relationships of the family have been aligned with a wide range of avian groups. An affinity with *Hesperornis* was suggested by Heilman, (1926) and Saville, (1957). Until 1931 the auks, loons, and grebes were all placed in the same order, *Pygopodes*. Tyler (1969) found no similarities in eggshells between grebes and loons and recommended they not be considered closely related. Storer (1960) noted that loons and grebes show convergent evolution. Storer (1956) proposed that loons diverged from a primitive larine stock sometime between the late Cretaceous and early Eocene, and placed loons immediately after the Charadriiformes and preceeding the Columbiformes (Storer, 1971). Most recently, a relationship between loons and gulls has been suggested by Sibley and Ahlquist (1972) based on egg white protein similarities. The karyotype of *G. immer* (Figure 1.) is very similar to that of *G. stellata* (Hamar, 1970). Both have a chromosome complement of 2n=88, and the sex chromosome, No. 4, is easily distinguised as the only large metacentric chromosome. There is no obvious similarity between loon karyotypes and those of other groups.

The Common Loon has been known by a number of scientific names in the past, among them *Colymbus glacialis*, *C. torquatus*, *C. imber*, *C. immer*, *Urinator imber*, *U. immer*, *Gavia imber*, and *G. immer*. The International Commission of Zoological Nomenclature decided in 1950 on the generic name *Gavia* (Forster 1788, Enchiridion Hist. Nat. 38) and the trivial name *immer* (Brunnich, 1764, Orn. boreal. 38).

The AOU check list (1957) recognizes no subspecies. Formerly two subspecies were recognized, *G. i. immer* and *G. i. elasson* (Bishop) (AOU, 1931). A size gradient has been defined with the smallest birds in the area around North Dakota, and larger individuals occurring to the northwest and northeast with the largest members on Baffin Island (Rand, 1947; Anderson *et al.*, 1970).

Figure 1. Karyotype of the Common Loon. The chromosome complement is 2n=88, and No. 4 is the Z chromosome.


Z
W

Loons are essentially allopatric during the breeding season. The Red-throated Loon is sympatric with each of the other three species in some parts of its range, although it prefers nesting on small tarns or ponds, and there is usually no direct habitat overlap. Where the ranges meet there may be some overlap between Arctic Loons and Common Loons, and an apparent hybridization between the two species was reported by Robertson and Fraker (1974).

The Common Loon has the most southern distribution of the loons; its breeding range extends approximately from 45° north latitude to the northern limit of the boreal forest in North America. There are also breeding populations in Iceland, Greenland, and Baffin Island (Palmer, 1962; Godfrey, 1966). Common Loons with young were reported from Scotland in 1970 and although it is known that some individuals summer there, this is the first account of ascertained breeding of which I am aware (Brit. Birds 1971, 64: 75).

Wintering distribution of the species is holarctic. In the eastern hemisphere they winter off the coasts of Norway and Great Britain, south to Algeria (Etchécopar, 1964; Witherby <u>et al</u>., 1940). In the western hemisphere they occur on all coastal areas of North America with particularly heavy concentrations along the mid-Atlantic and New England coasts, the eastern Gulf Coast, and the Pacific Coast from central California to Vancouver Island (Palmer, 1962; Bystrak, 1974).

The wintering portion of this study was made in an area where populations of Common Loons occur every winter, off the middle Atlantic coast of the United States. The breeding season portion was done at the southern limit of the species' range in north central Minnesota. Common Loons formerly bred further south, to northern Iowa, northern Ohio, and northeastern California (Bent, 1919), but the most southerly nesting records I have acquired during the course of the study were from Ramsey and Hennepin counties in the metropolitan area of Minneapolis and St. Paul, Minnesota.

My study areas were chosen because modifications in the biology, behavior, or populations of Common Loons should occur first at the limit of their range. An opportunity to assess potential flexibility could most readily be noted by comparing adaptations of this population with those that breed farther to the north and had been or were being studied there by others (Olson and Marshall, 1952; Munro, 1945; Sjölander and Ågren, 1972; Barr, 1973; Yonge, in prep.).

STUDY AREAS

Studies were carried out in three areas. Summer research was done in north central Minnesota and the winter portion was done on the Atlantic coast of Virginia, at Assateague Island.

BLACKDUCK

A 32-square mile tract in the Blackduck Ranger District of the Chippewa National Forest in Beltrami County, (47°40'N, 94°30'W) was used as the base for the habitat and nesting site selection portion of the study (Figure 2.). The study concerned primarily 11 small lakes in the area, each able to support only a single pair of loons, but some comparisons were made including data from two larger lakes in the area. Loons were known to use each of them at one time or another.

Lakes were eutrophic or dystrophic, with vegetation typical of the bog community. In some areas there were Red and White Pines* and Balsam Fir, but the predominant vegetation was aspen-birch. Logging occurred at some place within the area throughout my study. With the exception of the loggers, much of the area had no human encroachment during the summer, although hunting and ricing occurred in the fall.

ITASCA STATE PARK

Itasca State Park includes approximately 49 square miles of glaciated lake country surrounding Lake Itasca, the headwaters of the Mississippi River (Figure 3.). Vegetation is mixed deciduous-coniferous and contains several large stands of Red Pine, some over 250 years old. There are about 60 lakes plus numerous ponds, most formed by ice blocks either buried in glacial till or deposited in a pre-glacial valley. They range from those with shallow depressions of 3 to 5 feet to Elk Lake with a 90 foot deep trough. In addition to lakes within the Park, extensive observations were

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* Scientific names of all plants and animals are given in Appendix II.

Figure 2. Blackduck study area. Lakes shown are the following:

1. Anderson
2. Baumgartner
3. Benjamin
4. Carls
5. Chinamen
6. Coleman
7. Damon
8. Gimmer
9. Holland
10. Marie
11. Webster
12. Decker
13. Rabideau

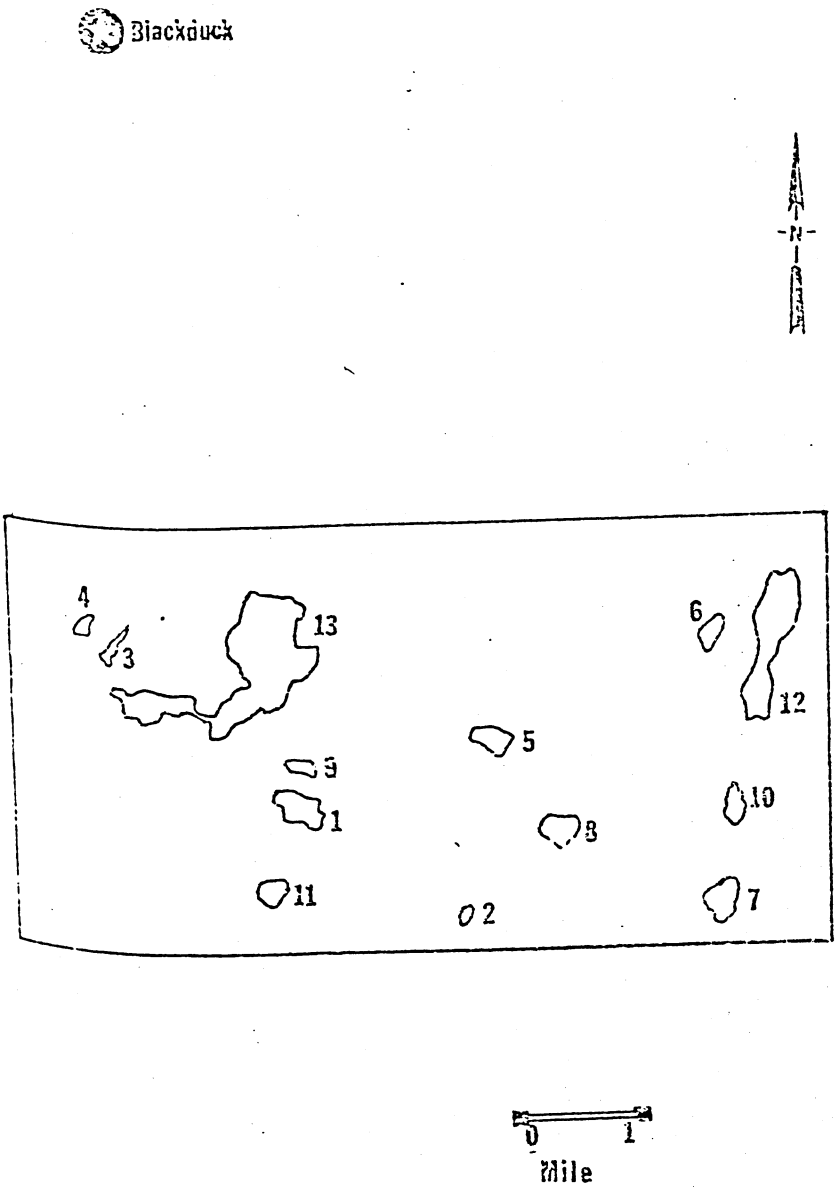
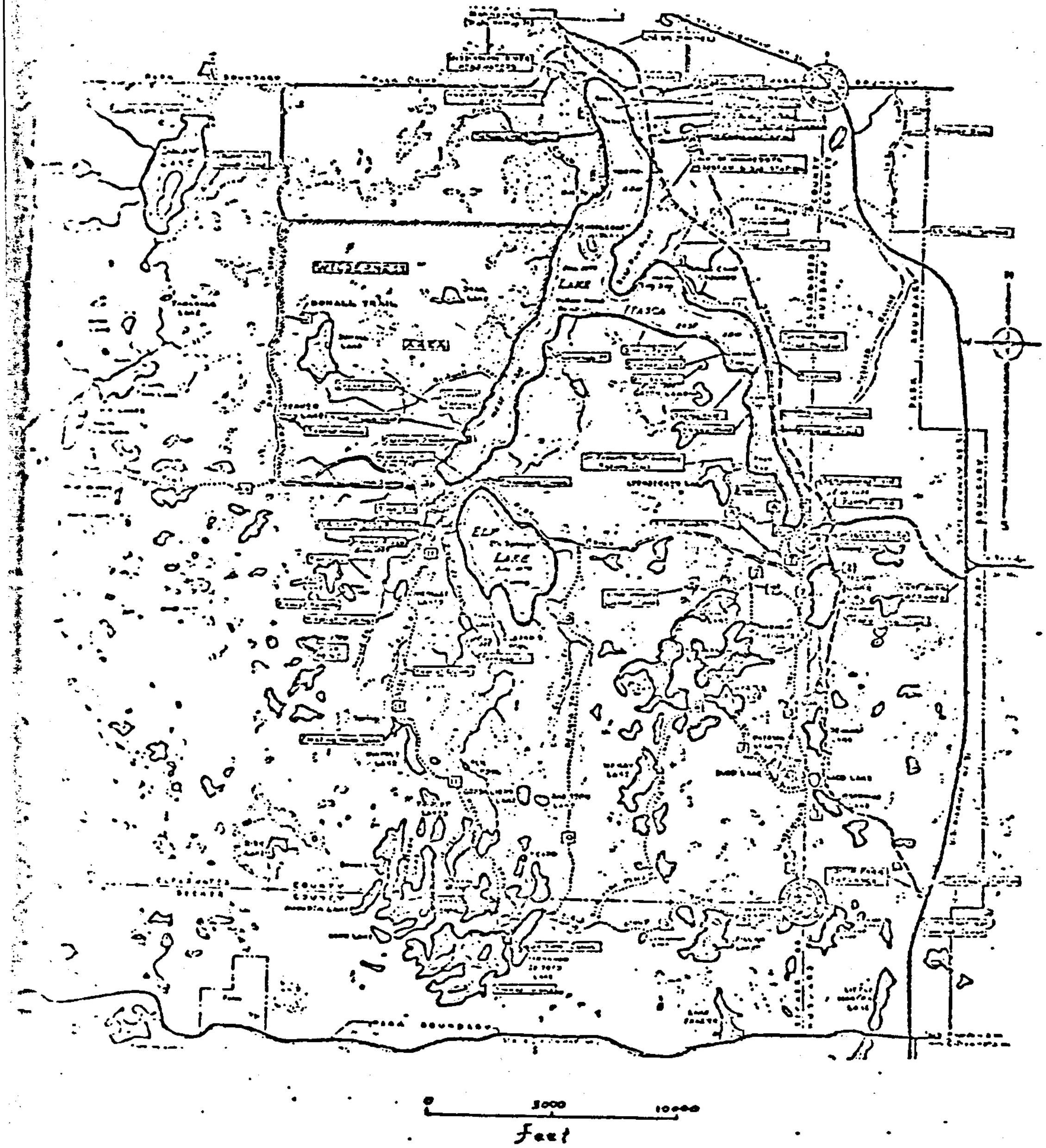

Blackduck
N
4
3
13
6
12
5
9
1
8
10
11
2
7
0
1
Mile

Figure 3. Map of Itasca State Park, Minnesota.


LAKE
ITASCA
ELK
LAKE
0
5000
10000
Feet

made on Lost Lake, located three-fourths mile east of the NE boundary of the Park.

ASSATEAGUE

Winter studies were conducted on the Atlantic coast at Chincoteague, Virginia. Some observations were made on the ocean side of Assateague Island, and some were made from Chincoteague Island, but most were made in Tom's Cove at the southern tip of Assateague Island National Seashore (Figure 4.). The cove is about 1½ miles across at the narrowest point, and about 3 miles in length. Mean tidal depths are shown on the map (Figure 4.), and at spring tides, it is about 14 feet deep. Although it is sheltered, there are usually whitecaps in the winter, and even on the calmest days waves were so large that observations from a small boat were impossible.

Tom's Cove is famous for its oysters and clams, and the waters around Chincoteague and Assateague are known to be excellent fishing grounds. The "watermen of Chincoteague" comprise the largest segment of the population. The Eastern Shores in general are noted for their abundance of wintering waterfowl and Assateague is one of the prime areas. Chincoteague National Wildlife Refuge is located on Assateague Island, and is the major wintering grounds of the Greater Snow Goose. Water birds associated with loons are discussed in the section on Winter Biology.

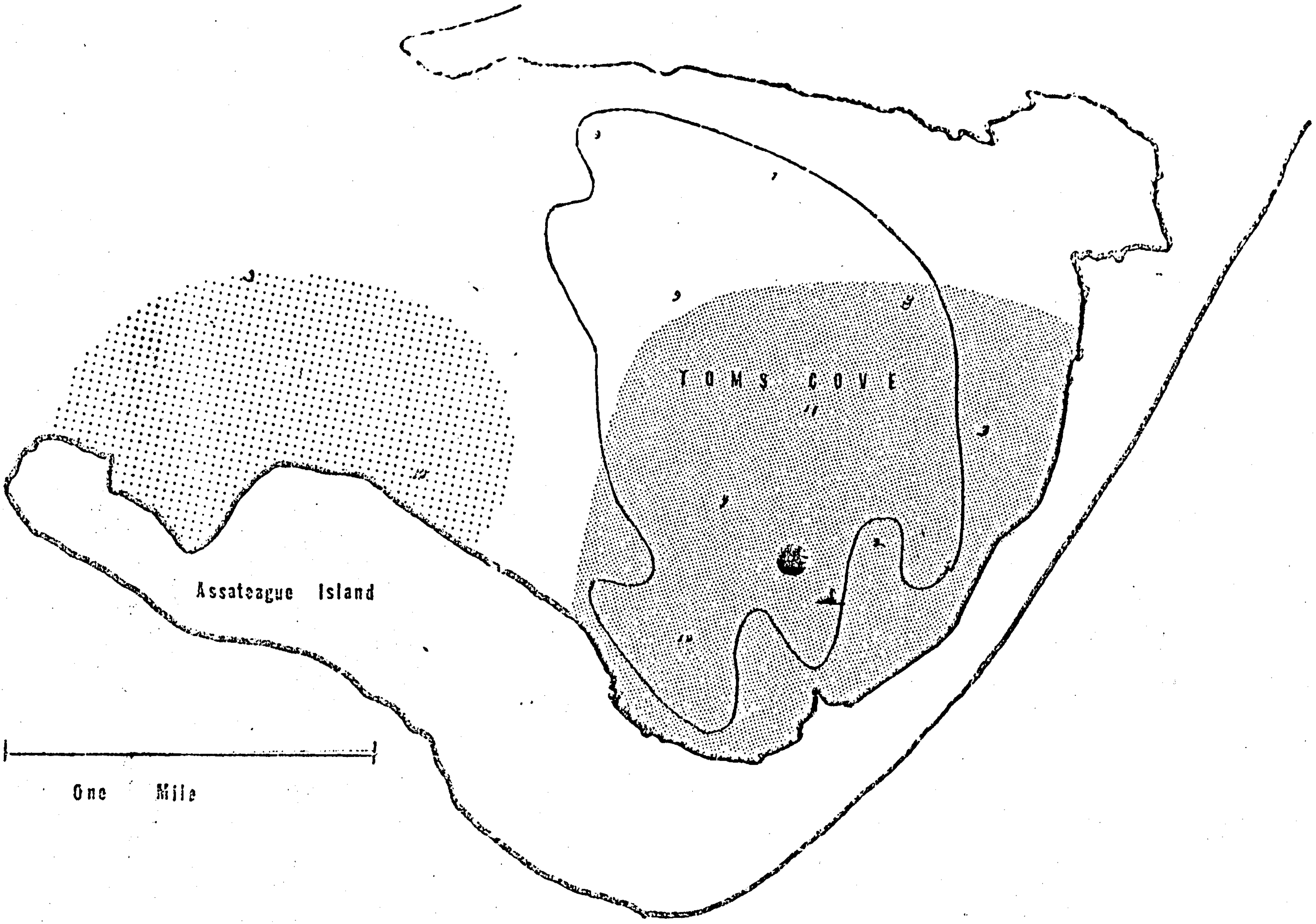
Figure 4. Map of Tom's Cove off Assateague Island, Virginia. The two study areas are designated as the Hook Study Area and the Factory Study Area. Symbols indicate mapped loons.

▲ Feeding loon

● Sleeping loon

░ Hook area

▒ Factory area


TOMS COVE
Assateague Island
One Mile

METHODS

Minnesota study lakes were small, all but one were less than 100 acres, and each comprised no more than a single loon territory. Capture of loons in order to band and mark them is exceedingly difficult and although I was successful in marking some individuals, adult loons from which behavioral data were secured were not color marked (discussed further on page 19). Individual pair members could be distinguished by differences in size, neck markings, and feather pattern variability.

Loons are monomorphic and determing sex in the field is difficult. I was first able to definitely sex a loon when I watched her lay an egg. Field notes which I had made earlier for that pair identified the pair members as "A" and "B" and indicated that "A" was always on top during copulations and was the only one to give the yodel, and that "B" was the one that laid the egg. Thereafter, pair members that yodeled and/or were on top during copulation were noted as males.

In most cases one pair member was larger than the other, and for those pairs that were sexed by behavioral methods, the larger one was the male. The head was larger, the bill was longer, and the overall body size was greater. Body length is difficult to measure from museum skins due to the variability in the way skins are prepared, but bill size and skull breadth are characters that can be measured accurately from museum specimens. Barr (1973) also found that males were larger than females, and determined by stomach content analyses that prey preference differed with the sex of the bird, males taking more large fish. This indicated that a larger head and longer bill length might be good characters for sex determination.

To test this, bills were measured at the culmen and skulls of skins and mounts were measured at the postorbital process to see if there were sufficient differences to permit their use in sexing adults (Table 1). Skeletal material was not used. Skulls of males were only slightly larger than those of females, and there was considerable overlap. Male bills were significantly longer than female bills ($P <.01$) but there was considerable overlap and I concluded that bill size could not be used either as a consistent indicator of sex. The only reliable method I used to sex birds in the field was by behavioral differences, and I recommend that unless additional data can be secured to confirm that within each pair the male is larger than its mate, size difference alone should not be used to sex loons.

Most observations were made several hundred yards from the birds using a 40X spotting scope. A folding chair blind was occasionally used, and at other times, observations were made from a car, but usually no blind was needed because of the distance. This assured that birds would not modify their behavior due to my presence. Loons were easily frightened from nests or nest sites when permanent blinds were erected. In 1971 I placed an artificial island just offshore from my living quarters, so instead of my going to the birds they came to me. Complete nest-building and egg-laying sequences were recorded from this site.

Table 1. Bill lengths and skull breadths of male and female Common Loons.

	Males	Females
Bill length		
N	60	52
$\overline{X}$	77.3 ± 0.37	74.8 ± 0.87
Range	60.7 to 93.1	59.5 to 89.4
	$t = 2.64$	$P < .01$
Skull breadth		
N	49	39
$\overline{X}$	47.8 ± 1.24	46.29 ± 0.61
Range	37.0 to 57.3	38.4 to 53.0
	no sig. diff.	

Specimens measured were from the American Museum of Natural History; the United States National Museum; James Ford Bell Museum of Natural History, University of Minnesota; Florida State Museum, University of Florida; Stovall Museum, University of Oklahoma.

Nest checks were made with the use of a small pram and outboard motor. Blackduck study lakes were checked from early May to September each summer, 1970-1974. Lakes with territorial pairs were checked several times from May through mid-July so that nesting and re-nesting could be ascertained, and late summer checks were made to verify fledging.

Water clarity readings were taken with a Secchi disc, water depth was measured by means of a fishing location water marker with a weighted line, and pH readings were taken with pH paper. Lake lengths were calculated from aerial photographs from the U.S. Forest Service Chippewa National Forest Headquarters. Data on fish species were secured from the Minnesota Department of Natural Resources Fisheries Regional office in Grand Rapids, and I did additional sampling with minnow traps baited with hamburger.

Super-8 movies and 35mm. slides were taken to record behavior for later verification with field notes that were recorded directly into bound notebooks, and vocalizations were recorded on a Uher 4000 Report L tape recorder at 7½ inches per second. Aerial photographs of Blackduck study lakes were made.

Other data were volunteered from the public via Project Loon Watch (PLW). Each year from 1971-1974 a questionnaire was sent to several hundred people who had expressed an interest in the study and a desire to help (Figure 5).

Lake sizes used for comparative purposes were taken from the Minnesota Conservation Department Bulletin No. 25, An Inventory of Minnesota Lakes, 1968.

Figure 5. Example of a Project Loon Watch questionnaire form.

PROJECT
LOON WATCH

1974

Return to: Judy McIntyre
Zoology Department
University of Minnesota
Minneapolis, Minnesota 55455

Your name and address:____________________

____

Please fill our a separate sheet for each lake. Write for more forms if needed.

State____________________

County____________________

Lake____________________

Size____________________

Homes on shore (circle one) 0 1 2 3 4 5 more than 5 Resort Campground

Use by man. Check highest value that applies. (Please check only ONE).

0. None (fall hunting only counts as none).
1. No boats.
2. Boating or canoeing irregularly.
3. One or two boats or canoes daily.
4. Daily use of boats, canoes, or sailboats; no boat motors.
5. Occasional use of boats with motor.
6. Daily use of one or two boats with motors.
7. Frequent use of boats with motors, as for fishing.
8. Occasional waterskiing and/or boat racing.
9. Frequent waterskiing and/or boat racing.

Date of your first visit this year____________________

Date water open sufficient for loon use____________________

Date loon(s) first came to lake____________________

Number on lake on above date____________________

Are loons present throughout the summer? (circle one) yes no irregularly

Total number of adult loons remaining on lake throughout the summer________

Total number of pairs for which hatching result was determined________
(includes both successes and failures)

Total number of young hatched by these pairs____________________

Total number of young which survived through summer____________________

Date young first seen____________________

Size of young on this date (check one)
1. Less than 1/3 length of adult
2. 1/3 to 2/3 length of adult
3. More than 2/3 length of adult

Date loons last seen____________________

Date of your last visit (December 31 if present year round)____________________

Number of young raised on this lake last year in which you observed young_____
What year was this?__________ Last year you checked lake__________

Please add any additional remarks on the back. If you see a group of 3 or more loons note 1.) date; 2.) time of day; 3.) number of loons; 4.) activity.

Winter observations in Tom's Cove were made from shore with a 40X spotting scope. A small boat was not successful as an observation post because of the waves which obscured visibility. The ruins of an old factory jutted out into the cove and from the slight elevation that the site offered, good observations were made. Direction and distance were calculated with the aid of a compass and spotting scope focus, explained more fully in the section on Winter Biology.

Loons were captured for banding and color marking by night-lighting. I used a method adapted from that described by Bishop and Barratt (1969). The man sitting on the bow wore a motorcycle helmet mounted with an airplane landing light (12 volts) 100,000 candle powered by a one-hp gasoline engine. A 17-foot Grumann guide boat with $9\frac{1}{2}$ hp motor was the most satisfactory equipment, but a nine-foot pram with a $5\frac{1}{2}$ hp motor was also used when the other equipment was not available. Birds were caught with a dip net with an eight-foot handle. Loons dive when approached and generally make a sharp underwater turn so that they cannot be followed in deep water, but on shallow lakes the landing light permits their being easily seen underwater so they can be pursued.

Each captured bird was marked with a U.S. Fish and Wildlife Service band and wing tagged with a colored plastic tag (Sa-flags, vinyl tagging by the Safety Flag Company of America). The tag was affixed by two grommets between the third and fourth secondaries, but was not fastened through the patagium. Juveniles had to be at least 6 weeks old before they were large enough to hold the band.

The tag did not impede flight, and it could be preened in with the secondaries when the loon was in the water. Wing tags were readily visible from a distance of several hundred yards whenever the birds did a Wing Flap.* Bands could be seen with a 40X spotting scope when the foot was extended for a Foot Waggle. Thirteen juveniles and three adults were banded during the study.

The karyotype was made by leucocyte culture (Shoffner _et al_., 1967) on a captive loon. The feather pulp squash technique (Shoffner _et al_., 1967) was tried on all birds wild-caught for banding in 1971 and 1972 but was unsuccessful. Because the Z-chromosome is the only large sub-metacentric one, Common Loons would be perfect subjects for initiating this method of sexing individuals and it should be pursued as a potential field technique for monomorphic species.

RESULTS

The format of this section follows the annual cycle of Common Loons beginning on one of their wintering areas of concentration. It will follow them through both spring and fall migrations, discuss their behavior and biology during their nesting season from habitat selection through fledging of the young in north central Minnesota, and will then present the results of toxic chemical analyses and population surveys.

*Displays are explained and illustrated in Appendix III

Appendix III presents a pictorial glossary of terms used to describe posturings and displays.

WINTERING BIOLOGY

Observation Methods

Observations were made from a 40X spotting scope mounted with a compass housed in wood, brass, and plastic to prevent metallic interference to the compass. The focus adjustment button was divided into 32 ridges. A standard was formulated by measuring the distance from the scope to a walking man at each one-ridge turn of the focus button. Observation points were located by triangulation with a lighthouse and an observation tower. Loon locations were recorded in the field as compass direction and focus button position. Observation and loon positions were then mapped on copies of a USGS map of Tom's Cove (Figure 4.), the compass reading was adjusted 8° west to account for the declination at 75°22'W, and the focus position was translated to feet. Mapping permitted interpreting placement of loons to compare their positions and spacing relative to tidal levels, sun time, and each other.

Interspecific Associations

Seabird assemblages of wintering coastal species have been described by several authors (see summaries by Nilsson, 1972; Cronly, 1973). Some of these studies have assessed avian distribution in terms of food resources and feeding strategies.

Horned Grebes, Brant, Common Goldeneyes, Bufflehead, Oldsquaw, Ruddy Ducks, Red-breasted Mergansers, Scoters, Red throated Loons, and Common Loons all utilized Tom's Cove. Interspecific feeding groups were not observed, but single Horned Grebes were frequently seen following Common Loons and diving just behind them. Commensal feeding in grebes has been described (Paulson, 1969) for four species, but has not previously been noted to occur between grebes and loons.

Horned Grebes, Common Goldeneyes, Ruddy Ducks, and Common Loons each formed a species-specific raft in the evening. The area utilized by each was similar in that they all concentrated over the deepest part of the cove (9 to 11 feet at mean low tide) but each raft was separate and there were no interspecific aggregations. Waterfowl rafting has been reported occurring offshore from the feeding area (Nilsson, 1972). A cove is circular, therefore offshore is in the center. Coves are protected from the strong wave action of the open ocean and are optimal rafting sites, and it is likely that several species used the same area because their requirements overlapped and the available site was small.

Loons were the last to flock each evening; all other species had formed rafts when the loons began to congregate. Goldeneye rafting began about one hour before sunset (agree, Breckenridge, 1953; King, 1960; Linsell, 1969), but loon aggregations were not formed until after sunset.

INTRASPECIFIC ASSOCIATIONS

My original purpose in making winter observations of Common Loons was to discover whether or not they engaged in flock feeding, thereby suggesting that perhaps the late summer flocking functioned as reinforcement mechanisms for winter behavior.

Red-throated Loons fed in small groups in the channel between Wallops Island and Assateague Island where the current was swift, and only occasionally were they seen in the bays and coves. On the other hand, Common Loons did not form feeding assemblages, but spent the day spaced and feeding singly in quiet water.

Loons often are reported drowned in fishing nets (Olson and Marshall, 1952; Bartonek, 1965; Parmelee et al., 1967; Vermeer, 1937a.) Off the coast of Virginia netting mortality peaks each year in March during windy weather when nets are set for mackerel and herring. Some of the local fishermen reported or brought me dead loons which had become entangled in their nets and although Red-throated Loons were sometimes caught three and four at a time, Common Loons were caught only as singles in any one set, giving additional evidence that the two species may utilize different feeding behavior.

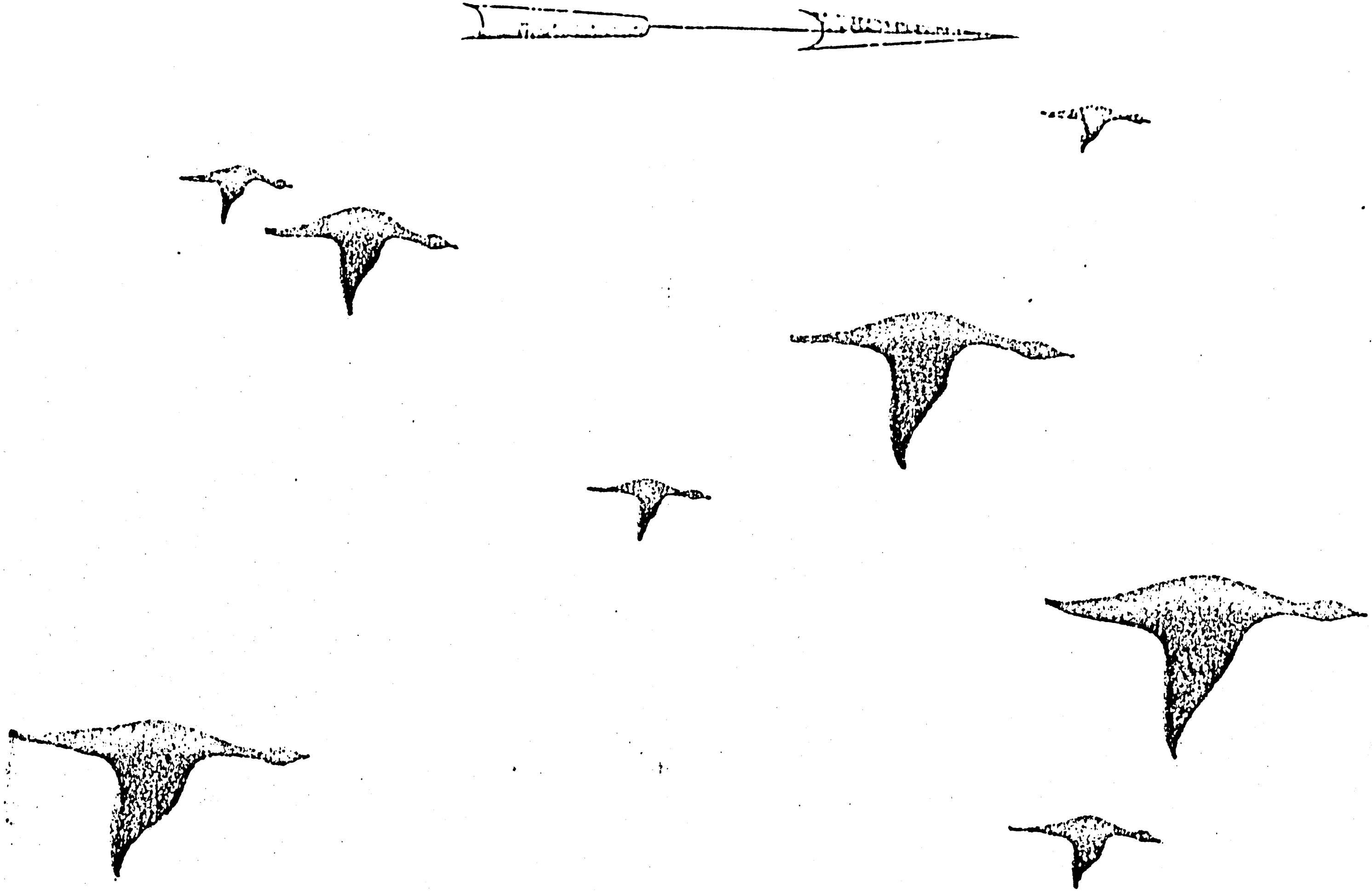
Some aggression occurred among Common Loons. The yodel, which is the territorial vocalization given during the breeding season, was occasionally heard, and twice I heard the tremolo call, which is used in aggressive and defensive activity during the summer. On 12 January a yodel was heard, then one loon approached another that was feeding. The feeding bird assumed the Aggressive Upright posture, then spread its wings and went into a Penguin Dance, after which the intruder ran from the area and the original resident resumed feeding.

From these three pieces of evidence, i.e. loons not observed feeding together, single bird mortality in fishing nets, and intraspecific aggression during feeding sessions, it appears that Common Loons do not engage in flock feeding on the wintering grounds.

Loons flew up and down the coast in loose aggregations throughout the period of my study. On 6 January I counted loons from a fishing boat as I moved down the coast about one-half mile offshore. In 11 miles, from 15:00 to 15:30, I counted 161 flying loons. Many flew singly; others were in extended cluster flight flocks (Heppner, 1974) of two to 46 individuals (Figure 6). About 90% of the birds were heading north. The same morning, I saw, but didn't count, large numbers also flying northward. Thus, loons were flying in the same direction both morning and evening, and it did not appear they were "flying in" and "flying out" of the cove. There was no regular flight to and from the cove at any time during the study.

The possibility still exists that flock feeding does occur offshore, or at night, but direct evidence for this is lacking. The clusters which I have described may be independent flights towards a common destination (i.e. offshore feeding) as Heppner (1974) has suggested is generally the stimulus for an extended cluster flight formation.

Figure 6. Typical loon formation as seen when they are flying up and down coastal areas.



Individual Spacing

Three methods were employed to calculate the space needed per loon:

1. Two areas, observed in Tom's Cove, each had groups of about 25 individuals. Because of the difficulty of seeing all birds at once due to distance, wave action, and frequent diving, 25 is a minimum number. The Factory Area was about 550 acres; the Hook Area, about 470 acres. With an estimate of 25 loons in each area, the average area ~~acre~~ was less than 20 acres per loon.
2. Individual distance was measured on the maps. There was much variability in spacing, and some sightings were made of two to five loons which were within 50 feet of each other. Sixty-five spacings were mapped and measured, and the average distance was 475 feet. If it is assumed this was the average radius describing individual distance, the space was divided into one loon per 16.6 ~~20.8~~ acres.
3. Movements of two loons for one hour each were recorded on different January days, and subsequently mapped and measured. One loon used 10.4 acres, the other 13.4 acres.

Evidence indicates that each loon needed 10 to 20 acres for its feeding area. The waters around Chincoteague are highly productive in fish and shellfish (loons were observed eating both), and the abundance in Tom's Cove has made this area known as one of the prime fishing and oystering areas in the United States. The annual Audubon Christmas Bird Count records large loon concentrations each year and in 1971, 641 Common Loons were reported in the area around Chincoteague (American Birds, 1972, 25:p.22), a record number of Common Loons from any single count. Because of the consistently high wintering population, and the abundant food supply in this region, the figures presented here represent wintering loon density in optimum habitat.

Activity Patterns

The number of loons engaged in each of four activities was counted every 15 minutes from low to high tide for five days to cover the full range of daylight hours (07:23 to 17:00) for the second week in January using tidal tables for Wallops Island, Virginia. Sequential diving, some culminating in fish or shellfish being brought to the surface was termed feeding; maintenance included preening, scratching, Foot Waggling, and Head Rubbing; sleeping was recorded when the bird had its head over its back in the dozing posture; and Drifting described a loon sitting on the water, head held low and facing forward, and not engaged in any of the other three activities.

The amount of time spent feeding from low to high tide was quite consistent from hour to hour, but there was a slight increase as the rate of rise slowed, and it declined at high tide. Sleeping patterns showed no tidal relationship. Maintenance behavior decreased at high tide, and Drifting increased, so that by high tide, over one-third of the activity consisted of Drifting (Figure 7).

Figure 7. Activity patterns in relation to tidal time.

▧ Feeding

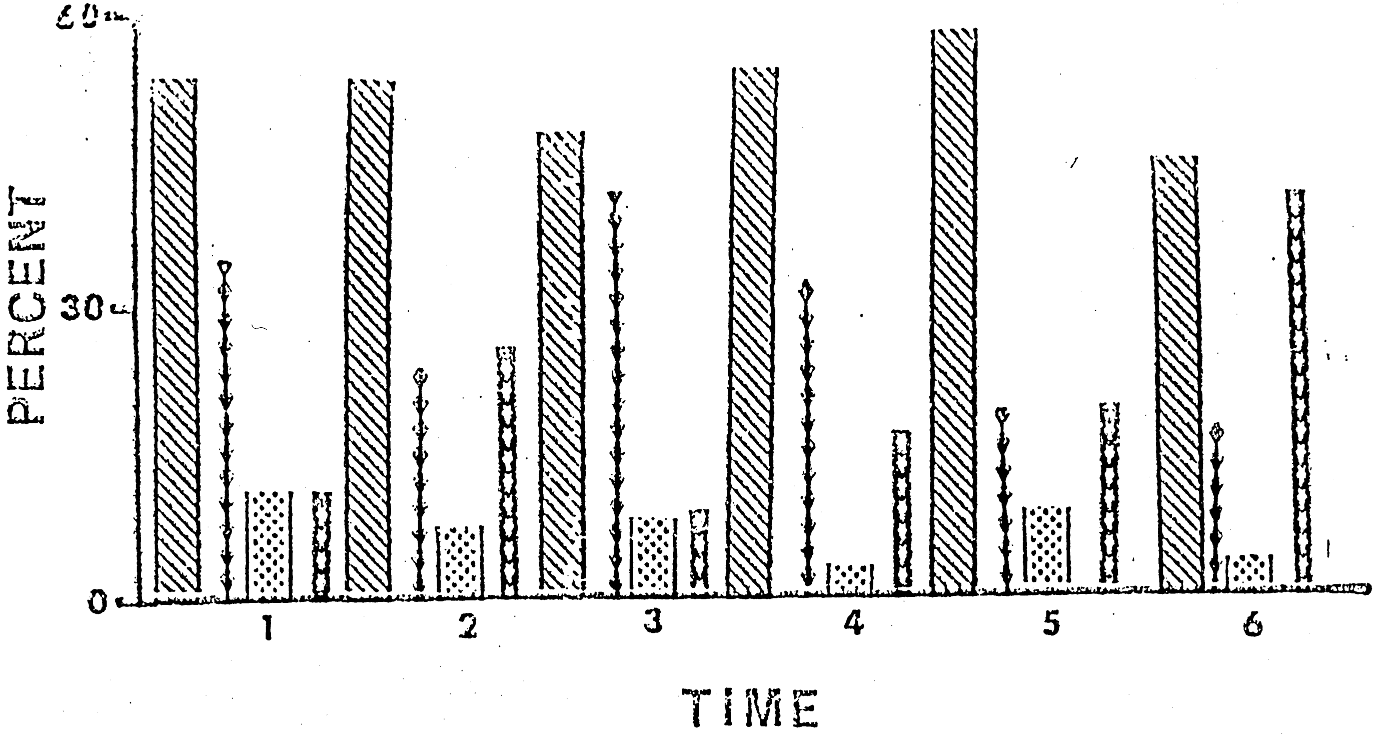
⧗ Maintenance

▒ Sleeping

⁑ Drifting

Readings taken during 5 days of flood tide, the earliest low tide at 07:23 and the last high tide at 17:00. Each group of 4 columns represents one hour. Water rise averaged as follows for each one-hour period:

Hour 1.	0.18 feet
2.	0.42
3.	0.46
4.	0.46
5.	0.24
6.	0.06


60
30
0
PERCENT
1
2
3
4
5
6
TIME

positions of loons feeding during ebb and flood tides were mapped to see if they changed as the depth of the water changed (Figure 8). Those feeding during flood tide were in deeper water, while those feeding during ebb tide were in more shallow water. There was not a significant correlation between feeding positions and changing water levels during flood tide ($r=.09$), but there was a highly significant correlation between feeding position and water level during ebb tide ($r=.76$, $t(20)=5.08$; $P<.001$). Loons stayed or moved closer to shore during ebb tides, and rather than moving their feeding areas to maintain a constant diving depth, shifted to shallow water to feed.

A sequence of observations from high to low tide was not made. However, the behavior of 29 loons was recorded during ebb tide in the course of the study. Most of that time (82.8%) was spent in feeding, the rest in preening and other maintenance behavior.

Behavior patterns throughout the day indicate that sleeping occurred primarily in the morning, feeding increased in the afternoon, and towards evening most of the loons drifted (Figure 9).

Feeding dives were timed to compare them with summer dives. They were significantly shorter ($\bar{X}=39.5\pm1.25$ seconds as against $\bar{X}=42.88\pm.012$ seconds in the summer, $P<.001$). They compared favorably with dives of wintering loons as recorded by Robinson (1923, $\bar{X}=34$ seconds), and Dewar (1924) at their preferred feeding depth, 12 to 20 feet ($\bar{X}=35.5\pm0.4$). Dewar (1924) suggested loons are bottom feeders. I concur. I commonly saw them bring flatfish and shellfish to the surface indicating at least some of their feeding was done on the bott

Figure 8. Comparison between position of feeding loons by height of tide and 6' contour line. Loon feeding during:

✷ Ebb tide

▲ Flood tide

◆◆◆◆ Six foot contour line

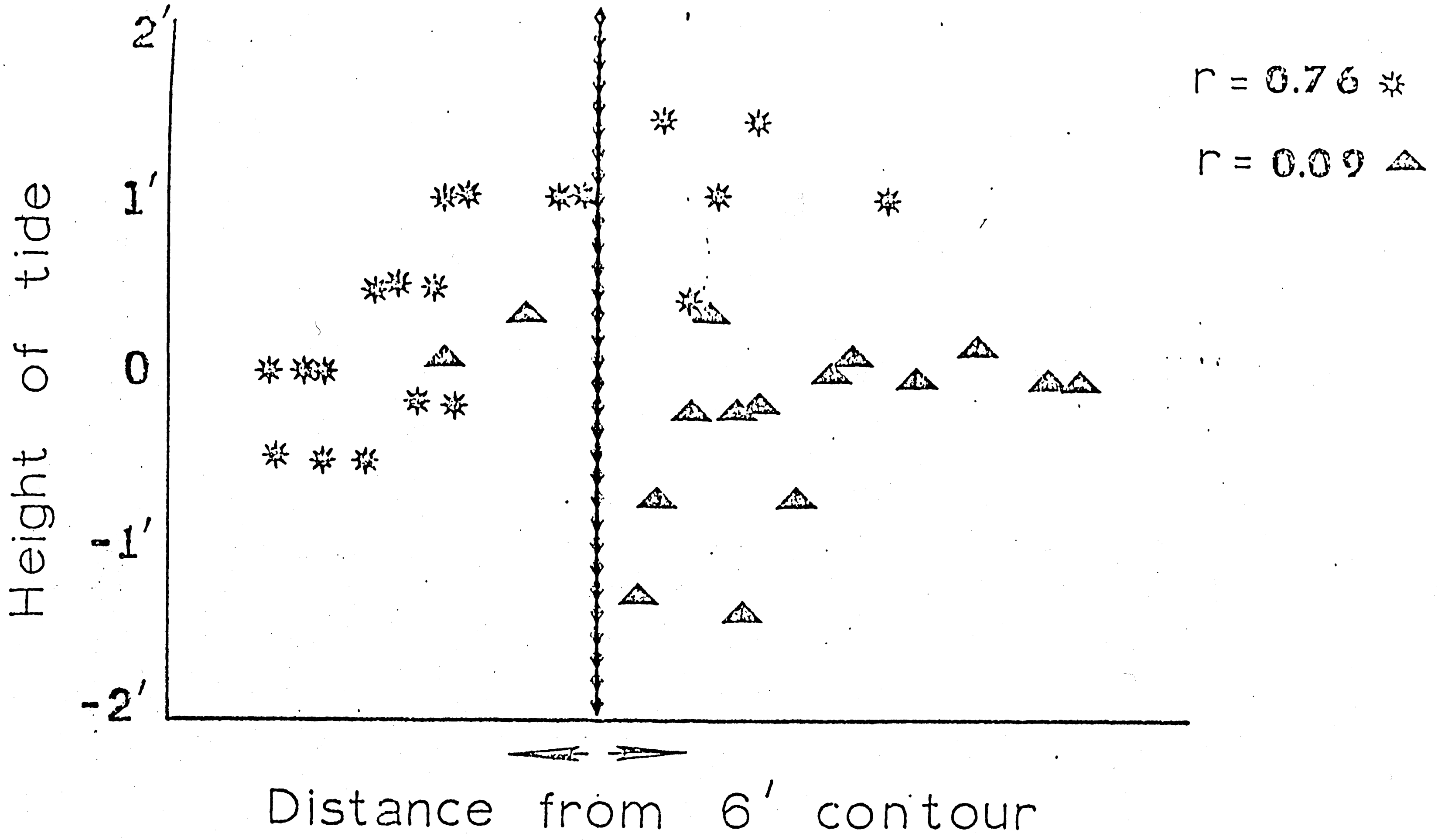

2'
1'
0
-1'
-2'
Height of tide
Distance from 6' contour
r = 0.76 ☼
r = 0.09 △

Figure 9. Activity patterns in relation to sun time.

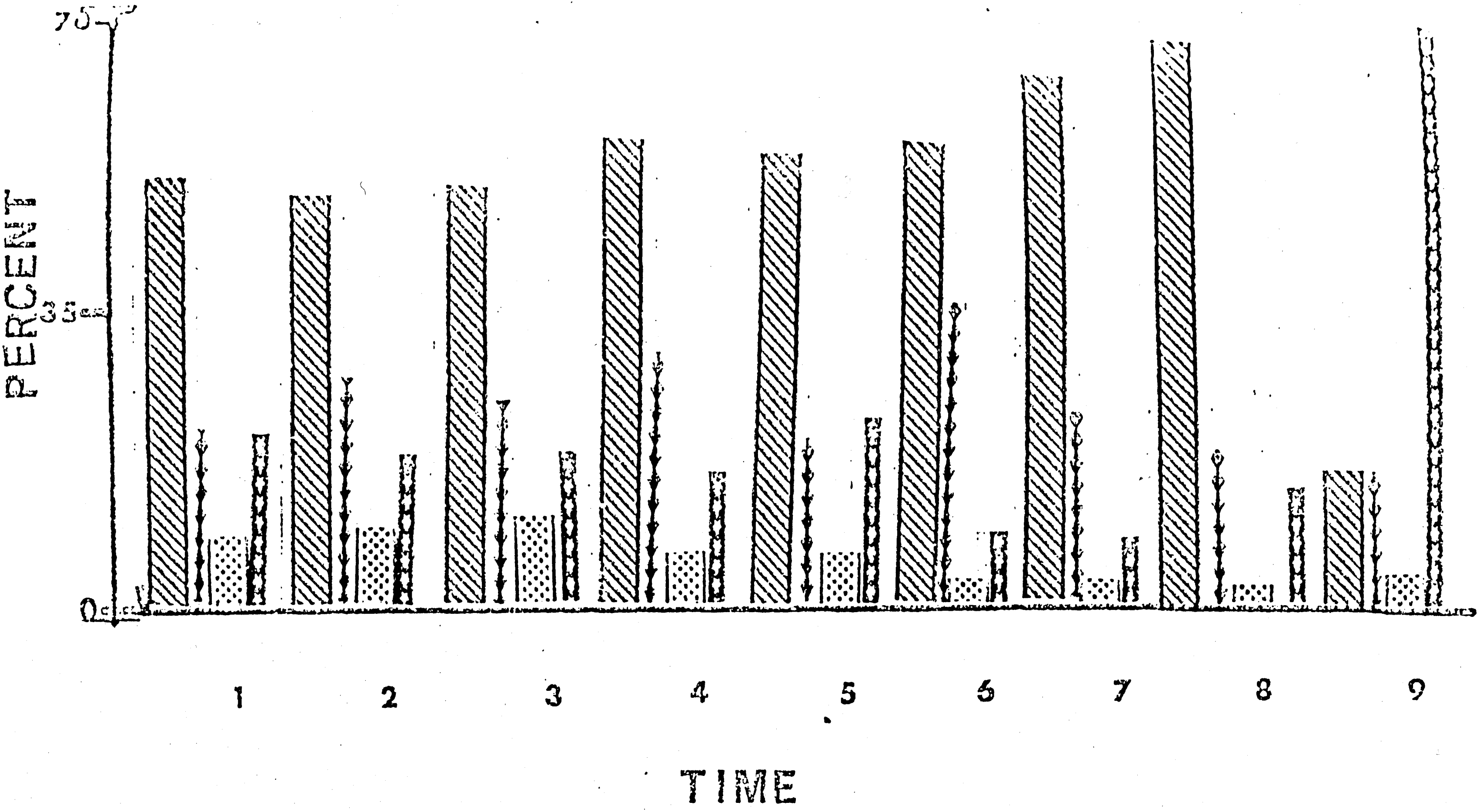
▧ Feeding

◆ Maintenance

▒ Sleeping

■ Drifting

Time covered is 08:00 to 17:00. Only three birds could be sighted before 08:00 and they were feeding. Each group of four columns represents one hour.


70
35
0
PERCENT
1
2
3
4
5
6
7
8
9
TIME

Evening Flocking

Late in the afternoon loons stopped feeding, alternately preened and slept for about half an hour ($\overline{X}$=28 minutes), and drifted to the center of the cove to form a loose aggregation. Flocking was correlated with sunset time (Figure 10). Cessation of feeding, preening, and beginning of drifting began close to sunset and is probably related to lowered visibility for feeding (agree, Barr, 1973). Preening and other maintenance activity stopped and rafts were assembled about 20 minutes past sunset ($\overline{X}$=19.67±3.38 minutes). Although the location was not precisely the same each evening, the same general area in the deep part of the cove was used each night (Figure 11). Loons from outside the cove did not fly in to join the raft. I counted from seven to 31 loons on different evenings, but variability may well have been due to weather conditions such as fog and rain that considerably hampered visibility on many evenings.

Numbers during March were higher, and on 18 March there was a flock of more than 100 birds in the cove. On 19, 20, and 21 March there were also large numbers. Loons were seen in Tom's Cove through the first week in April, but none could be found there after the second week which suggests that the larger groups probably were pre-migratory flight aggregations.

Discussion

There are several advantages to loons for wintering in a marine environment. The freezing of breeding lakes surely functions as the major selective pressure for fall migration and the most

Figure 10. Nightly rafting of Common Loons in Tom's Cove.

◓ Sunset

* Cessation of feeding

✱ Rafts formed

✺ Large flock of over 100 loons.

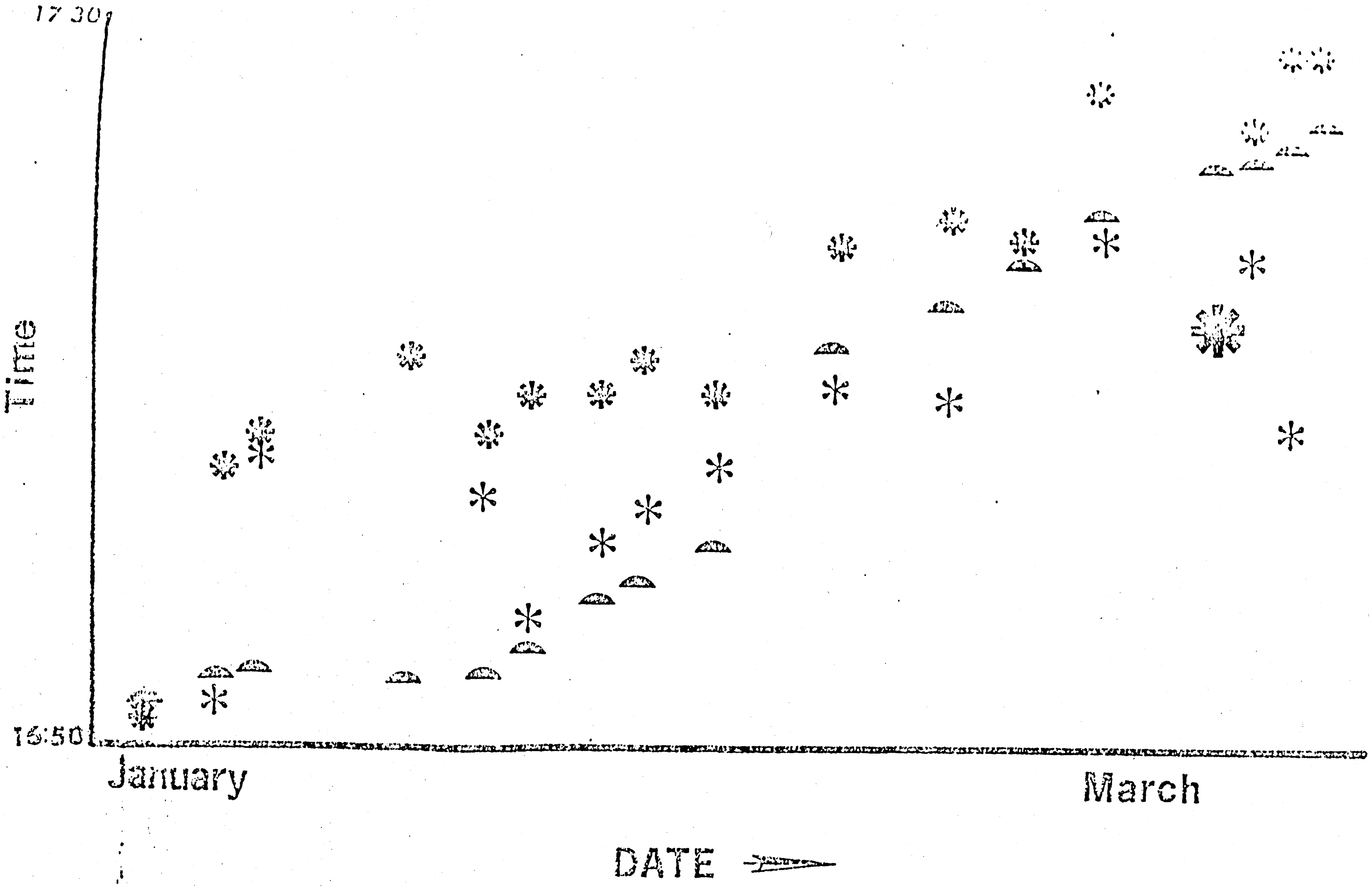
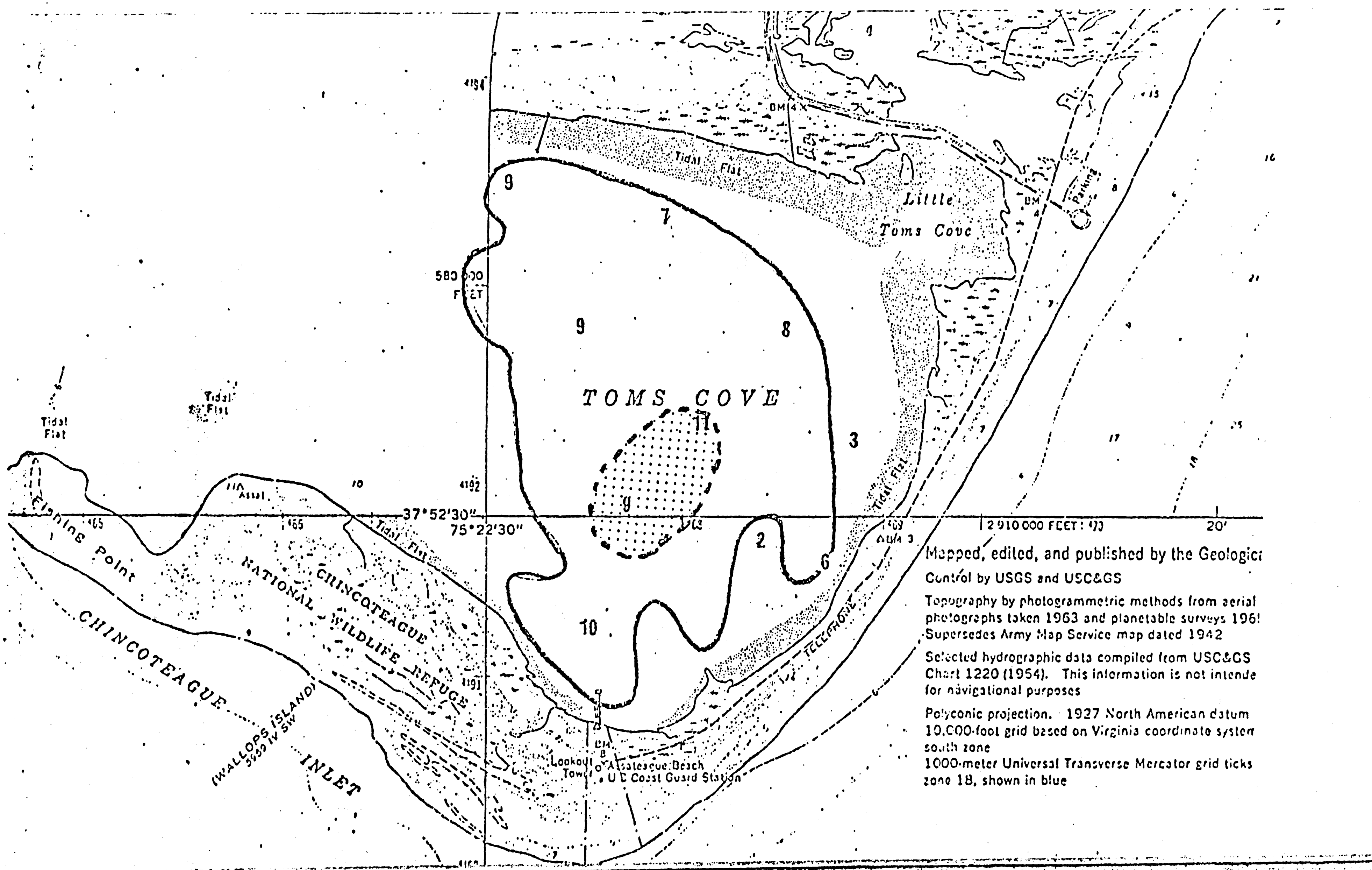

17 30
Time
16:50
January
March
DATE

Figure 11. Rafting location on the wintering grounds.



Mapped, edited, and published by the Geologic

Control by USGS and USC&GS

Topography by photogrammetric methods from aerial photographs taken 1963 and planetable surveys 196

Supersedes Army Map Service map dated 1942

Selected hydrographic data compiled from USC&GS Chart 1220 (1954). This information is not intende for navigational purposes

Polyconic projection. 1927 North American datum

10,000-foot grid based on Virginia coordinate system south zone

1000-meter Universal Transverse Mercator grid ticks zone 18, shown in blue obvious destinations are coastal areas because of the large expanse of water that will remain open throughout the winter. Some loons do remain on inland lakes during the winter (Bent, 1919), but most do not.

Adult loons have a complete prenuptial molt from January to March (May, 1930; Woolfenden, 1967; and my observation during this study). An extensive contiguous coastal wintering range permits unrestrictive mobility while the loons are flightless during their simultaneous remigial molt.

Summer diving times which I recorded were taken at depths comparable to those in Tom's Cove (six to 15 feet). The shorter diving time as well as the smaller required feeding area per loon in the winter indicate that food may be more abundant and/or more easily captured on the coast than on fresh water lakes. A clue to both of these possibilities is given by the spacing of loons along the coast and around the perimeter of the cove. This assures a maximum area of active tidal movement for each bird and permits a smaller feeding area than is needed in the summer on fresh water lakes. Barr (1973) found that prey (fish) conditioned to avian predators (loons) were less easily captured. A partial turnover of prey items twice daily with each incoming tide brings some naive prey to the loons feeding area and increases capture efficiency.

Another advantage for birds in a marine environment has received little attention but should be considered as an interesting and perhaps important benefit of a salt water wintering area. Aspergillosis is a common disease in both captive and wild loons (Locke and Young, 1967; Barr, pers. comm., and I have also found it to be a problem with loons I have handled.) It appears to be a potential threat in the event of stress, as Aspergillus sp. may be present even in healthy birds. Potential growth of Aspergillus mycelium is rapid, and damage to the air sac system is irreversible. Kaben and Schwarz (1970) in a series of experiments with Aspergillus showed its growth is retarded in the presence of salt. It is possible the circulation of salt through the supraorbital glands helps to prevent growth of this fungus.

There is intraspecific interaction throughout the winter. Some loons were seen by twos when they were sleeping, very early in the morning or towards evening. Leebody (1892) indicated that Common Loons remained in pairs off the coast of Ireland during the winter. I hesitate to call these pairs because of the implication they are mated pairs; they could as readily be pairs of siblings. In the fall siblings remain together, but most pairs of mates do not. I saw no loons feeding by twos. Leebody (1892) stated that pairs held a joint feeding territory, but did not indicate they fed cooperatively.

Common Loons off the Virginia coast never engaged in flock feeding but did congregate each night and there are several possible advantages for this. Loons may feed together at night, but lowered light levels and poor visibility raise questions as to the likelihood this occurs. On the other hand, large schools of mackerel and herring are near the surface at night, especially in late winter, and there is an opportunity for a rich and available food source at this time. Rafting would serve to unify birds that were scattered throughout the cove during the day should they move out to the open ocean later at night. Birds of some other aquatic species do feed at night. Feeding by cormorants is not too different from that of loons and visibility problems would be similar, yet it is well known that cormorants do feed at night. The Japanese fishermen of the Imperial Household, the men who train and fish with cormorants, do their fishing at night (Yamashita, pers. comm.).

Another cause for rafting behavior may simply be the necessity for gathering in the same location due to the necessity of sharing the same site. There is less possibility loons would be washed ashore during low tide if they remained offshore. In a cove, "offshore" is in the center and is the smallest portion of the cove relative to the perimeter. What should perhaps be looked at are the behavioral mechanisms that have evolved to reduce aggression and permit rafting associations.

Loons migrate in large groups (Trautman, 1940; ~~Hochbaum, [illegible],~~; Hochbaum, 1955), generally during the day, although some nocturnal migrations also occur. The large concentrations which were noted in March were no doubt pre-migratory gatherings. But even throughout the winter, nightly rafting might also serve to reinforce behavior essential to migratory aggregations which form later.

Activity was mediated to some extent by both tidal and diurnal influences. Rafting time and cessation of feeding followed sun time. Feeding intensity during the day followed a tidal rhythm. Feeding dropped abruptly at the end of the day because light conditions decreased foraging efficiency. Superimposed on the light rhythm was the influence of ebb and flood tides. Intensive feeding and movement of the birds into shallow water during ebb tide indicated there was a lag effect of prey items behind the receding tide.

During the winter, space is more limited and day length is shorter than in the summer on northern fresh water lakes. An abundant food source combined with tidal influence to increase feeding efficiency offer maximum benefits for wintering loons.

MIGRATION

Spring

Migrations occur during an extended time period over a broad area (Palmer, 1962). Both coastal and overland flights are seen, but there are three major migration routes: a western route along the Pacific coast, with some birds continuing to Alaska and some flying overland to the northeast to southern British Columbia; a northward flight along the Atlantic seaboard (Palmer, 1962); and a third comprised of a funneling of Gulf and Atlantic coast overland migrants through the Great Lakes to northwest Canada (Preston, 1956; Arbib, 1963; this study).

There ~~are~~ is a paucity of banding data, but they suggest multiple overland routes south of the Great Lakes, a northwest-southeast direction north of the Great Lakes, and east of the Rocky Mountains, and a northeast-southwest direction west of the Rocky Mountains (Figure 12). American Birds Seasonal Reports also provide ample evidence for many overland migrants, but the large concentrations consistently reported are over the Great Lakes of Erie, Huron, and Ontario. Many other stopping points inland attract from a few to several hundred loons (Figure 12; Forbush, 1912, 1925; Gabrielson and Jewett, 1940; Trautman, 1940; Hochbaum, 1955; Burleigh, 1958; Imhof, 1962; Arbib, 1963; Mengel, 1965; Sutton, 1967; Kohel, 1972).

Spring migration through Minnesota is comprised partially of birds crossing Wisconsin from Lake Michigan (Kohel, 1972); partly from birds following the Mississippi River through Illinois and Iowa; and partly from birds moving northward through the center of the state (Figure 13). Small, but annual reports are received from the areas mapped, and occasionally 10 to 20 individuals are seen in Freeborn and Rice counties. Centerville Lake in Anoka County has been reported as a major spring stopover (Olson and Marshall, 1952), but I received no PLW reports from it. I also questioned several of the lakeshore residents, but none were aware of spring loon concentrations, nor did I see loons when I checked in the spring of 1972. Lakes in Minneapolis, principally Calhoun, Harriet, Cedar, Lakes of the Isles, and Nokomis, are annually host to migrating loons, as is Lake Como in St. Paul. The arrow crossing

Figure 12. Migration patterns of Common Loons across the United States as compiled from banding records, and American Birds Seasonal Reports.

—— North - South movement
◆◆◆◆ South - North movement
Banding recovery data

✱ Spring Concentrations

▼ Fall Concentrations

● Concentrations both spring and fall

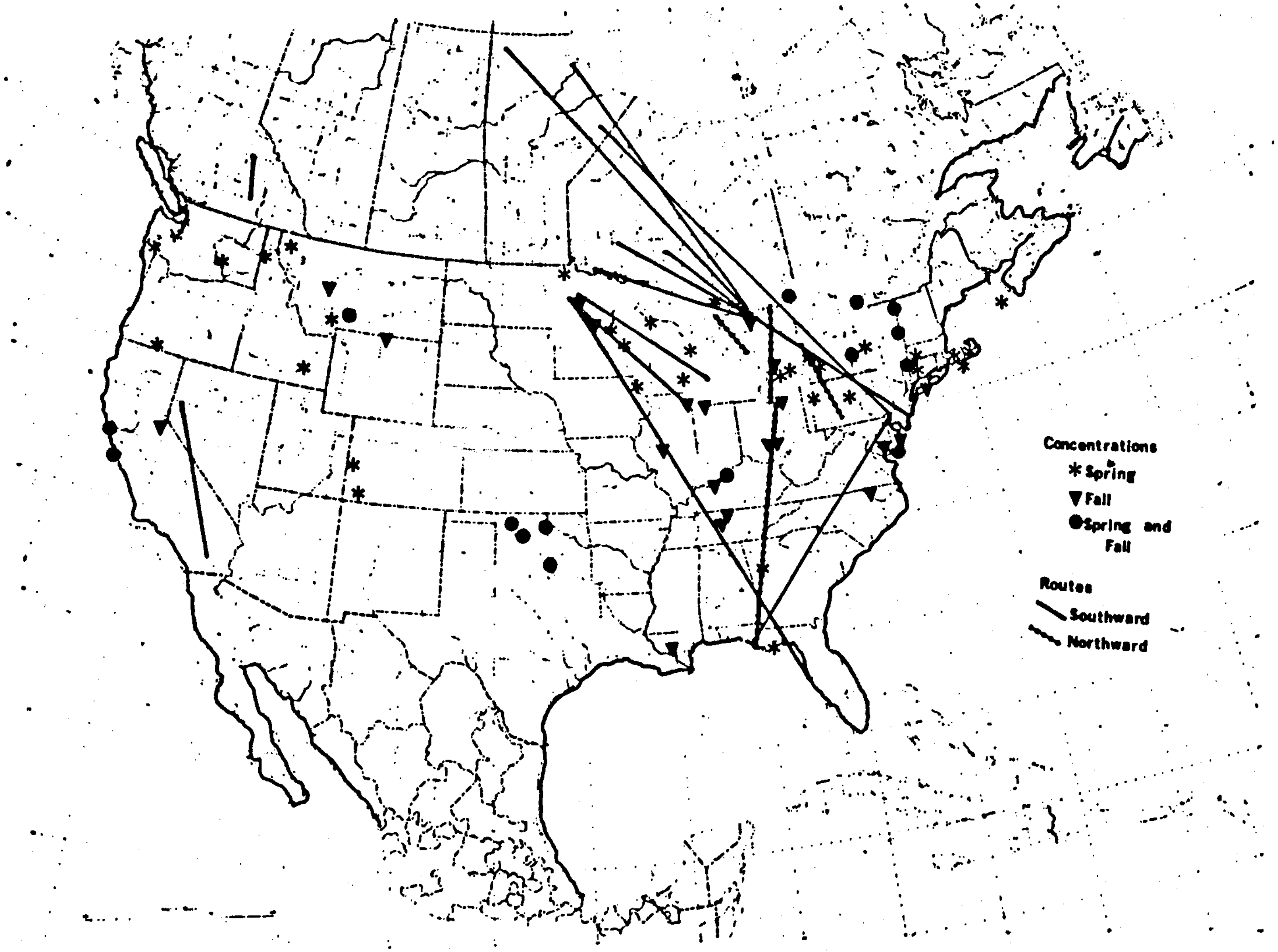
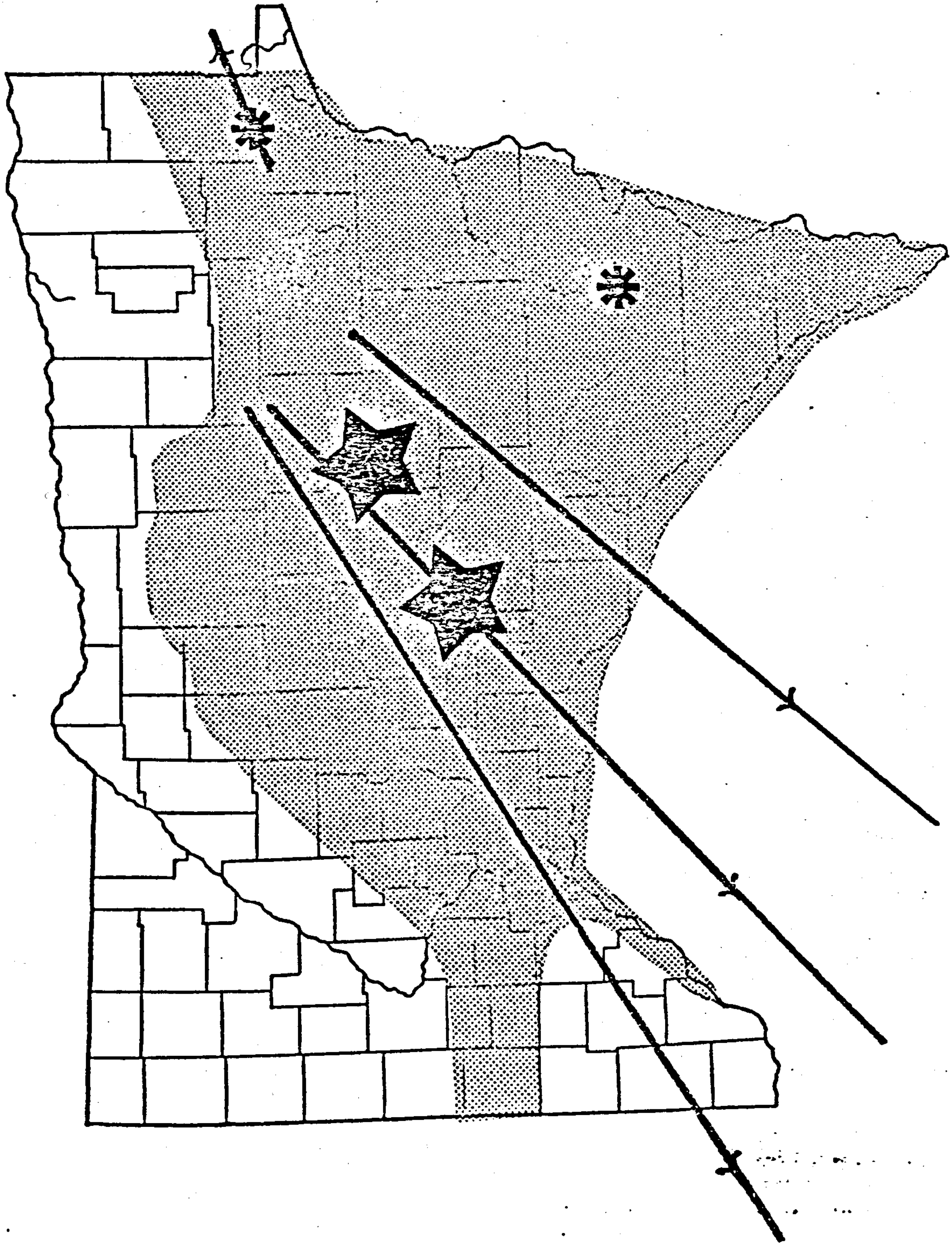

Concentrations
* Spring
▼ Fall
● Spring and Fall
Routes
Southward
Northward

Figure 13. Migration patterns of Common Loons across Minnesota.

- ✱↘ Spring movement as monitored for a two-week period over a single site.
- ↘ Fall movement from banding recovery data.
- ✱ Spring concentrations frequently noted.
- ★ Fall concentrations frequently noted.
- ▦ Migration records as compiled from Project Loon Watch reports.



the northwest of the state (Figure 13) indicates compass-monitored flights recorded every morning in late April and early May for two weeks. It is a traditional flyway over which loons are seen every spring (Berg, pers. comm.).

Spring records indicate that early coastal departures begin in mid-March, and many inland sightings have been reported by late March (American Birds Seasonal Reports, and this study). The earliest Minnesota arrival on record was 15 March 1974 on the Mississippi River in Wabasha and Winona Counties. Tufts (1961) stated the first arrival in Nova Scotia was 7 April; late May is arrival time in Iceland (Sjölander and Ågren, 1972); and loons reach Baffin Island by early June (Palmer, 1962). Early dates in the west include 20 March in Pocatello, Idaho (American Birds 1974, 28:828); 4 April in Ennis, Montana (American Birds 1971, 255: 772); and 8 April, in Fortine, Montana (American Birds, 1973, 27: 796). Late departures include 6 May 1974 from San Bernadino, California, 28 May from Ocean Shores, Washington, 31 May 1972 from North Carolina, and 4 June from Alabama (American Birds Seasonal Reports, 1970-1974). In 1973 Vaughn (pers. comm.) reported major departures from the Eastern Shores at Chincoteague, Virginia from 8 to 21 April, but noted there were still about 100 present early in May.

These perhaps represent the widest range of dates, but many separate accounts and a summary by Palmer (1962) show that migration extends over several weeks. Migration lasts from 1 April to 12 May in western Pennsylvania (Preston, 1956); occurs during the last three weeks of April and the first two weeks of May in Ohio (Trautman, 1940);

extends from mid-May to early June in Massachusetts (Forbush, 1925; Griscom and Snyder, 1955); continues from 20 April to 16 May in Maine (Palmer, 1949); was recorded for the entire month of April over Missouri (Widman, 1907); and is seen from the middle to the end of April in British Columbia (Munro, 1945). In Minnesota, arrivals are from 23 March to 27 May.

Peak date in western Pennsylvania is 22 April (Preston, 1956); and is late April in the Cariboo Parkland region of British Columbia (Munro, 1945). Over the eastern Great Lakes there are often several peak days in a single year, usually from 15 April to 8 May. Along the Atlantic coast, heavy migration is later, and loons are common until 25 May over New Jersey, and at top numbers at the end of May in Massachusetts (Forbush, 1925).

In Minnesota, monitoring of 305 lake arrivals from 1970-1974 gave a median date of April 23. There were a few as early as late March, and many (14.8%) in May, mostly in the northern tier of counties and, it may be that most of those are coming across the Great Lakes.

Fall

Fall migration extends over a two to three month period, and movements do not appear to be different than spring routes (Figures 12 and 13). Arrivals along the Atlantic coast have occasionally been reported as early as August (American Birds 1974 28: 33; and Vaughn and Grody, pers. comm.). Initial departures begin at the end of August or early September (Olson and Marshall, 1952; Palmer, 1949; 1962). Birds move from smaller to larger lakes, and departures continue until the lakes freeze, which is in November in Minnesota. Arrivals at the southern part of their wintering range have been reported as early as 26 September in Florida (Am. Birds 1972, 26: 51), and 27 October in southern Texas (Am. Birds 1973, 27: 83), but normal arrivals to these sections of their wintering range are during November.

In Minnesota, departures extend over a longer period than spring arrivals do. The first to leave do so in early September, but many remain until November when the lakes freeze. There are reports of loons being seen in December, but loons I have captured and/or examined at that time have been injured or malformed and incapable of flight.

Mille Lacs Lake, Minnesota, is a traditional stopping place for hundreds of loons. They begin to arrive in late September, and the peak usually is around mid-October. In 1972, 1973, and 1974 large rafts were counted on 20, 13 and 15 October respectively. On 26 October 1966 there were large numbers, and on 11 November 1969, 500 loons were still present (Campbell, 1970). The Great Lakes is a major concentration area, and Kettle Point in Lake Huron consistently records hundreds, and in some years, thousands, of migrating loons (Perkins, 1965; Fay, et al., 1965; and American Birds Seasonal Reports).

Daily Schedule

Palmer (1962) stated that loons are primarily diurnal migrants and Williams (1973) found they left the Gulf Coast on northward flights between one-half hour past sunrise and 09:30. Hochbaum

(1955) described a flock of several hundred passing over Ithaca, New York at dawn during a fall migration, and Arbib (1963) noted the heaviest portion of flights occurred before 10:00. Trautman (1940) also saw all migrants during the day, but alluded to the possibility they may also migrate at night because they sometimes landed on Buckeye Lake, Ohio at daybreak.

PLW reports gave several references to daytime flights. On 4 and 5 November 1972 several hundred loons were seen flying over Woman Lake south of Leech Lake, Minnesota, beginning about an hour past sunrise and another report describing May flights for two weeks noted all were from early to mid-morning. I have observed the beginning of flight activity on Mille Lacs Lake in the fall just at daybreak, and have not seen loons fly to the lake but have seen them take off at that time. The group of young which I watched depart from Lake Itasca in November 1973 left at 08:20.

Behavior

Some authors note loons migrate singly or in small groups, Preston, 1956; Palmer, 1962; Arbib, 1963), and other reports state they go in large loose flocks (Dunlop, 1915; Olson and Marshall, 1952; Hochbaum, 1955). Trautman (1940) saw a migrating group which was so spread out (from 30 to 200 feet between individuals) that small flocks of ducks passed through the loon association and didn't disturb them. Bent (1919) and Todd (1940) implied loons migrate as mated pairs. Preston (1956) tested this idea mathematically by counts of odd versus even numbers of loons at migratory stops and concluded they do not. Some of the loons which I watched during fall migration at Mille Lacs Lake were in twos but most were not; of 56 loons feeding in one bay, five were in groups of two, 17 were singles, and 29 were in groups of three or more. One of these "pairs" was comprised of an adult and a young. Discounting those two, only 14.3% were possibly mated pairs.

Birds seen in twos and noted as mated pairs may in fact be siblings. Two young which I wing-tagged in 1973 were together most of the time from September to November, behaved towards each other much as mates do, and migrated together in November. Birds seen as two may also be individuals of the same sex, as there is no sure way to determine sex of these birds (agree, Preston, 1956).

Fall migrants watched in mid-October began at 7:30 to fly and swim into the bays from the open water where they had been at daybreak, dove alone or in small groups, but did not feed cooperatively. Individuals did not remain in any one area and there were three complete rotations in front of my observation site in a one-half hour period. Because they were in different stages of molt, adults were easily told apart, but the young had no distinctive markings. By 09:00 large numbers of loons had moved farther out although there were still more than 50 in each of the three bays on the west side of the lake.

I circled the 132,000 acre lake to see if there were loons on all sides. The wind was WNW and loons were most easily seen in the calmer waters of the west side, however there were loons all around the lake, and along the east side as many as 15 to 20 could be seen at each sighting, spaced at least 100 yards apart, and about 100 to 400 yards offshore. By 16:30 most had stopped feeding, and by 17:45 they assembled in a loose raft, preening and drifting far out in the open water. I counted a minimum of 175 individuals; in addition there was a smaller group of 21, plus other groups out too far to count. I estimate there were 300 to 400 loons offshore from just one bay that I kept under observation until dark. Sunset was at 18:32.

Discussion

Loons do not fly in formation but in extended cluster flight flocks (definition, after Heppner, 1974). The same pattern is used by loons in winter excursions along the coasts, and during summer rallies (Figure 6). There are many reports of single or small group migrants, but there are also many records of large numbers of loons flying at the same time.

Wind, a major determinant of migration timing (Gauthreaux and LeGrand, 1974) and availability of open water in the spring, may cause some build-up of loons enroute. Fall freeze-up accounts for concentrations, for by the time loons have reached Mille Lacs Lake or the Great Lakes, most loons that summer in northern Canada east of the Rocky Mountains have left their breeding lakes due to ice cover.

If the major interior flight occurs in a northwest-southeast direction as the map indicates (Figure 12) then stopping places along this route, as well as along coastal routes, would draw large numbers of birds, while the north-south and east-west movements should be smaller. This accounts for the smaller numbers found in western Pennsylvania (Preston, 1956) and along the Appalacian and Texas-Nebraska routes). There are apparently traditional stopping places at many inland locations, but when large numbers of loons are recorded at one time at some of those in the southern part of the United States, they are accounted to be "rare" aggregations. Sufficient records attest to the fact that some are routed inland, but stops may be brief, may not occur during every migration, and may not always include large numbers of individuals.

Large groups of migrating loons are annually seen in Minnesota during the fall, usually at traditional sites. In the spring, various lakes report loon concentrations. Loons begin to gather at the end of September on Mille Lacs Lake, before the major fall departure from Minnesota's breeding lakes. They may be primarily Canadian migrants, or non-breeding Minnesota birds. Mille Lacs is a large (132,510 acres), shallow (35 to 40 feet) lake with several bays and an abundant source of fish (Eddy and Underhill, 1974). In the spring when loons follow ice break-up, rivers or lakes with river inlets or outlets provide the first open water. Gatherings are likely to occur on whatever water is available when most lakes are still frozen. In the fall, large lakes freeze later than small lakes. Mille Lacs, only a one-day journey from the Great Lakes for birds that may have a flight speed of nearly 60 mph (Bent, 1919; Preston, 1951), is an excellent departure point for this lap of the migration.

Two of the birds which I banded in Minnesota were recovered on or near Lake Michigan. It is possible loons which nest in central Minnesota may also move to the Great Lakes in the fall. From there it is one day to the Atlantic coast and two days to the Gulf of Mexico; the Great Lakes have an abundance of alewives, a favorite food (Peterson, 1965), and they remain ice-free later than other lakes in the fall. The Great Lakes are probably used as a stopover both by birds which continue to the Atlantic or Gulf coasts, and by those which may over-winter on them. In a mild year they do not freeze, and although the information is sparse, indications are that some birds do not continue to the coasts.

There are sufficient records over the years to indicate there is a funneling-fanning pattern between the Great Lakes and the two coastal areas. Although there has been one recovery of a Minnesota banded bird on the Gulf coast of Florida, there are not sufficient records yet to predict where the wintering site of Minnesota summer residents is located, or whether in fact, there is only one discrete area. Brodkorb (1953) stated that Florida loons were small and should be called _G_. _i_. _elasson_. Although there are no longer two subspecies recognized, there is a size gradient and Minnesota-North Dakota-Manitoba is the region of smallest individuals (Rand, 1947; Anderson _et_ _al_., 1970).

The behavior of loons at stopping points along migration routes is similar to that on their wintering grounds. They remain in the open water during the night; move close to shore in the morning, either to pick up grit, vegetation, crayfish, fish, or perhaps all four, then move farther out to alternately feed and preen during the day.

Molt patterns on adults served as individual markers and indicated they moved around during the early morning. It is not known if an individual remained in a single area after 09:00 while feeding. The large rafts that formed on the open water in the evening may have been composed of many smaller groups. Those that were close in and could be counted contained about 20 individuals; those on the wintering grounds also contained about two dozen individuals.

There is a great deal of variability in behavior from pair to pair in late summer. I have documented the behavior of some pairs in which the time spent away from the territory differs greatly between the two birds. Barr (1973) also found that one member of a pair spent a different amount of time away from the young than the other did, the time schedules were not the same for the two sexes. On the other hand, many pairs (for example on Lake Itasca and Mary Lake) remained together until fall; and on other lakes, even when no young were raised, some pairs still remained late in August. Sample sizes of such examples are too small to adequately reflect the full range of pair behavior, but there is reason to assume loons possess individual differences like other animals do. If a loon pair is together when migration begins, they probably migrate together. The small numbers which are seen in twos may or may not be pairs, but the majority of migrants are not paired.

Loons may migrate as groups or singly. There is not the same selective advantage of group migration that benefits some other species such as formation flying or cooperative feeding. However, weather factors may be important and if there are a limited number of available stopping places, especially late in the fall and early in the spring, these factors would influence the concentrations which occur at these times.

Their closest intraspecific contact is during the early morning and at night when they are rafting. Behavior during these times closely parallels late summer behavior between siblings, and winter behavior of all loons. It is advantageous for the birds to adopt behavior that will permit closer contact than during the day while they are stopped and feeding because there are limited stopping sites enroute and there is a greater probability that loons already assembled be able to leave together and maintain contact with each other, yet extended over a broad area, will be able to locate such stopping sites.

The long period of pre-migratory gatherings attests to the post-breeding necessity for reestablishment of social communication. Flight vocalizations during migration permit cohesion without the necessity for close physical contact. Nightly rafting permits a daily re-socializing and maintains a cohesion to facilitate migration.

BREEDING BIOLOGY

Arrival

Arrival time was examined to see whether it correlated more closely with ice break-up or with calendar date. Arrivals were also examined to see whether or not loons arrived as mated pairs. Data presented are from PLW reports (1971-1973) in conjunction with my findings.

Lakes opened later in 1971 and earlier in 1973 than they did in 1972. If loons followed ice break-up, they should have arrived later in 1971 and earlier in 1973 (Figure 14). They did, but arrivals were more closely synchronized with lake openings in a late year than in an early year. There was an average lapse of three days in a late year, five days in an average year, and eight days in an early one. In all years, more than a third of the loons came during the first three days after there was open water on a lake. In 1973 there were fewer that arrived on the first day of open water, and arrivals were spaced out for a longer time than during the other two years.

Arrival times that were reported for the same lakes each year (N=48) showed that arrivals agreed more closely with ice break-up than with calendar date.

In 1973 there was not a single peak arrival day as in 1971 and 1972 (Figure 14). When lakes used as breeding territories thawed early, arrivals contined over many weeks and loons did not congregate on only a few bodies of water. When lakes thawed late, a back-up occurred on those lakes or rivers that opened early and when other lakes opened later, occupants flew directly to them, creating a single peak day.

Table 2. gives the numbers of individuals first seen on arrival, but it is not known whether or not they were the territorial occupants of the lakes, in fact, aggregations reported were undoubtedly composed of migrant loons. For example, many respondents stated on questionnaires,... "first loon arrived (date given), was alone on the lake until (date) when second came;" or..."pair first seen today..."

Figure 14. Spring arrival to Minnesota lakes in 1971 (A), 1972 (B), and 1973 (C).

● ● ● Open Water

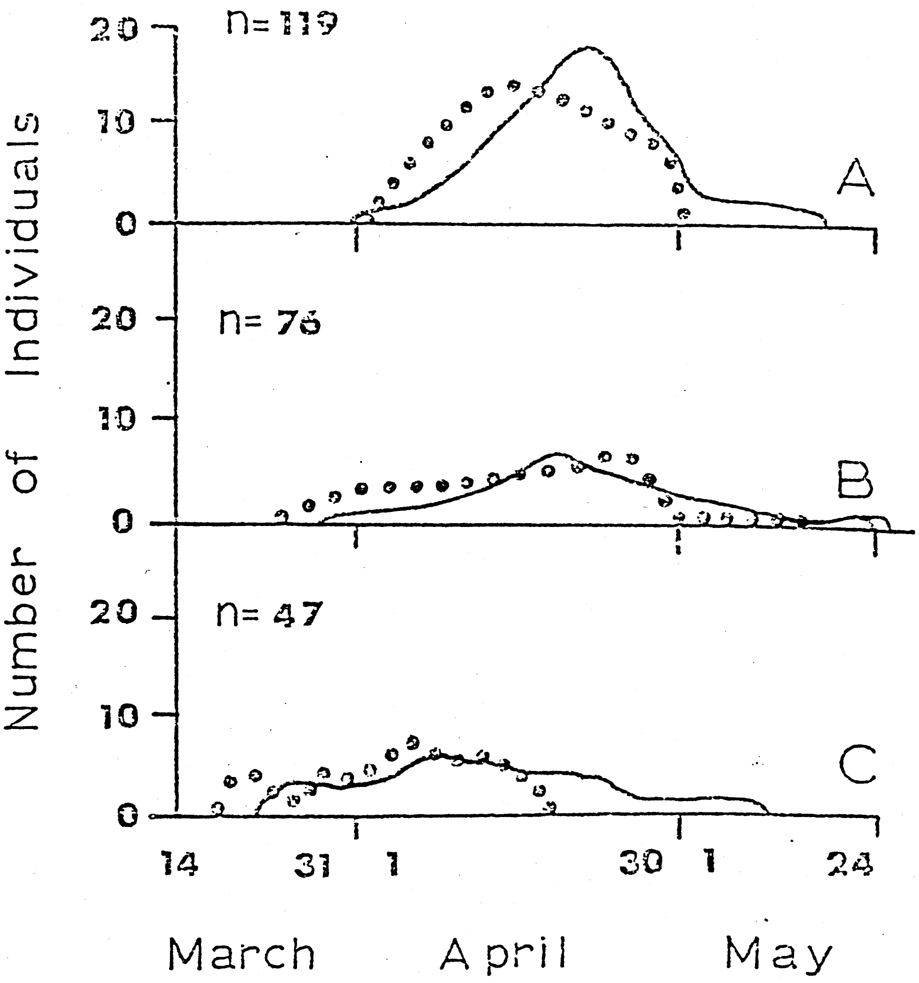
——— Arrival of the Birds

D. correlates arrival times for the three years with calendar dates.

— — — 1971 late lake opening

━━━ 1972 average lake opening

● ● ● 1973 early lake opening


Number of Individuals
20
10
0
n= 119
A
n= 76
B
n= 47
C
14
31
1
30
1
24
March
April
May

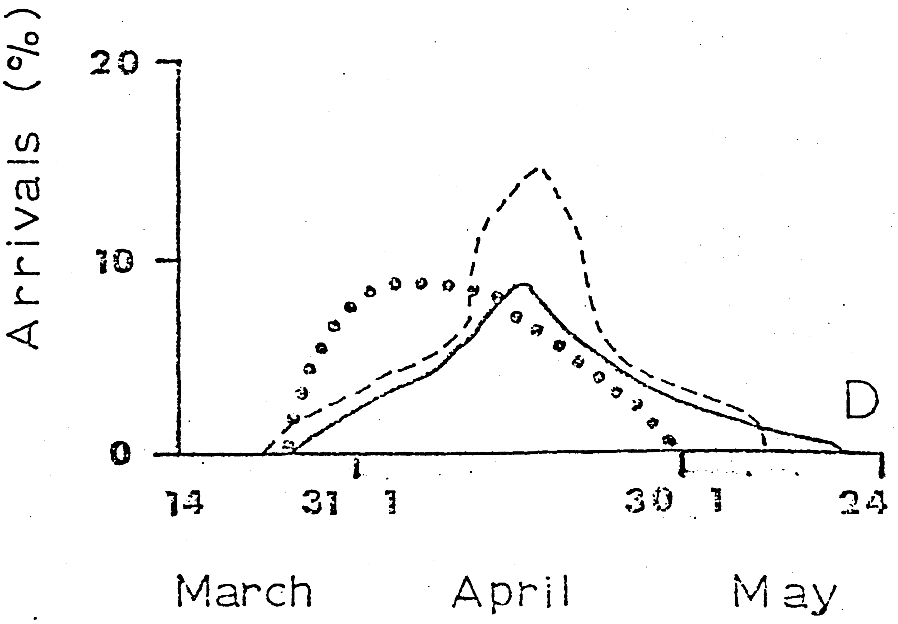

Arrivals (%)
20
10
0
D
14
31
1
30
1
24
March
April
May

Table 2. Time period throughout which the first loon arrival to each lake was recorded.

YEAR	TIME SPAN
1971	March 28 to May 16
1972	March 29 to May 27
1973	March 26 to May 5

The first loons to arrive on the study lakes stayed and established territories based on their behavior such as territorial defense, and yodel vocalization. If loons did not remain as mated pairs through the winter, most should arrive as singles. A comparison of single versus paired arrivals in 1971 and 1973 (a late year and an early year) showed there were significantly more single arrivals when the lakes opened early (Chi-square test, X^2=8.54, $P<.005$).

Site affinity confers many benefits and there is some evidence that loons have adopted this behavior (McIntyre, 1974). It is possible that pair members are the same individuals from year to year, and if site affinity occurs for both males and females, it is an easy mechanism to assure re-pairing of former mates without the necessity of maintaining a year-long pair bond. In the few cases for which I could determine the sex of the first bird to arrive, males arrived first. Mates arrived within two weeks, frequently in a day or two.

A back-up on available open water in a late year caused a peak arrival time and increased the probability that both pair members arrived the same day. PLW reports showed that equal numbers were seen as singles and pairs in average and late years, but that in early years, twice as many were first sighted as singles. If loons remained paired throughout the winter, there would be no difference in paired and single first sightings.

Habitat Selection

Distribution in Minnesota

Loons have traditionally been associated with large deep lakes of the northern boreal forest. Although some descriptions note that loons breed on both large and small lakes in both open and forested areas (Palmer, 1962), most accounts specify a preference for large deep wilderness lakes (Bent, 1919; Witherby et al., 1940; Arbib, 1963; Sutton, 1965). Vermeer (1973b), in surveying parts of central Alberta to find an area suitable for a study of Common Loon nesting requirements, found no loons on shallow lakes and confined his observations to lakes utilized by sport fishermen. Olson and Marshall (1952) stipulated one of the two major requirements was... "an open expanse of lake, completely devoid of any emergent vegetation."

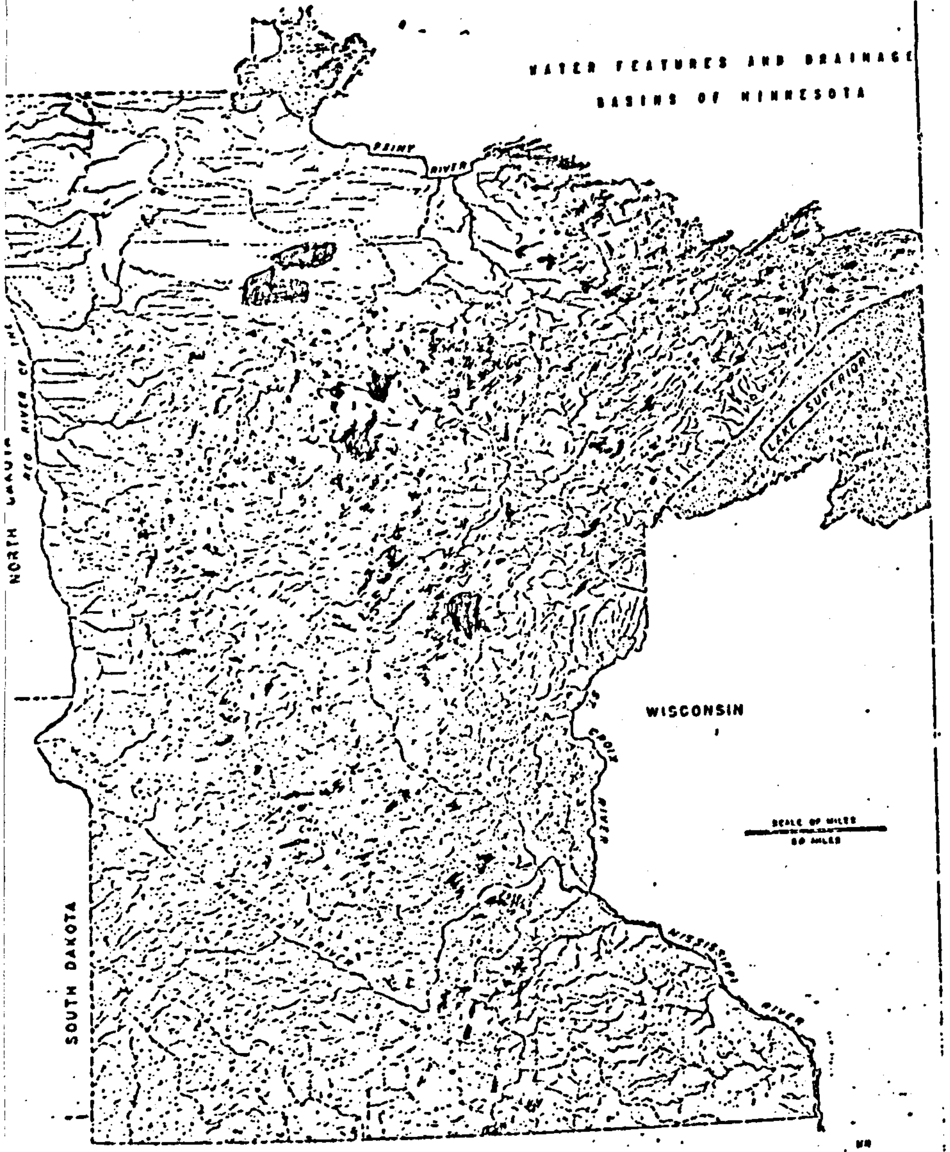
Distribution in Minnesota was looked at to see how closely it agreed with these suggestions. It does closely follow lake distribution (Figure 15.), but loons do not nest on all lakes, even in counties with the greatest lake concentration, such as Crow Wing, Beltrami, or St. Louis.

Figure 15. Loon distribution compared to lake distribution in Minnesota.

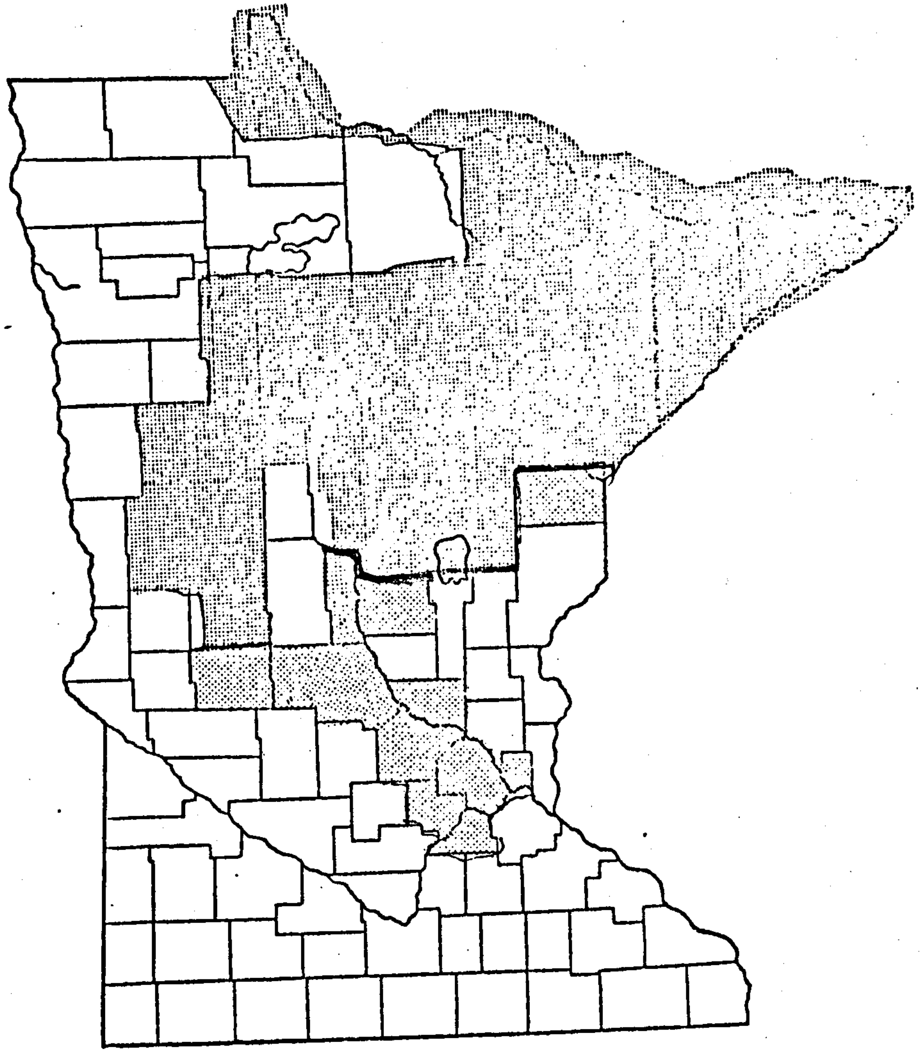
A. Lake distribution

B. Loon distribution

▦	Most lakes reported (PLW) from this region have pairs of nesting loons.
▒	Most lakes in these counties do not have pairs of nesting loons but there are a few reports (PLW) of territorial pairs every year.


WATER FEATURES AND DRAINAGE
BASINS OF MINNESOTA
RAINY RIVER
LAKE SUPERIOR
NORTH DAKOTA
RED RIVER OF THE NORTH
SOUTH DAKOTA
WISCONSIN
ST. CROIX RIVER
MINNESOTA RIVER
MISSISSIPPI RIVER
SCALE OF MILES
50 MILES
IOWA

A.



Loon territories include some shallow or deep, small or large, eutrophic, dystrophic or oligotrophic, remote or urban, clear or turbid lakes. To determine which features are optimal, which are essential, and which destroy a lake for loon habitat, I used data from the two study areas supplemented by PLW reports to assess the relative merits of several features.

Lake Size

Very few loons had territories on lakes smaller than 10 acres, but half of all larger lakes had resident pairs and nearly all lakes larger than 50 acres (79.3%) had at least one pair of territorial birds (Figure 16). However, most of the large Minnesota lakes that were reported to have no resident loons are located near the metropolitan area of Minneapolis and St. Paul or in the southern part of the state, south of the present breeding range. North of 46° latitude, 94.3% of the larger lakes had pairs of loons.

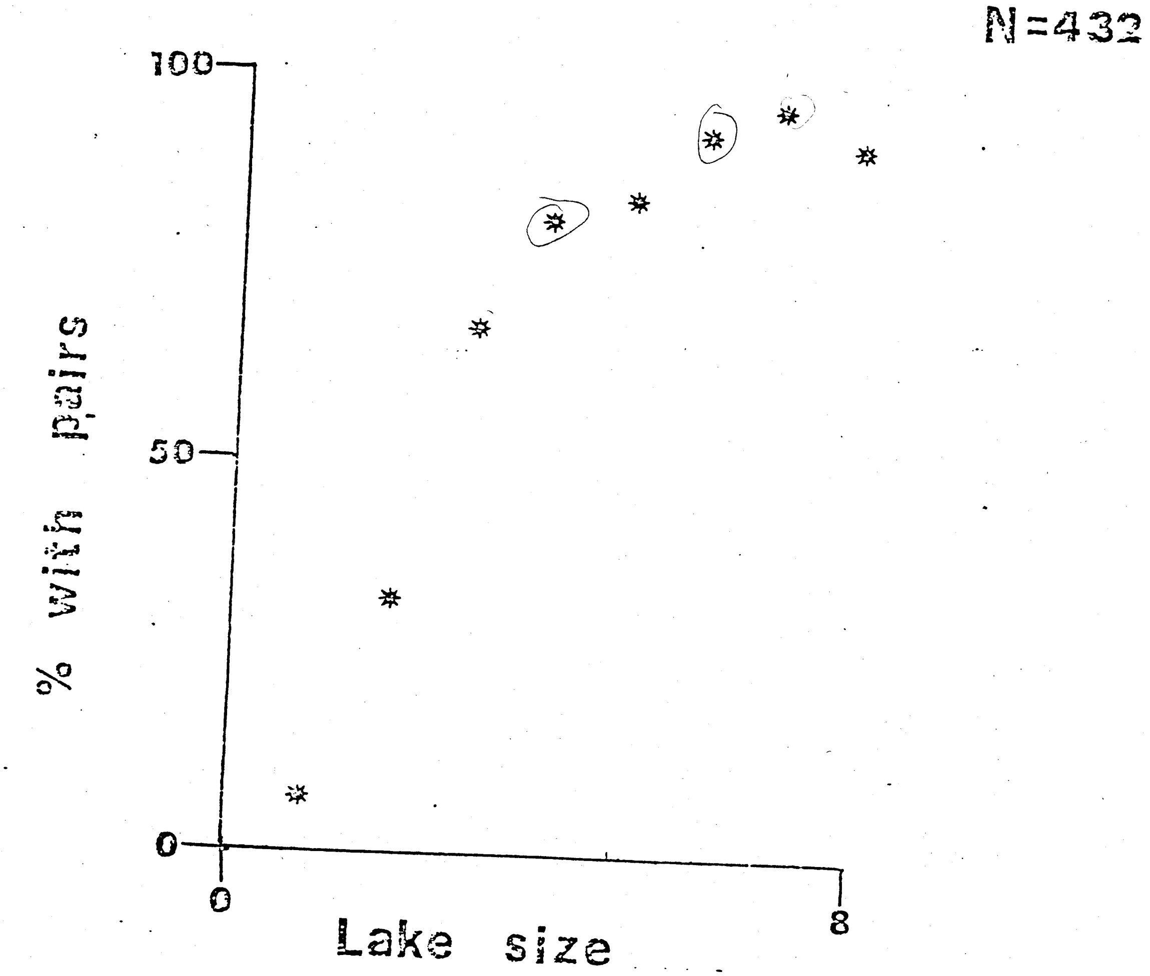
In Itasca State Park, all lakes larger than 50 acres had pairs, but fewer lakes under 50 acres did than the proportion reported on by PLW respondents. There is doubtless some bias from public sampling because small lakes with no game fish receive less recreational use, hence would not be reported in the survey, while on the other hand, I surveyed all lakes irrespective of their size, fish population, or other features that make lakes attractive to the public.

The criterion assigned for "lake success" was the presence of at least one fledged brood. If both one-chick and two-chick

Figure 16. Proportion of lakes with resident Common Loons correlated with lake size.

Lake size code:

1.	0-10 acres
2.	10-25 acres
3.	26-50 acres
4.	51-100 acres
5.	101-200 acres
6.	201-500 acres
7.	501-1000 acres
8.	> 1000 acres


N=432
100
50
0
% with pairs
0
8
Lake size

broods occurred on a single lake, the status of "two-chick brood success" was attributed to that lake. Rationale for this is that a lake that contains a pair with a two-chick brood must be of sufficient quality to permit achievement of the optimum annual reproductive potential.

The presence of broods was plotted against lake size (Figure 17 and Table 3). Few loons using lakes smaller than 25 acres raised young, and none raised two-chick broods, but half of all lakes over 50 acres had loons with young. If the lake was over 50 acres, it made no difference how large it was; the probability of successfully raising a brood did not show a direct correlation with size. However, the probability of raising a two-chick brood was greater on larger lakes than on smaller ones. Very few lakes with resident loons were smaller than nearby lakes with none, indicating loons did not select a small lake in favor of a larger one. Some large lakes with loon territories also had large areas with no loons and/or single residents, while nearby smaller lakes had breeding pairs. Based on the premise that optimum habitat is that which permits the opportunity to maximize productivity, size is apparently not the only consideration in territorial selection.

Nesting Islands

Physical and biotic factors were examined on the Blackduck study lakes (Table 4). All lakes were 25 to 114 acres, large enough to accomodate just a single pair of loons; eutrophic; contained fish; and had at least one portion of shoreline that was flat,

Figure 17. Brood size correlated with lake size. Lake size code is the same as given for Figure 16.

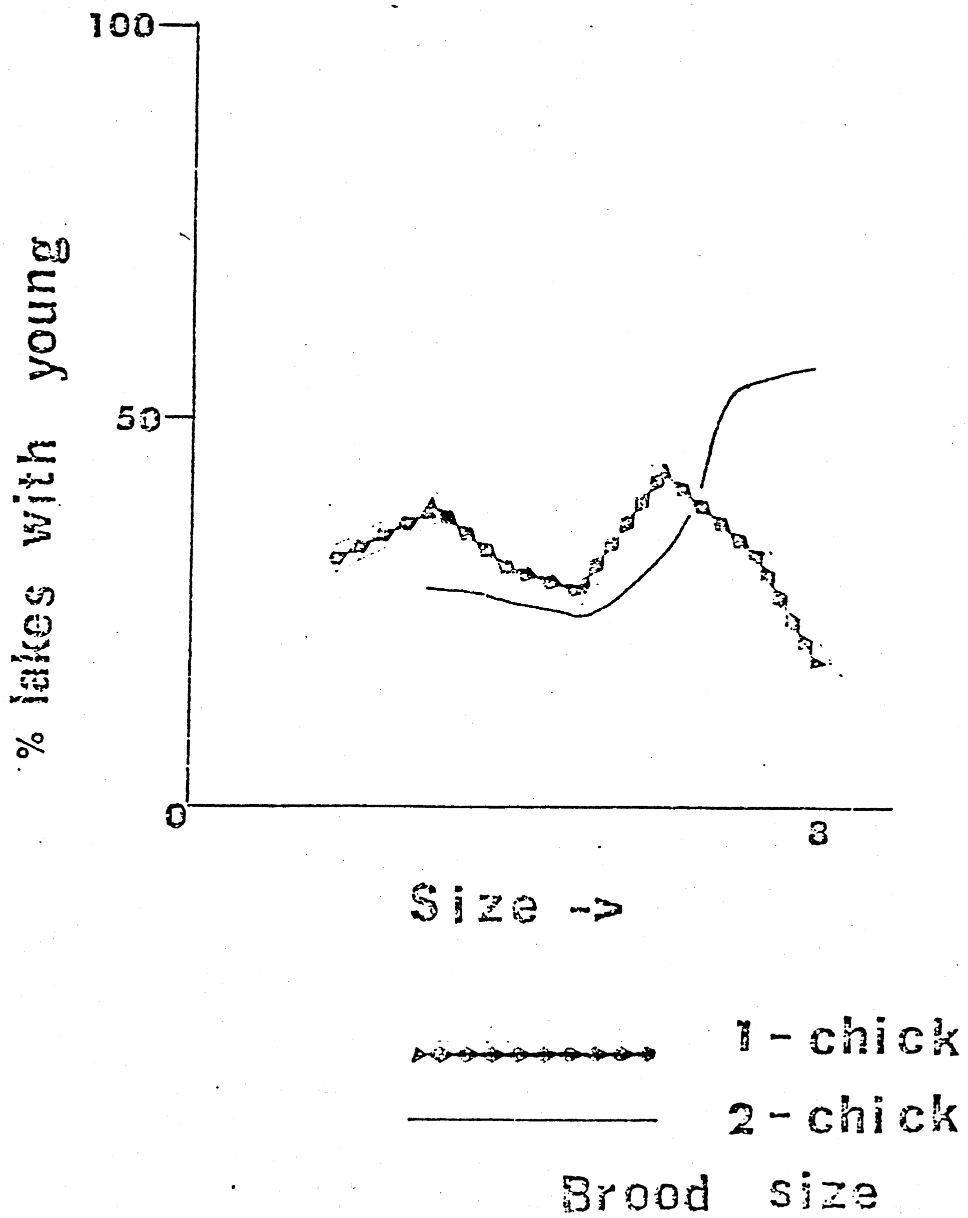

100
50
0
3
% lakes with young
Size ->
1-chick
2-chick
Brood size

Table 3. Young correlated with size of lake. Number given is percent of total in each class.

Lake Size	No Young	One-chick Brood	Two-chick Brood	N
1	100.0	-	-	1
2	66.7	33.3	-	15
3	33.3	38.1	28.6	21
4	43.3	30.0	26.7	30
5	48.0	28.0	24.0	50
6	28.0	44.0	28.0	25
7	36.7	33.3	30.0	30
8	24.0	40.0	36.0	25
9	16.7	50.0	33.3	12
10	50.0	16.7	33.3	6
11	9.1	9.1	81.8	11
12	-	100.0	-	2
13	42.8	28.6	28.6	7
14	25.5	18.1	56.4	55
				284

Code for lake size:

1 1~~0~~ - 10 acres
2 11 - 25
3 26 - 50
4 51 - 100
5 101 - 200
6 201 - 300
7 301 - 400
8 401 - 500
9 501 - 600
10 601 - 700
11 701 - 800
12 801 - 900
13 901 - 1000
14 > 1000

Code for fish species

1	*Salmo gairdneri*
2	*Coregonus artedi*
3	*Umbra limi*
4	*Esox lucius*
5	*Notemigonis crysoleucas*
6	*Pimephales promelas*
7	*Catostomus commersoni*
8	*Catastomus* sp.
9	*Ictalurus nebulosus*
10	*Noturus gyrinus*
11	*Culaea inconstans*
12	*Micropterus salmoides*
13	*Ambloplites rupestris*
14	*Lepomis macrochirus*
15	*Lepomis gibbosus*
16	*Lepomis* sp.
17	*Pomoxis nigromaculatus*
18	*Perca flavescens*
19	*Stizosledion vitreum*
20	*Etheostoma nigrum*

Code for recreational lake use same as given on Project Loon Watch questionnaires.

Table 4. Physical and biotic parameters for the Blackduck study area lakes.

Lakes	Acreage	Length (feet)	Direction of Longest Length	Maximum Depth (feet)	Water Clarity (in feet)	pH	Fish	Recreational Use Category	Presence of Nesting Pairs
Anderson	114	3135	NW-SE	10	6.5	4.5	4,5,6,9, 18	2	+
Baumgartner	27	990	N-S	12.5	6.5	4.5	3,11	0	+
Benjamin	36	2640	NE-SW	125	18	5.0	1,3,4,7, 9,13,14, 15,17,18, 19,20	8	+
Carl's	25	1650	NE-SW	45	2.5	4.5	4,9,12, 14,15	2	-
Chinaman	72	2310	E-W	5.5	3.5	3.5	3,11	0	+
Coleman	52	2310	N-S	22	4.0	4.5	4,8,9,11, 16	2	-
Damon	72	2640	N-S	10	3.0	4.5	9,11	0	-
Gimmer	77	2062	E-W	9	2.5	4.0	3,11	0	+
Holland	30	1650	NW-SE	19	3.5	4.5	9	0	-
Marie	49	1650	N-S	12	2.0	4.5	2,4,9,18	5	-
Webster	70	1980	non-directional	17	6.0	4.5	3,4,9,11	8	+

No attempt was made to determine all fish species present. Sampling showed there were at least some fish in all lakes.

sheltered, and composed of vegetation typical of the bog community. Half the lakes had islands, either naturally anchored portions of vegetation or sedge mat away from the shore, or artificial ones, previously constructed by the Forest Service for use by Ring-necked Ducks (Mathisen, 1967), some of which had been utilized by loons as nest sites (Mathisen, 1969). At the end of the 1970 nesting season, artificial islands were built on all lakes in the study area with none (Appendix IV). Lakes used as territories in 1970 were used again in subsequent years; lakes without pairs did not acquire them. The addition of nesting islands did not enhance the lakes, but islands did influence nest site choice as discussed in the section on nesting.

Human Disturbance Factors

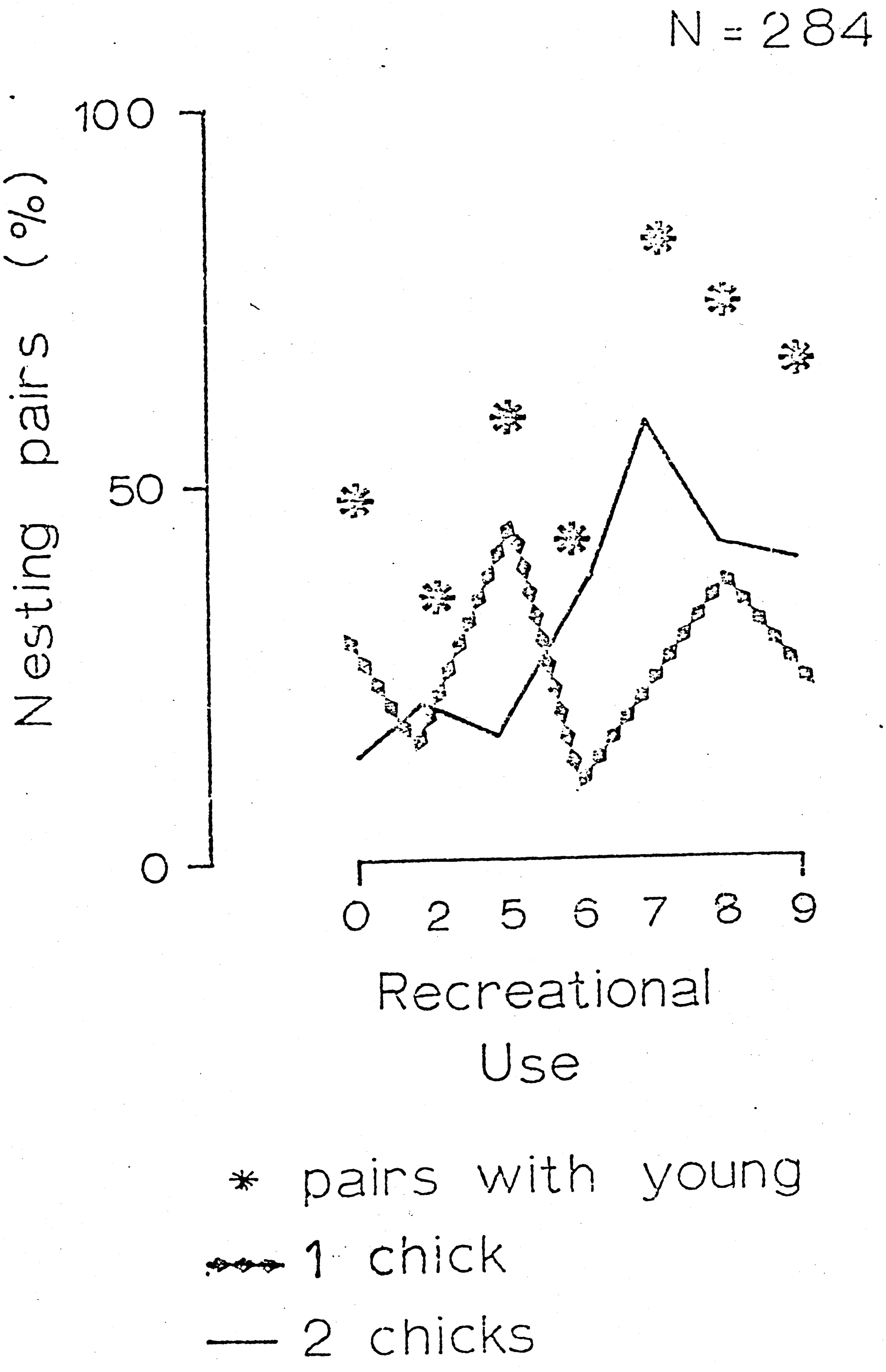
Recreational lake use had no effect on whether or not a particular lake was used for a loon territory. The sample size for my study areas was small, and there was a much larger one available from the PLW reports as discussed earlier (p. 56). Presence, absence, and size of loon broods was used as an indicator of the quality of habitat (Figure 18).

If recreational use has no effect on loon productivity, there should be no difference among lakes of varying use categories, but there was a significant difference (R x C test, df=6, $X^2=34.07$, $P < 001$). If the difference signified that disturbance provided an adverse effect, there should have been a negative correlation, but the opposite happened, for a positive linear relationship between productivity and recreational use

Figure 18. A. Proportion of nesting pairs with young correlated with recreational lake use.

B. Proportion of one-chick and two-chick broods correlated with recreational lake use.

Lake use values are those given in the PLW questionnaire (see Figure 5, p.18).


N = 284
Nesting pairs (%)
100
50
0
0
2
5
6
7
8
9
Recreational Use
* pairs with young
1 chick
2 chicks

was shown.

An increase in the number of lakes with broods could still indicate decreased productivity if brood size decreased with increasing use, i.e., increased one-chick and decreased two-chick broods. To test this, I assumed brood sizes would remain in the same ratio regardless of human use if disturbance did not affect productivity. In my study areas there was a ratio of 49:51 one-chick to two-chick broods (N=40); FLW reports gave a proportion of 48:52 one-chick to two-chick broods (N=188); and these suggest an expected ratio of about 50:50. There was a significant difference using this expected ratio when brood size was correlated with recreational use (RxC test, df=6, X^2=14.704, P<.05). However, there was a positive, not negative correlation between two-chick broods and increasing recreational use (Figure 18).

Because more than half the lakes were larger than 200 acres (153/284) and had a use index greater than 7 (172/284), it is possible that lake size masked the effects of the use factor. Lakes with use indices 7 and 8 (high use) were lumped and productivity assessed with respect to lake size (Figure 19). There were significantly more large lakes with loon broods (R x C test, df=12, X^2=21.0, P<.05). Use categories 0 and 2 (minimal use) were combined (Figure 19) and there was also a significant increase in productivity with lake size (R x C test, df=8, X^2=15.59, P<.05). Lake size does seem to play a major role in potential habitat quality but it should be noted that

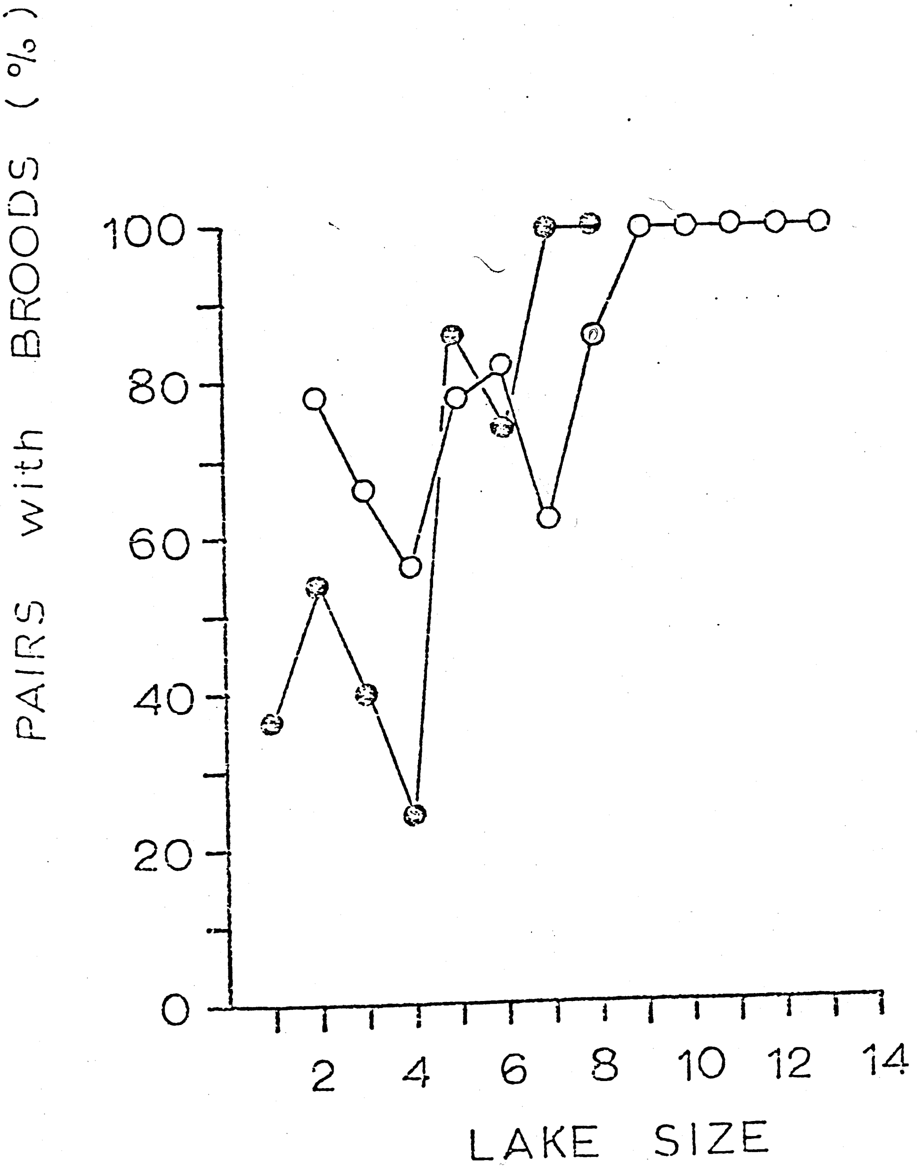

PAIRS with BROODS (%)
100
80
60
40
20
0
2
4
6
8
10
12
14
LAKE SIZE

Figure 19. A. Proportion of nesting pairs with broods correlated with lake size on lakes of heavy recreational use (Classes 7 and 8, N=118, open circles).

B. Proportion of nesting pairs with broods correlated with size on lakes with minimal or no recreational use (classes 0 and 2, N=82; closed circles).

all lakes larger than 400 acres with nesting pairs had at least one successful brood, whereas only lakes over 700 acres had a minimum of one brood per lake where human use was intense.

Discussion

There was no one factor that determined a lake was not suitable loon habitat. Loons in both Blackduck and Itasca State Park study areas nested on shallow lakes with emergent vegetation, deep lakes with no islands, lakes with no game fish and with turbid water, and small bog lakes; they also nested on deep clear lakes with fish and little human disturbance, and this seems inconsistent with previous findings. However, those lakes not used as nesting lakes were turbid and more than 10 feet deep.

A shallow lake with low clarity still permitted visibility to the bottom. As Barr (1973) has pointed out, one pair and two chicks need about 1050 kilograms of fish during a 15-week period. The great amount, frequency of parental feedings, improbability of the young going elsewhere to learn to forage and length of pre-fledging period, require that food be easy to secure, and plentiful from June to September from the territorial lake. Barr's (1973) experiments showed that loons are opportunistic feeders and take what is easiest to secure. On the basis of these findings, shallow eutrophic lakes with mudminnows should provide habitat equal to that of deep trout lakes. All study lakes had fish, but their availability to loons was dependant on visibility. Deep lakes with low visibility offer escape for a pursued fish, but shallow ones, even with low visibility, offer no such refuge from a foraging loon.

Gimmer Lake is an excellent example of the loon's adaptability to low water clarity. Gimmer is a bog lake, completely filled in the center with emergents, primarily water lilies, and has a channel nine feet deep along one side. Sampling proved there were fish in the channel as well as in the more vegetated areas, but loons used the side opposite the channel exclusively, where the maximum five foot depth permitted such densely growing emergent vegetation that even a canoe can not get through in late summer. During the five years I checked the lake, I never saw a loon in the channel, but visibility there was only 2.5 feet by Secchi disc reading. The preference for the heavily vegetated side may be explained in easier foraging in the shallow water.

Lakes in this study were eutrophic. Lakes studied by others (Olson and Marshall, 1952; Barr, 1973; Vermeer, 1973b) were oligotrophic. Oligotrophic lakes are not as productive as eutrophic ones and generally have more large, but fewer small fish. Large fish make these excellent lakes for sport fishermen, but do not necessarily provide a prime food source for loons. Rather, large fish may be a potential threat to loon chicks, as has been suggested for some other birds, for example grebes (LaBastille, 1974). Eutrophic lakes are known to be higher in productivity of fish small enough to provide a useable prey for loons. Hildén (1965) noted that birds are generally stenotopic at the edge of their range and eurytopic in the center.

This he explains by increased density in the center with subsequent pressure to utilize a greater variety of habitat types. Population density may be greater farther north in the loon's range (indications of this are available from studies such as Yonge, in prep)., but loons are more eurytopic at the southern edge.

This disparity may be a result of the various habitat types available to loons in an area of eutrophic lakes. If oligotrophic lakes provide a minimal food source per area unit, then large lakes must be used, as small ones could not provide sufficient food for a pair with young. But the eutrophic lakes at the southern limit of the breeding range have a higher fish productivity and loons are able to use both large and small lakes for nesting. A large and stable population utilizing a variety of habitats should thus be found at the southern limit of the breeding range until increasing eutrophication causes decreasing water clarity, or lakes become so shallow they dry in late summer.

The positive correlation of productivity with increased recreational use does not support previous opinions concerning the adverse effects of human disturbance on loons (Olson and Marshall, 1952; Ream, 1968; Barr, 1973; Dunker and Elgmork, 1973). If loons and humans both prefer clear lakes with an abundant supply of fish, then these data may represent a requirement overlap and not a cause-effect relationship. The greater success of two-chick broods on lakes of high use could be incidental and actually the results of an abundant food supply.

Heavy sport fishing pressures, artificial stocking, and high nutrient levels all serve to increase the supply of fish small enough to be used by loons.

I have frequently seen loons leave their nests when fishermen stopped and stayed in one spot near or in emergent vegetation, providing they were close to the nest. Passing boats generally do not cause an incubating bird to leave its nest, but a slow-moving or stopped boat does cause nest-exiting. Fishermen are rarely aware this occurs as their first sighting of the loon is after the bird has slid off its nest, swum underwater, and emerged out in the lake. Olson and Marshall (1952) and Ream (1968) discussed a similar problem on the canoe routes of the border lakes. There canoeists stopped and/or camped on islands where loons were nesting, and, unaware that they were disturbing the birds, caused nest desertion.

Another disturbance follows nest-finding by humans. In 1971 I watched from the opposite shore while boats and canoes made trips to view and photograph a loon nest with eggs on Webster Lake, a find originally reported to other campers by an excited tourist. Twenty-four hours later the pair were still in a different part of the lake and they never returned to the nest site.

Lakes in use category 7, those with heavy recreational fishing pressures, have the greatest proportion of reproductive success. This agrees with the supposition that food is the limiting factor in habitat selection. Data presented in

Figures 18 and 19 indicate that recreational fishing does not greatly conflict with loon reproductive success except on small lakes, but my observations indicate that fishing may lower productivity. Summation and analysis of PlW data masks the adverse effects of human use that I have observed. Lakes in use category 7 are optimal loon habitat and expected fledging rate is higher than, not equal to, overall expectancies.

There was a decline in the probability of two-chick broods on lakes of the highest use categories, i.e., those with much water skiing and/or boat racing, on small lakes only. These activities usually occur in the center of large lakes while loon nests and the rearing of chicks are confined to the littoral portions. However, the increased likelihood of several nesting pairs on larger lakes doubtless permits bias to the results as I presented them, and total productivity per water acre should be assessed. This is touched on in the section on Populations, and those data indicate that a more detailed study should be made.

The ultimate factor in habitat selection by Common Loons is for lakes with an abundant supply of small fish and water sufficiently clear to permit efficient foraging. Selection of large lakes is a proximate factor which increases the probability that a nesting lake not go dry in the summer. Common Loons will utilize smaller eutrophic lakes as long as the fish supply is adequate and available, recreational use is at a minimum, and shoreline development is negligible.

Courtship

Description

Loon courtship has been variously described as elaborate, simple, aquatic, terrestrial, aerial, diurnal, nocturnal (Huxley, 1923; Roberts, 1932; Keith, 1937; Yeates, 1950; Olson and Marshall, 1952, Drury, 1961; Palmer, 1961; Southern, 1961; Parmelee et al., 1967; Sjölander, 1968; Lehtonen, 1970; Tate and Tate, 1970; Sjölander and Ågren, 1972; Dunker, 1975). That which I observed was simple, aquatic, and diurnal. I could not make observations at night, and it is possible nocturnal courtship did occur.

The displays used in courtship and copulation are defined and illustrated in Appendix III. and a quantification of percent of time spent in each is given in Table 5. No displays are unique to courtship and all are used in other social situations. Displays between mates involved turning the head, hiding the bill, and tucking the head low with subsequent lessening of the visibility of neck and throat stripes. In threat situations, such as defense of young against human intruders or nest protection from raccoons, the neck was held high, the bill directed forward, and slightly down, and wings held out from the body.

Some accounts have been given of running and flight displays (Southern, 1961; Palmer, 1962), but I believe these are aggressive displays, probably given in territorial defense. The components described for them are definitely agonistic and could not serve to strengthen a pair bond.

Table 5. Displays used in Common Loon courtship and the percent of time spent on each. (N=31 sequences monitored).

Displays	Percent
<u>Diving</u>	
Short Dive	54.8
Splash Dive	12.9
Circle Dive	6.5
Jerk Dive	3.2
<u>Head Posturing</u>	
Bill Dipping	45.1
Facing Away	38.7
Head Throw	25.8
Bill Flick	19.4
Modified Pelican Posture	6.5
Head Jerk	9.7

Both sexes used the same displays, often at the same time, while they were swimming near the shore. Sjölander and Ågren (1972) and Sjölander and Ågren (in press) have indicated the same occurs for Common Loons in Iceland and Yellow-billed Loons in Alaska, and termed it "search swimming." I would prefer to call it Slow Swimming because of the implication that "search swimming" is used to search for something and, as a term, it is perhaps reading the behavioral conclusion into the description.

There was no uniformity of sequences used, their order, or the amount of time spent in each from one courtship bout to another; neither was there uniformity between those bouts that ended in copulation and those that did not.

Short Dives are quiet, brief dives, usually given simultaneously by the pair, and are significantly shorter than feeding dives ($N=16$, $\bar{X}=6.5$ seconds, $P<.001$ shorter than feeding dives). Splash Dives, Circle Dives, and Jerk Dives are described in Appendix III. Diving was used in 64.5% of all sequences.

Bill Flicking is an abbreviated Bill Dipping, and a Head Throw is a quick Head Rub, but used in a social situation rather than for maintenance.

The soft "mew" vocalization was used during courtship. It is a call that I have heard only between family members, between mates, and from parent to young, and it was given during 25.8% of the courtship sequences.

The earliest courtship that I observed was on 28 April 1972, the day after the second pair member arrived on the territorial lake. The latest I saw was on 24 June 1970 and occurred a week after the fourth and final nest attempt by that pair, was composed of only Bill Dips and a single Head Throw, and concluded with a successful copulation. Courtship and copulation lasted through May and June, and displays were the same throughout the period.

When pair members were not engaged in courtship displays but were close to each other, a modified Pelican Posture was assumed for much of the time. The white throat patch is hidden with this posture, and bills are minimized which serves to lessen the aggressive quality of a face to face confrontation.

Most courtship occurred in the morning from 06:00 to 10:30 and in the late afternoon or evening, after 15:45. One sequence was seen from 10:50 to 11:07 just prior to nesting and subsequent egg-laying. Courtship was never seen at noon or during the early afternoon.

Twenty-six of the 32 sequences I watched occurred in the morning, but two factors may have biased the sampling. First, many of these were observed at the time I was on a daily monitoring schedule that included observations from 07:00 to noon. Secondly, territorial defense is required more frequently in the morning than in the evening, and courtship sequences were interrupted at times by an intruder landing in the territory. Resumption at a later time was counted as one sequence because it contained all the components of a complete sequence. In fact, if the original sequence had been completed, there may not have been another. This is speculative, but it should be pointed out that the preponderance of morning courtship notations may not indicate a behavior that would be engaged in if there were no interruptions.

Discussion

Sjölander and Ågren (1972) state that G. immer uses very little special behavior preceeding copulation which could be termed courtship. I concur if they mean there are no displays used solely for courtship. However, there is one difference in our observations. They described courtship only as formalized Bill Dipping followed by mutual Splash Diving. Birds which I observed employed Bill Dipping and Splash Diving before copulation, but courtship also included all the components listed in Table 5.

Although Common Loon courtship is not spectacular, posturing shows there are elements typical of the dualistic nature of courtship display many other species exhibit. Jerk swimming and Splash Diving are aggressive, but they alternate with appeasement behavior such as Pelican Posture and Facing Away.

Copulation

Description

Copulation, as opposed to courtship, was very stereotyped, with precisely the same behavior engaged in every instance I observed (12 times, copulations involving four pairs). Preceeding one copulation, I could not see the pair before they were on land to note which bird initiated copulation. In the other 11 instances, the female went to land first six times, and the male did five times. In 11 separate instances, the male went to shore following a courtship sequence, waited, and invited, but the female did not follow.

When the male preceeded the female, he climbed on shore, pointed his bill along his side in the direction of the female, or picked at the vegetation, gave the new call, and with his head lowered so that his bill touched the ground, he waited until the female approached. (This might be termed "inviting"). If the female responded and approached the male, he slid off the site and waited until the female climbed on land, then he mounted her and stood on her shoulders with his head directed forward over her head. Cloacal contact lasted from three to 15 seconds, and the male dismounted immediately afterwards by walking over whichever of the female's shoulders was nearer to the water. He never "pivoted" as described by Tate and Tate (1970). The female stayed longer, up to eight minutes. She sometimes engaged in nest building activity before leaving the site.

When the female was the first to climb ashore, the male followed immediately in all instances except one, mounted and copulated with her. In those instances when the male "invited" and the female did not respond, he waited as long as several minutes, kept his back to her, and continued to give the "mew" call.

Some nest-building activity usually followed copulation. Both pair members engaged in preening and bathing activities following copulation. No post-copulatory displays were seen. Although most copulations were early in the morning, there was a range of times (Table 6.).

Table 6. Time of day when copulations occurred.

05:41
05:47
05:48
07:35
09:10
09:48
11:00
16:05
17:45
21:25

Discussion

Sjölander and Ågren (1972) said copulation was initiated by the female. Their observations were for only two pairs of loons, and for six copulations. My records give data for four pairs and 11 copulations. Due to individual differences and the small number of observations either of us have, it is possible that either sex may initiate copulations. More data from more pairs are needed.

Sjölander and Ågren (1972) also found that most copulations occurred early in the morning. Because there are not 24 hours of daylight in my study areas as there were in the Icelandic region they studied, I do not know if loons in Minnesota also copulate between 03:00 and 05:41.

Copulation platforms have been described (Huxley, 1923; Tate and Tate, 1970). Sjölander and Ågren (1972) found no evidence of such a structure. This may be a matter of semantics. All copulations by one pair seen in 1971 were on the structure that later became their nest and building movements attending copulation and frequently incorporated into post-copulatory behavior, were expanded into full nest-building for this pair. For another pair, also in 1971, copulations occurred at the same site over and over until late in the season. Vegetation which had been pulled to this site did indeed make it resemble a "platform" but the actual nest was built at another location.

Other pairs in other years chose various sites for copulation, the same site as in former year, a future nest site, never the nest site, and all degrees of variables within this range. I assume loons may copulate at any site that provides a sufficiently sturdy foundation so they do not sink when both birds are on it. Loon nesting lakes frequently have only one or two such sites; sturdy, near the water, or on a small island or clump of sedge. Nest-building movements are a part of both pre- and post-copulatory behavior. They may function both to assist in self-stimulation for actual nest-building, and to help form the substrate for additional copulations. Something resembling a "platform" is thus the result of repeated copulations. An actual "platform", probably not, but the individual variability of loon behavior and accomodations of each lake indicate that both views may be honest assessments.

At no time, either in courtship or copulation situations, did I see aerial flights, overwater chases, or anything other than the quiet, almost understated, displays described. Pair members may engage in overwater chases, aerial flights, duetting, but I have interpreted this as territorial defense. None ended in copulation.

Courtship displays differ from aggressive displays with the inclusion of Facing Away and modified Pelican Posturing. Copulation may be initiated by either pair member, occurs on land, involves no ordered displays, is regularly followed by nest-building, and includes no ritualized post-copulatory display. It occurs most commonly in the morning and evening. Courtship and copulation may be components of pair behavior for more than two months, beginning with arrival on the territory. Because loons may re-nest several times over a two-month period, it is advantageous for them to maintain sexual readiness in the event of nest loss.

Nesting

Nest Site

Nest site selection among birds has been shown to be determined by availability of nesting materials, fluctuating water levels, proximity and/or visibility to the nearest neighbor, predator pressures, height and/or density of vegetation, thermal micro-environment, and proximity of food, (Emlen, 1954, Bongiorno, 1970; Verner and Engelson 1970; Burger 1972, 1974; Calder, 1974).

Within the Gaviidae it has been suggested that proximity to deep open water, wind direction, predator pressures, firm substrate, cryptic coloration of the background, shadows, and human disturbance are important factors (Olson and Marshall, 1952; Palmer, 1962; Lehtonen, 1970; Dunker and Elgmork, 1973; Vermeer, 1973b; Dunker, 1974). Site preference was checked for its relevance to food availability, wind direction, substrate and human interference, as well as whether or not it was located on an island. Optimum conditions were considered to be met based on the success:fail ratio.

Food Availability

Feeding was usually done only by the pair member not incubating. Only once did I see an incubating bird leave its nest, feed, and return to continue incubating. The off bird generally fished away from the nest, a strategy perhaps designed to call attention away from the nest site, and it appears that proximity to food is not a factor in nest site location.

Directional Placement and Recreational Use

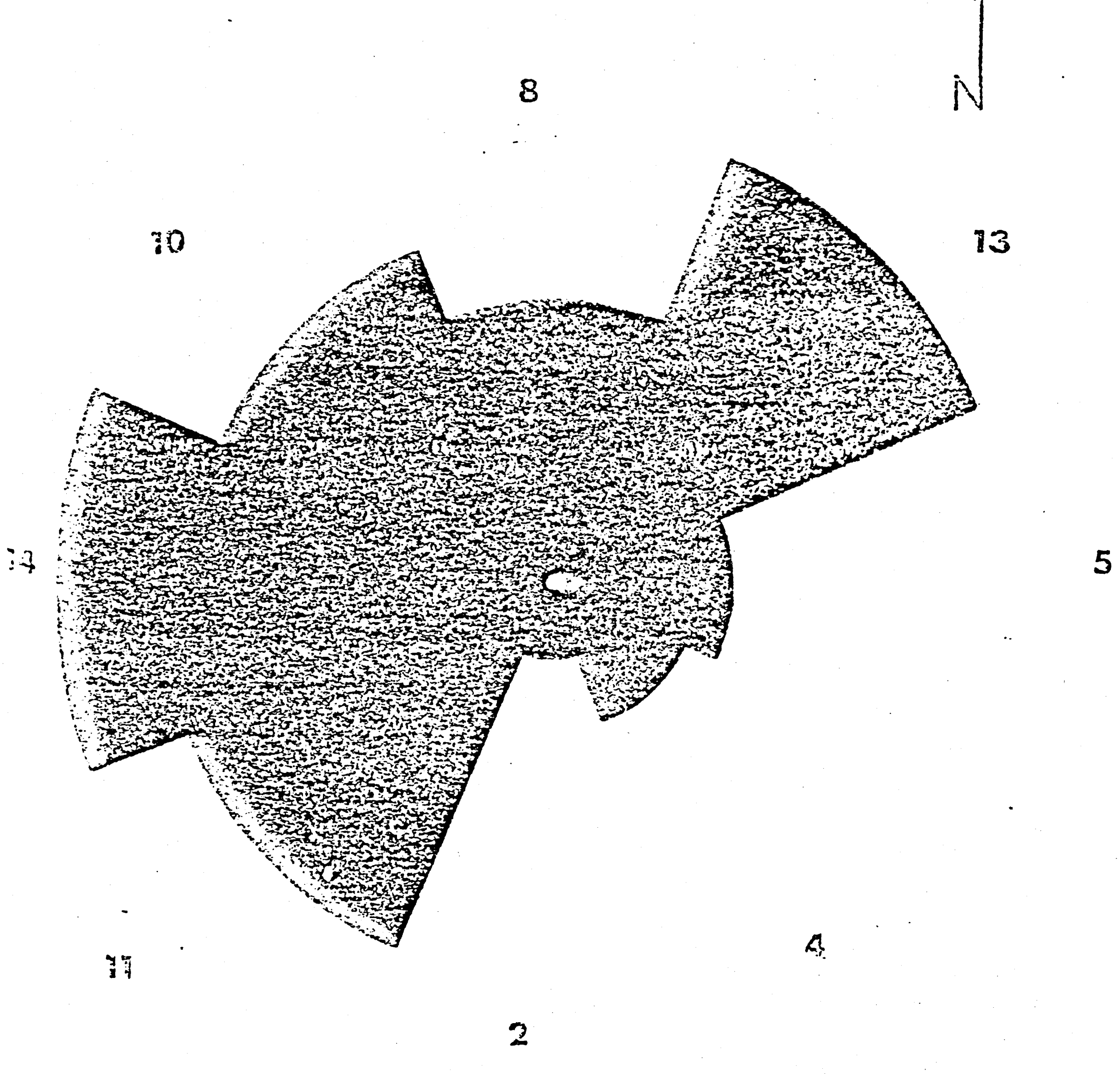
The location of all nests by their position on the lake was charted (Figure 20). Most were on the north and west sides. Because prevailing winds are from the NW, strong wave action more commonly occurs on the south and east sides. The north and west are more protected and nests placed there would have a lowered probability of wash-out from waves.

Prevailing winds shape shoreline (Figure 21). While it is true that loons place their nests to minimize flooding (Olson and Marshall, 1952; Vermeer, 1973b), the proximate cause of selection for north and west sites seems to be choice of substrate.

Directional placement with respect to the areas of most intensive human disturbance was also examined. Some lakes had recreational use (N=5), but on other lakes there was no human disturbance during the nesting season (N=6). Use versus non-use on nesting lakes was examined and found to make no difference to nest success (Figure 22) Chi-square test, $X^2 = .419$).

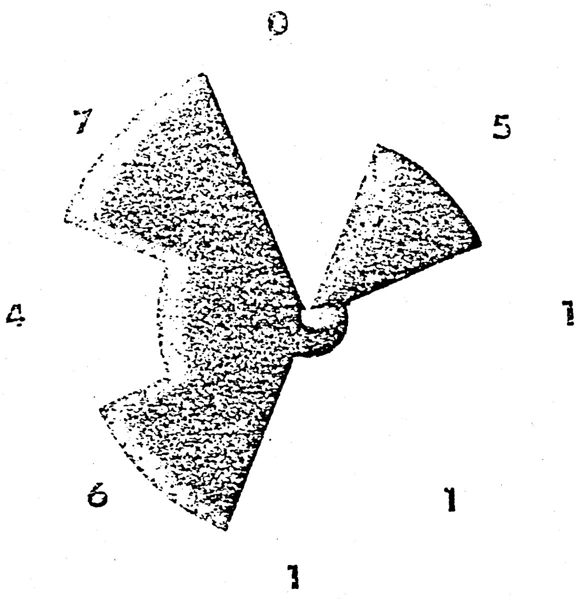
All lakes were used at least for fall hunting or ricing. Although this activity still rated them a "0" disturbance factor, it necessitated a point of access which was usually a boat landing. One lake had a campground, one a public beach, another a private beach, and two had boat landings.

Figure 20. Nest locations. Numbers represent number of nests in each direction.

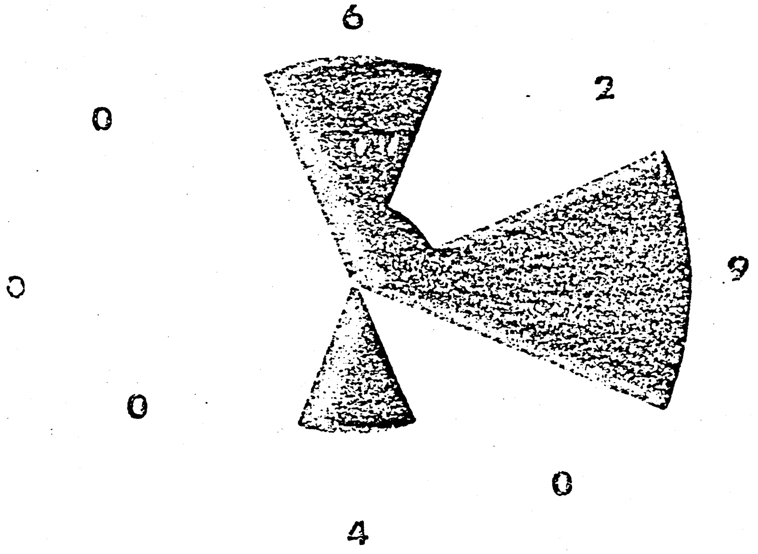


NEST SITES

Figure 21. Condition of all shores on the study lakes. Numbers indicate numbers of lakes.

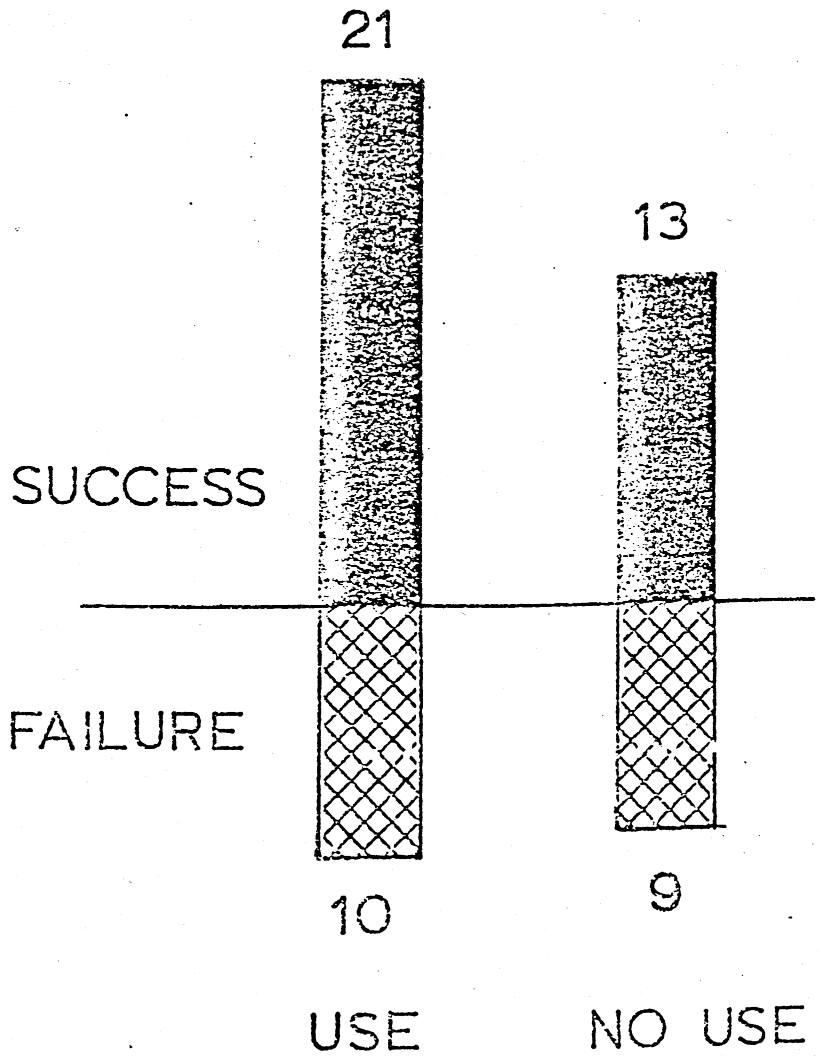


SEDGE MAT



CLEAN SHORE

Figure 22. A comparison of nesting failure and success on lakes with and without recreational use.

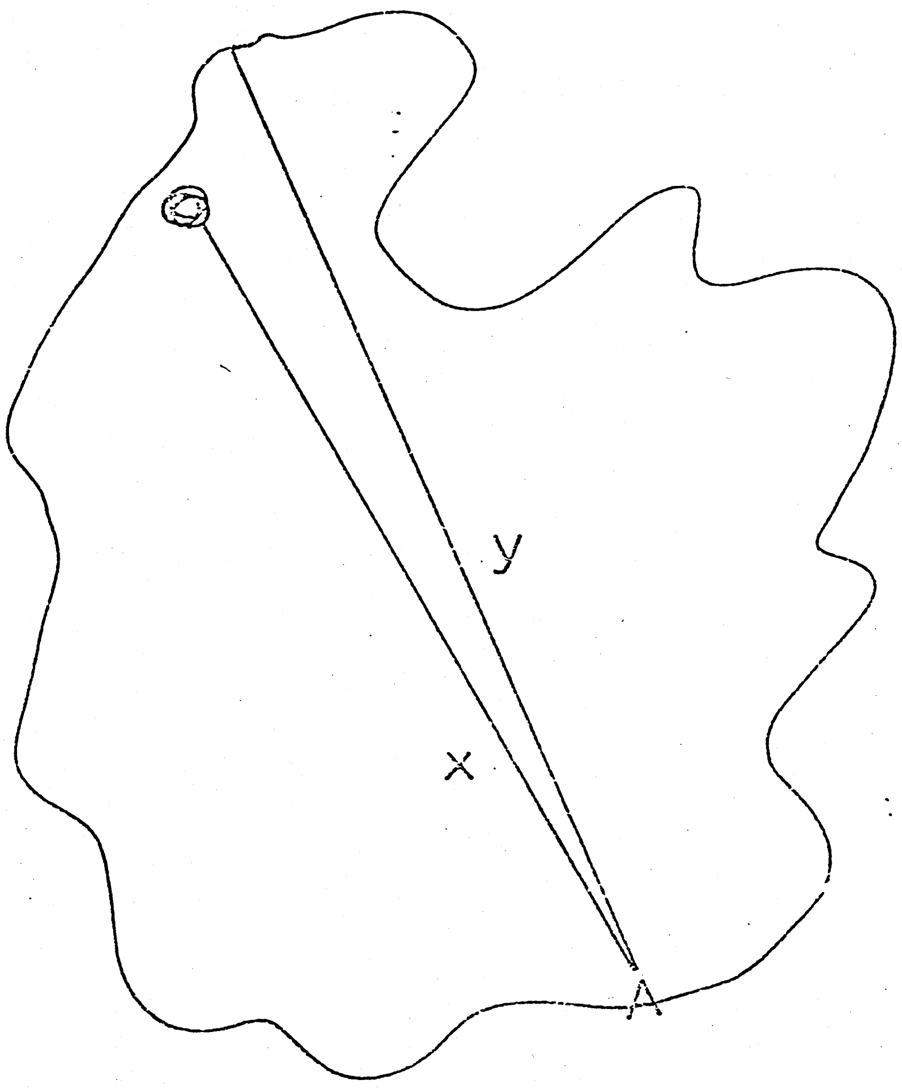

21
13
SUCCESS
FAILURE
10
9
USE
NO USE

It seemed possible that nest placement may have been partially determined by recreational use, so distance from the point of lake access to nest site was measured and compared between lakes with disturbance during the nesting season and those with none. To standardize this figure for all lakes, the distance from the access to the furthest point on the lake was measured (y) and distance from access to loon nest was measured (x) and distance standardized by $D=\frac{x}{y}$ (Figure 23; Table 7).

Nests on lakes with disturbance during the nesting season were farther from access than those without; nests on islands were closer to access than those on the shore or sedge mat; and successful nests were farther than unsuccessful ones, but no differences were statistically significant. Each possible combination of the three was examined with each other. The greatest distance difference was between nest sites that were successful, not on islands, and on lakes with use, compared with unsuccessful nests on islands on lakes with no use. There was not a significant difference between these combinations (t-test for SE of the difference of the means, t=1.815, df=17).

There did not seem to be a relationship between site preference and human access position. A firm shore is optimal for boat launching, and if such a spot can be found, particularly one near a road, it will be used. The same is preferred substrate for a beach or campsite. Because

Figure 23. Hypothetical lake, nesting site, and access point illustrating method used to calculate access-nesting site ratio.



Λ access

◎ nest

Table 7. Relationship of human access points with positioning of loon nests.

Situation	$\overline{X}$	N
Lakes with use	0.660	41
Lakes with no use	0.521	20
Island nests	0.577	31
Other	0.632	31
Successful	0.649	23
Unsuccessful	0.578	39
On islands		
With use		
Successful	0.678	8
Unsuccessful	0.645	5
No use		
Successful	0.557	7
Unsuccessful	0.485	11
Not on islands		
With use		
Successful	0.701	8
Unsuccessful	0.611	21
No use		
Successful	0.0	0
Unsuccessful	0.595	2

this is more likely to be found away from the preferred substrate type for loon nests, there is probably very little potential conflict.

Islands

Half of all nesting occurred on islands (1970-1974). Islands were not available on all lakes until 1971, and data from this time on is more germaine to answer the question of preference relative to open water (Figure 24). (See Appendix IV. for explanation of the construction of artificial islands.)

When islands were available, 88% of all nests were built on them. This is in close agreement with island preference as noted by Yeats, 1950; Olson and Marshall, 1952; Lehtonen, 1970; Vermeer, 1973b. However, the ability of loons to use other sites when islands were not available agrees well with others (Munro, 1945; Sage, 1972; Dunker and Elgmork, 1973). Lakes with islands added increased nesting success by 58.9% (Chi-square test, X^2=11.1, $P<.005$).

Distance from island nest site to shore was measured and correlated with success (Figure 25.). It did not affect success. Water depth did show a significant position correlation with nest success (Figure 26.). (A t-test for the SE of the difference of the means gave a statistic of $t=2.61$, $df=19$, $P<.02$.) In all cases when a nest island was in water less than half a meter deep, there was a nesting failure.

Figure 24. Success and failure of nesting attempts as related to the positioning of the nest.

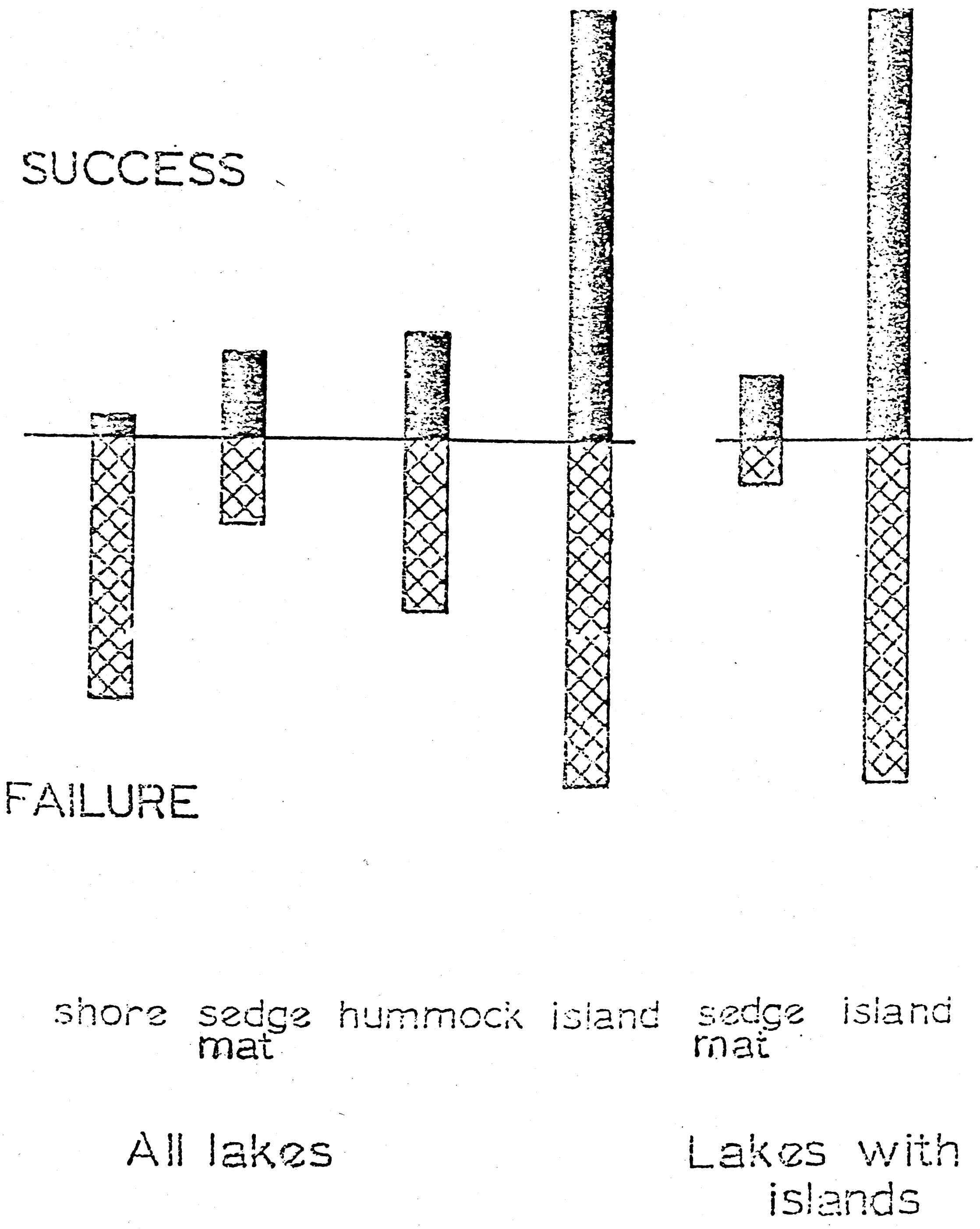
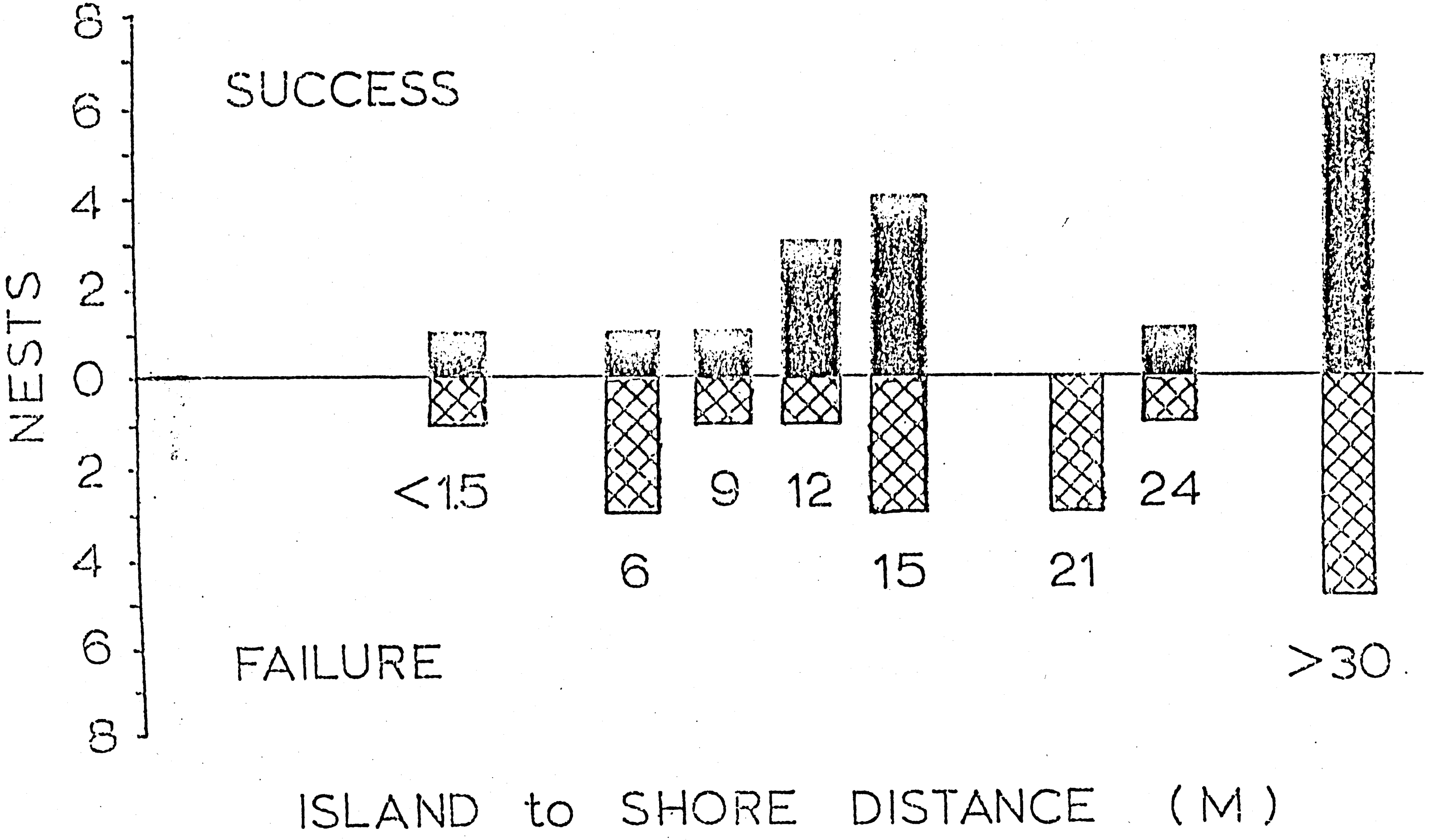
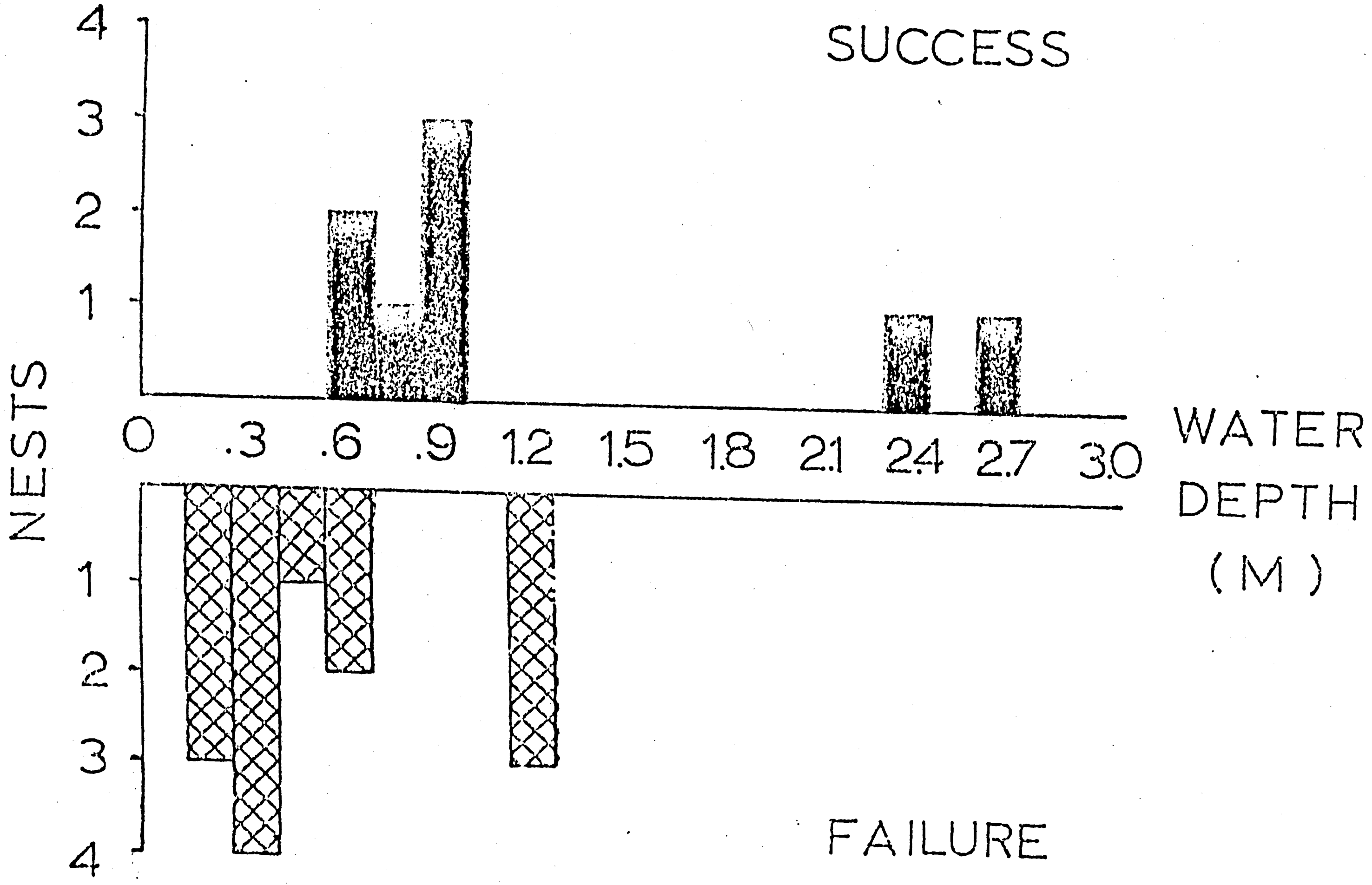

SUCCESS
FAILURE
shore
sedge mat
hummock
island
sedge mat
island
All lakes
Lakes with islands

Figure 25. Success or failure of nests as related to the distance of the nesting island to shore.



NESTS
8
6
4
2
0
2
4
6
8
SUCCESS
FAILURE
<1.5
6
9
12
15
21
24
>30
ISLAND to SHORE DISTANCE (M)

Figure 26. Success or failure of nests as related to the depth of water by the nest site.


SUCCESS
4
3
2
1
NESTS
0
.3
.6
.9
1.2
1.5
1.8
2.1
2.4
2.7
3.0
WATER
DEPTH
(M)
1
2
3
4
FAILURE

Causes of Nest Failure

All unsuccessful nests were examined for causes of failure and the possible relevance to location of the nest site. Predation accounted for more than 75% of all nest losses, but for only 46% of island failures. On lakes with islands sedge mat nest failures were the result of predation. Flooding and desertion, the latter partially caused by human disturbance, accounted for most other losses.

Crows were the only avian nest predator noted. There were no ravens on the study areas in the summer. Crows were seen pe~~a~~rching over and flying down to loon nests, and eating loon eggs. In addition, shells were found with small holes as described by Rearden (1951) for eggs destroyed by crows, and others were found which looked like those as shown by Sowls (1955). I made predator track traps to identify mammalian predators (see Appendix V.). In 1970, track traps were made around three former loon shore nests; in 1972 four artificial loon nests were made, two on the shore and two on islands. Predators were identified by the tracks they left in the sand-clay mixture. There was no avian predation; all losses were due to ~~animals~~ mammals.

Results of 118 trap days indicated the major predator was a raccoon and other losses were from skunks. Mink tracks were found in only one instance, and the egg was not taken. The deer "predation" was scored because a deer stepped on the egg and broke it (Table 8.).

Most losses and all initial losses happened at night, and none occurred on islands. Frequency of predation increased after initial discovery of the nest, so that 1972 tests were discontinued after a week due to acclimitization by the predator with consequent maximum predation (Figure 27.).

Discussion

Island nests did incur some predation, but island test sites did not. Loon activity associated with nest relief and not the nest and egg *per se* may draw attention to the nest and alert avian predators. Deep water beside the nesting island increases the loon's ability to leave and return undetected, and may explain the importance of water depth in site selection.

Mammalian predators are not hindered by water which permits wading, but many prefer not to swim. Deep water may confer some additional benefits to loons by deterring some mammalian predators.

Predators have good memories and return to the site of a successful predation which offers a selection pressure against re-nesting on the same site in the event of a nest failure. On the other hand, if a site has a successful nest one year, the probability that the same site will provide a safe location the following year is greater than the probability that a new, randomly selected

Table 8. Results of the predator track trap tests.

1970 TESTS

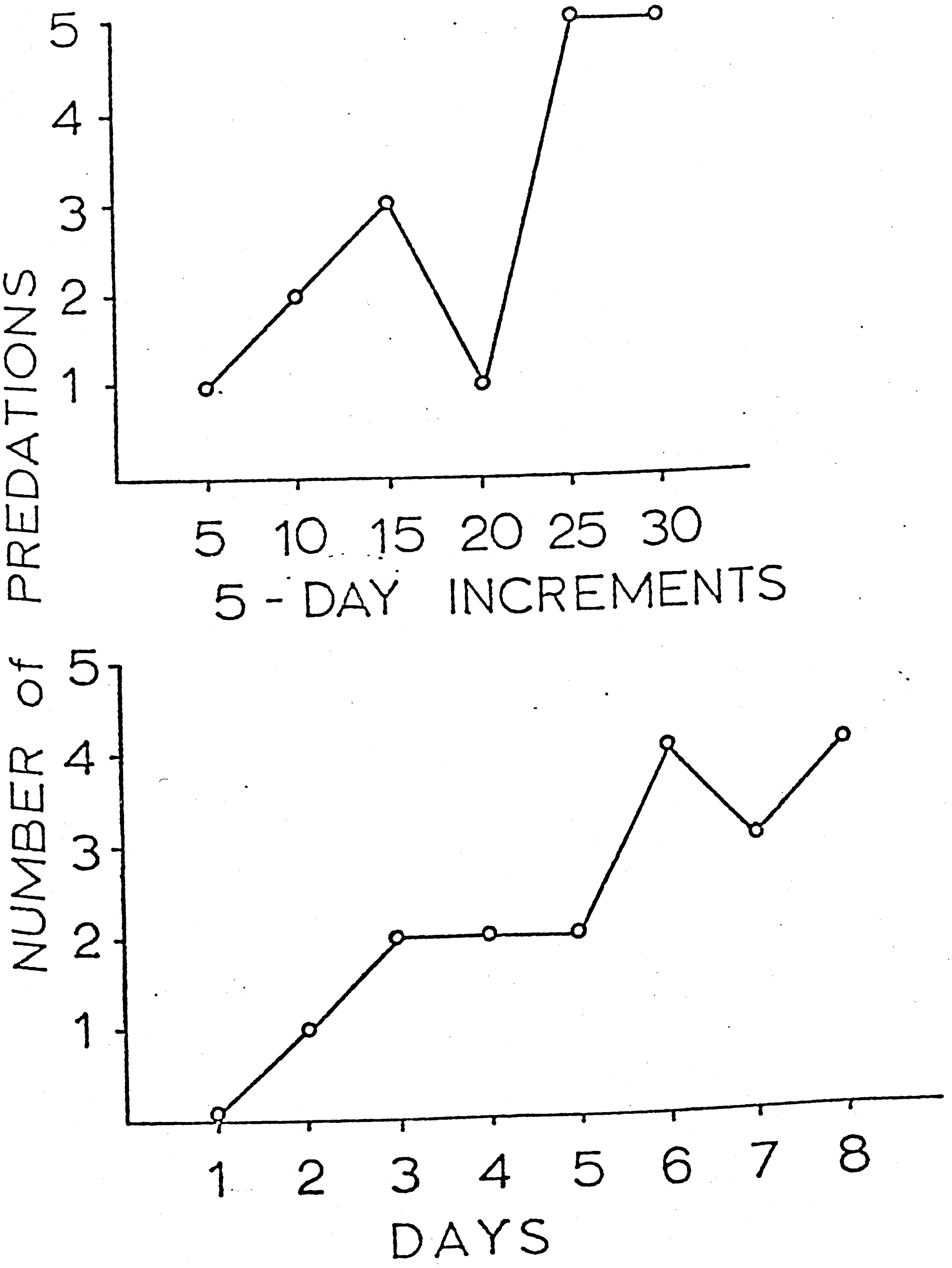
Predator	N
Raccoon	12
Skunk	3
Unknown*	2
Total	17
Total trap days	90

1972 TESTS

Shore				Island
Day		Night		
	5		13	0
Raccoon	4	Raccoon	12	
Other (Deer)	1	Other (Skunk)	1	

*The rumpled nest and condition of eggshells indicated predation was by raccoon.

Figure 27. Frequency of predation of the predator track trap tests as related to the length of time the test had been run.


NUMBER of PREDATIONS
5
4
3
2
1
5
10
15
20
25
30
5 - DAY INCREMENTS
5
4
3
2
1
1
2
3
4
5
6
7
8
DAYS

and untried location will. Site affinity showed a significant correlation with success (Figure 28.) because the nest site was changed in almost all cases following a failure, while retention of the same site was proportionately greater following success.

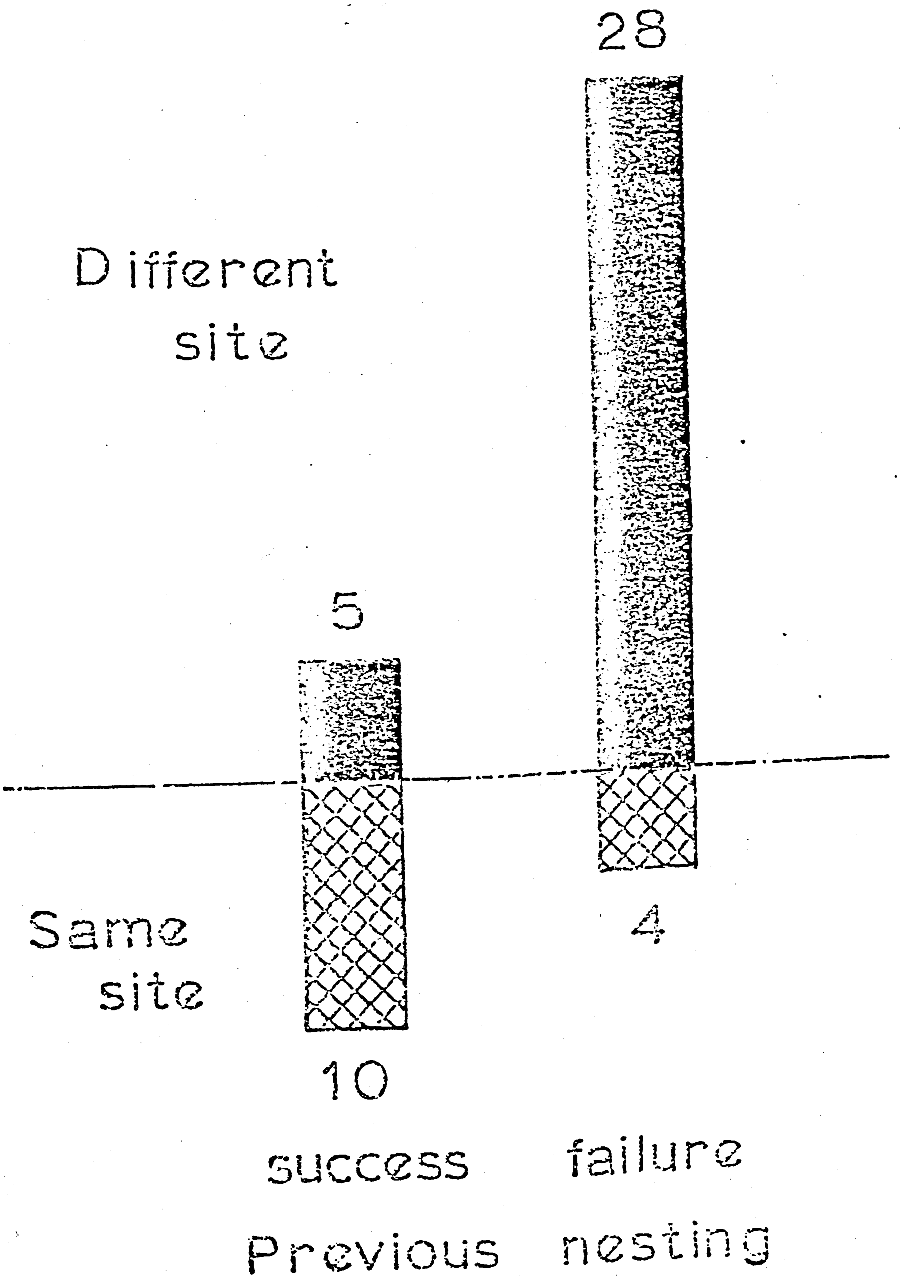
Numerous studies of other species show there is a high degree of site affinity explained by increased success via maintenance of a large colony size, retention of a mate (Austin, 1949; Mendall, 1958; Cooch, 1965; Johnson, 1967; Richdale and Warham, 1973).

Lehtonen, (1965) Lindberg (1968) and Sjölander (in press) indicated that Arctic Loons retain the same nest site from year to year, while Dunker and Elgmork (1973) thought a change was mandatory.

None of these studies compared site change with success or failure. This seems to be the important factor in retaining or changing the site. Olson and Marshall (1952) found that most replacement clutches within a breeding season were laid in a new nest site. Selection for retention of a successful site has been mentioned, and there is another advantage that bears discussion.

It is imperative that northern breeders begin nesting as soon as possible. Although there was a time lag between spring arrival and onset of nesting among pairs on my study areas, more northern populations nest a few days after their arrival at the breeding lakes (Sjölander and Ågren,

Figure 28. Nest site affinity including both re-nests and nests from year to year.


28
Different
site
5
Same
site
4
10
success
failure
Previous
nesting

1972). Site affinity could reduce time spent in site searching and permit more rapid onset of nesting.

The ultimate factor in selecting a nest site is its suitability as a location protected from wind and waves and its safety from predators. The proximate factors, deep water and use of islands, make it appear that nests are built away from areas of human disturbance. This is probably coincidental.

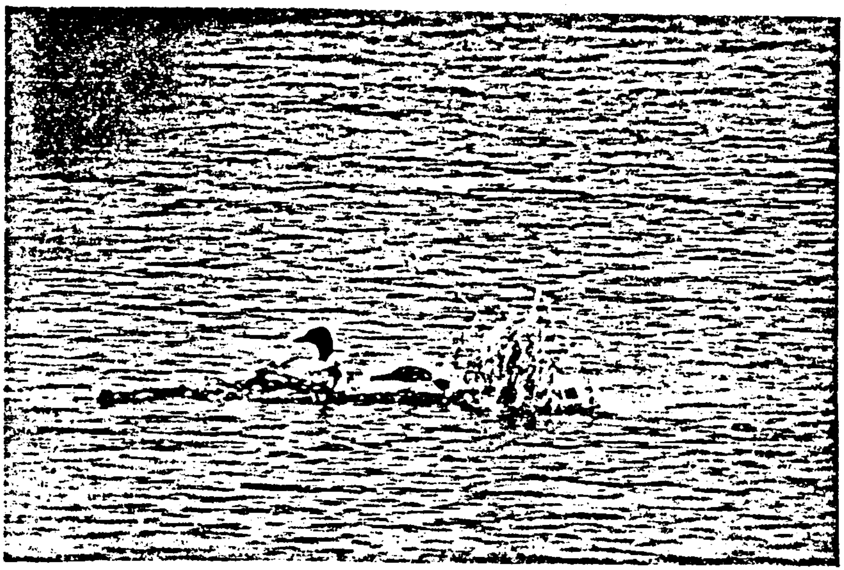
Nest-building Behavior

Description

Nest materials were secured by two methods, retrieving and pulling. Retrieving meant the birds dove and brought materials from the lake bottom. Pulling was done as the bird sat on the nest platform and pulled living vegetation and root materials from the island. Materials were placed on the nest by sideways-throwing as was described for Red-throated Loons by Drury (1961). Only once was a loon seen to carry materials to the nest from a distance by swimming to the site with material in its bill. When vegetation was thrown, it landed on the site, back in the water, or even on the back or tail of the loon. Placement on the nest was done with a lucky throw or because the loon was on or near the nest.

Both pair members built at the same time, and late in nest building (i.e., for this pair, on the last day before egg-laying), I observed one loon in the lake diving and retrieving material which was placed on the nest and rearranged by the mate (Figure 29.). Whether this should be termed cooperative building is questionable as no passing of material from one loon

Figure 29. Pair of loons on Lost Lake building a nest on an artificial island.



directly to another was seen.

Table 9. gives the times spent in nest-building by one pair of loons from the onset to the laying of the egg, for a first nest; replacement nests may be built more quickly. Although this pair used parts of four days, actual nest-building time was a little more than three hours for the male, and a little less than three hours for the female. Both the number of sitting periods and the total time was evenly divided between the pair members. This is not in agreement with Sjölander and Ågren's (1972) findings that the female did most of the building, nor with Lehtonen (1970) who stated that the male built the nest.

Although some building behavior followed mating, the actual nest is not necessarily built on the copulation site. I watched copulations of four pairs at various times during the study. Two pairs utilized a copulation site for a nest site; the other two never did.

Initiation of nest-building at a location which subsequently became the nest was by either male or female. I determined which pair member selected the nest site by presenting an artificial structure and keeping it under continuous observation. The pair came together to the island; the male made the initial nest-building attempt, and was later joined by the female.

Site selection by two other pairs was recorded. Members of one pair built nests in two different areas, and the one

Table 9. Summary of nest-building activities by one pair of loons. Total observation time was 87 hours.

	Minutes Spent		Times on Nest	
Date	Male	Female	Male	Female
May 11	49	28	12	13
12	0	0	0	0
13	26	28	7	7
14	106	110	16	16
Total	181	166	25	26

which eventually became the nest was the one the female had been building. Another pair went ashore 38 times during a four-hour period on the first day of nesting, and 11 of the 38 trips were to the site that became the nest location. The female went the first two times, then throughout the four-hour period either male or female made visits and nest-building movements there, the male six times, and female five times.

Sjölander and Ágren (1972) stated the male chose the nest site in Iceland, but my evidence suggests that either sex may choose the site.

There were no differences in behavior during original and replacement nest-building. Re-nesting is further discussed in the section on eggs.

Discussion

Harrison (1967) proposed sideways throwing as the most primitive form of nest building and noted it was derived from aggressive behavior. He also wrote of the derivation of sideways-throwing from its evolution as a direct sequence to copulation posturing. In Facing Away, vegetation may be encountered with the bill when the head is turned and a logical next step is to move some vegetation. Arranging and rearranging of nest material is thus a sequence to Facing Away and indicates minimal additional development of behavioral posturing specifically associated with building a nest.

Harrison (1967) suggested that for birds that build this way, the size of the completed nest is determined by the availability of material. The ultimate stimulus which determines the final nest structure for Charadriiformes is a tactile response; nests are built to exclude the dampness of the substrate. The ultimate stimulus for loons may also be a tactile one, and the degree of firmness in the substrate may dictate the final size.

As a secondary effect, a large, and especially a high loon nest will remain less damp than a small low one if it is built on boggy substrate and it will have greater protection from flooding or wave action. Availability of materials is greater on sedge mat than on rocks or gravel, and more so in lakes with aquatic vegetation than those without. However, muskrat houses are also damp and contain much material that could be manipulated and rearranged. Muskrat house nests that I have seen have been essentially the same as they were before loons nested on them. They are substantial, high above the water, and firm.

A "pre-conditioning" for incubation has likely been selected for as indicated by the numerous times loons go on and off the nest during several days of construction. If this does serve as a "pre-conditioning" then both pair members should share in nest building because both incubate. They both do.

Nests

Description

Loon nests have been described by many authors (Appendix VI, VII). Those on my study areas were remarkably similar to each other (Figure 30.). Both contained much wet and rotting vegetation, although A. was a nest completely built by loons, while B. was made on muskrat workings, with little added vegetation. I attempted to discover the stimulus to build since there is a considerable variability in nests throughout the species' range. I have seen nests late in incubation in other areas with virtually no nest material used and eggs on the bare ground or duff and C. is an example of the latter.

I presented loons with platform islands of varying firmness made with a base of plywood and sand, gravel, or vegetation placed on them. Sedge mat islands were also offered. They used only sedge mat islands. It would be worth further investigation to see if it is height above water, firmness of the substrate, availability of vegetative materials, or a combination of these factors which determines the type of nest a pair will build.

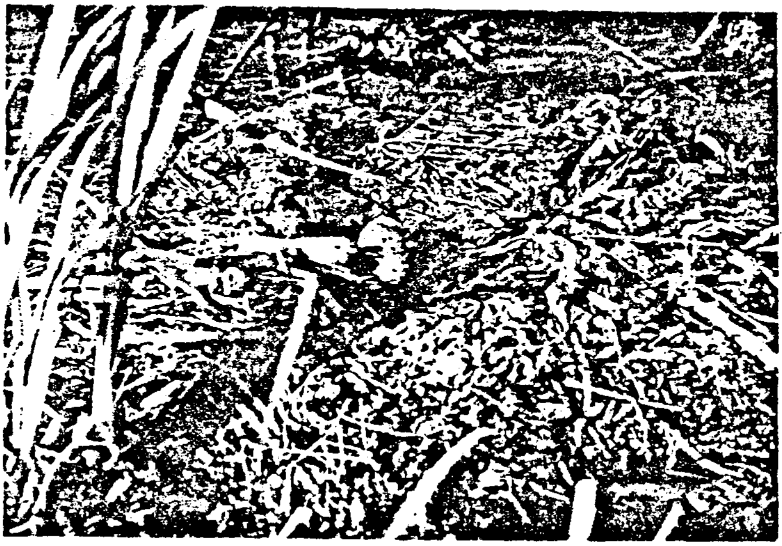
Two loon nests were collected from artificial islands that had been made for the loons just prior to their nesting, so it was known that all materials were placed there by the loons immediately before and during a single incubation period. They were collected on the day the young left the nest, thus no additional material was added, carried off by other animals, or washed away. One weighed 20 pounds, the other, 40 pounds.

Table 10. gives the vegetative composition of 15 loon nests. All but one contained at least one species of sedge,

Figure 30. Loon nests.

A.

B.



C.

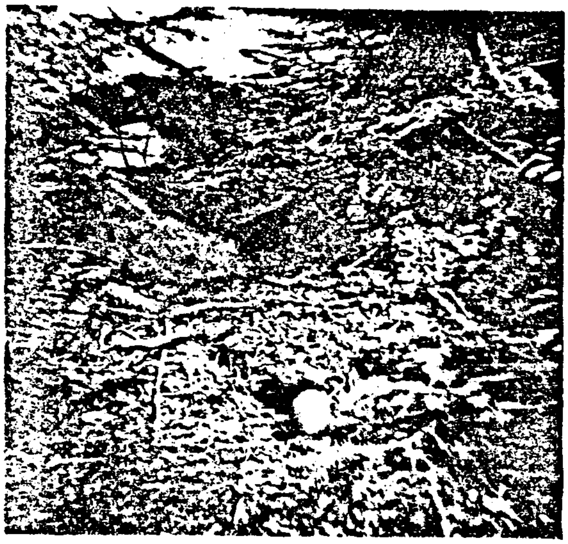


Table 10. Vegetative composition of 15 Common Loon nests by species.

Plant Species	Present in N Nests
Alnus sp.	2
Campanula aparanoides	2
Carex aquilitus	1
Carex crawfordii	2
Carex sp.	10
Dryopteris thelypteris	4
Eleocharis sp.	3
Dulichium arundinaecaeum	1
Hypericum virginicum	2
Iris versicolor	1
Lycopus uniflores	3
Moss (not Sphagnum)	5
Pinus resinosus	1
Pinus strobus	1
Salix sp.	1
Scuttelaria epilobifolia	3
Sphagnum sp.	1
Thuja occidentalis	1
Typha latifolia	7
Calla palustris	1
Scirpus acutus	6
Utricularia sp.	2
unidentified rhizomes	3

and nearly half used some cattail material. As these species were common to all lakes investigated, it is not surprising some material from these was used in the loon nests. However, if the quantity of each type is checked, it can be seen that most of the nest material was composed of clumps of roots, rhizomes, and decayed vegetation, and stems and sticks added rigidity (Figure 31.). Clumps averaged 23.6 grams wet weight, and were $\bar{X}$ =22 mm^3, range, 2mm.x 1.5 mm. x .5mm. to 10 mm. x 11 mm. x 2.5 mm.. One nest contained 218 distinct clumps plus more loose material of the same type that may have originally been placed in the nest as clumps.

Forty-seven nests were measured (Table 11.). This is in agreement with nests from the Knife Lake Region (Olson and Marshall, 1952). There was no significant difference between nests from which chicks successfully hatched and those that failed. There was a significant difference between first and replacement nests (N=20) in their outside dimensions but not in their inside width or depth (t-test for SE of the difference of the means, $t=3.42$, $P<.01$). Nest sizes did not change during incubation, as noted by Olson and Marshall (1952). Eight nests that were known to be new averaged 24.5" outside by 10.6" inside, slightly larger than the average of the 45 nests measured at all stages through hatching.

Figure 31. Composition of one loon nest by vegetation types by weight.

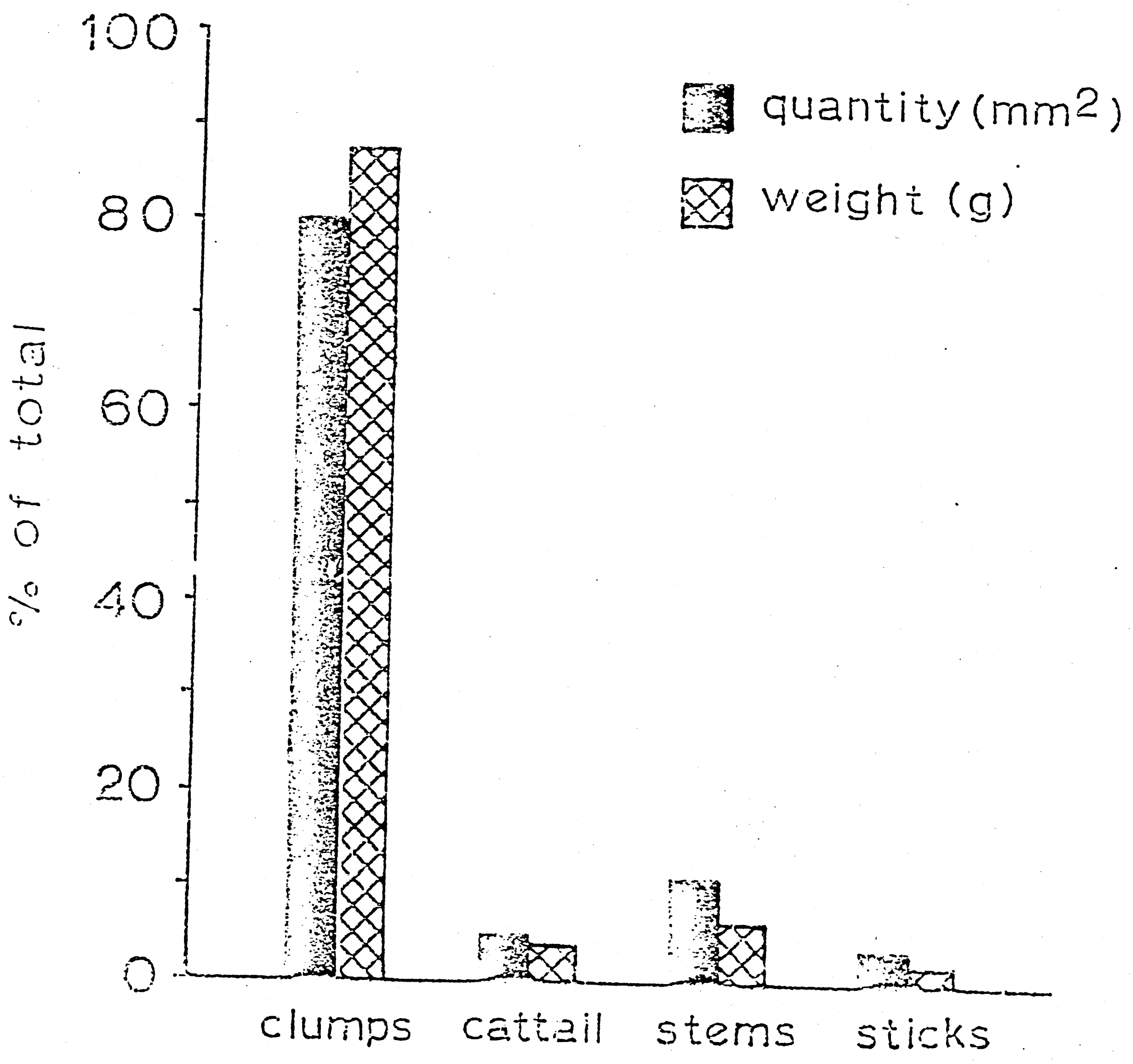

100
80
60
40
20
0
% of total
quantity (mm2)
weight (g)
clumps
cattail
stems
sticks

Table 11. Measurements of Common Loon nests in north central Minnesota.

	Outside ($\bar{X}$)	Inside ($\bar{X}$)	Depth ($\bar{X}$)
All nests	22.4 ± .82	9.59 ± .59	1.22 ± .084
Successful nests	21.5 ± .916	9.5 ± .76	1.26 ± .88
Unsuccessful nests	22.4 ± 1.54	9.24 ± .298	1.29 ± .008

Discussion

Nests of G. immer are composed of any available materials. Those in my study areas were large bulky structures. Olson and Marshall (1952) found that nests in their areas were virtually non-existent as actual structures when nesting commenced, but increased in size as incubation proceeded. Nests in this study were not significantly different in size from beginning to end of incubation. The substrate on which nests were built was spongy and there were no lakes with large rocky outcroppings like there are in the Knife Lake Region. A substantial substrate is required to support the weight of the nest, an incubating bird, or both pair members as sometimes both adults are on at once (more than 60 pounds), to prevent the egg from being submerged.

Beecher (1942) postulated that specialization reduces adaptability. Loons breed on the ephemeral fresh water lakes of glaciated areas. Many are shallow and subject to water level fluctuations from beaver workings, rainfall, or may undergo rapid eutrophication. Loons must nest near water because of their specialized leg placement and a broad spectrum of useable nest sites permits them to utilize a wider range of nesting habitat. Their opportunities for nesting are considerably broadened because they can alter the available substrate by changing the form of the nest. The mechanism that permits and guides this flexibility is likely a tactile response.

Eggs

Shape and Size

Terms describing birds' eggs have been standardized into 12 variants of the terms elliptical, subelliptical, oval, and pyriform (Palmer, 1962). Loons' eggs have been described as elliptical to long oval (Palmer, 1962) subelliptical and oval (Anderson _et_ _al_.), and asymmetric, with a negative bicone (Preston, 1969).

Anderson _et_ _al_. (1970) refined variables by evaluating eggs from seven regions and assessing geographical variability. Their results indicate volume is the single best variable to use in mapping a cline because of its highly significant difference among regions. Eggs from this study were subelliptical and oval and averaged 87.6 mm. X 55.6 mm. (N=53 eggs). Shape and size were virtually the same as previously described for Minnesota (Anderson _et_ _al_., 1970; Olson and Marshall, 1952, $\bar{X}$=86.8 mm. X 55.0 mm.). I used the method of Anderson _et_ _al_ (1970) for volumetric determination in order to most accurately compare my results with theirs. They used a correction factor (CF) of 0.62 and 0.64. Eggs in my collection for which I could determine volume by water displacement showed a CF of 0.63. Most eggs that I measured subsequently hatched and thus were not available for volumetric determination by any other method than with use of the following formula:

$$V= 0.63 \left[\pi \left(\frac{B}{2}\right)^2 L \right]$$

where B= width and L= length.

Volumes of eggs from this study fit well with the cline presented by Anderson et al (1970). The average for Region 4 (Minnesota, Wisconsin and Michigan) was 140.5 ± 3.3 and for Region 3 (Alberta and Manitoba) it was 128.0 ± 2.4. Minnesota is geographically located at the border of Regions 3 and 4 and if there is a cline it is expected Minnesota values would fall between the two. They did; $\bar{X} = 134.1 \pm 1.74$ cm^3 (N=53).

The L/B ratio from this study (1.58) is the same Anderson et al (1970) described for eggs from Region 4. Eggshell thickness was also measured and compared, but those results are presented in the section on Toxic Chemicals.

Color

Colors varied from olive to brown, but most had a greenish brown or brownish olive ground color and dark brown or black splotches. Egg color varied within a clutch and from one individual to another. Some single clutches contained plain and splotched eggs, light and dark eggs, and/or green and brown eggs. Egg color may not vary from region to region. Eggs from my study area were laid in nests made of vegetation (see nest description) and were cryptic with respect to their background. Some loons in other parts of their range lay their eggs directly on the ground. Eggs which I have seen in these circumstances did not differ in color, and also blended in with their backgrounds.

Background color may be kept variable because of the absence of selection pressures operating for any single color. The alternative is that there is selection for color variability within a clutch because two eggs of the same color are more visible than are two eggs of different colors, providing they both reasonably approximate at least some of the substrate color.

Clutch Size

Table 12. gives the numbers of eggs in clutches and their outcome. There were twice as many two-egg clutches as there were one-egg clutches, if by clutch is meant the total number of eggs in a nest at one time, incubated together, and hatching either synchronously or sequentially. However, many of the one-egg clutches were not a complete egg-cycle but were part of a two-egg clutch (one lost to flooding, predation, etc.) or were the second egg component of a laying-cycle for which the first egg had been lost. There were only seven one-egg clutches that were known to represent complete laying cycles.

Olson and Marshall (1952) reported approximate equal numbers of one-egg and two-egg clutches. The difference between our findings may be the result of greater loss of one egg of a laying cycle or a higher population of one-egg laying cycles among loons in their study area.

Table 12. Common Loon clutches from north central Minnesota.

Clutch Size	N	Hatching Results Success	Failure
1	18	5	13
2	32	19	13
3*	1	collected	

* It was not verified that the three-egg clutch was from the same female. Pesticide residue analysis showed that two eggs were nearly alike in all residue amounts tested, and one was dissimilar in all results.

Hatching success for two-egg clutches was significantly greater than for one-egg clutches (Chi-square test $X^2 = 4.607$, $P < .05$). Olson and Marshall (1952) also found two-egg clutches to be more successful and concluded that the critical period between the laying of the first and second eggs permitted more ready desertion. That no doubt does provide an explanation for some of the single egg loss. However, there are also other possible causes for the differential success rate.

Predator tests which I conducted indicated that mammalian predation at a known site increased after the first predation. A test nest was visited and the egg taken each time a fresh one was placed in the track trap after the nest had been located in one series of tests; and in the other, the frequency of predation increased with the duration of the testing period. Some eggs recorded in this study or by other investigators as one-egg clutches may have been part of a two-egg laying cycle. Both eggs may have been laid in the same nest, either as a two-egg clutch or the second may have been laid after the first had been lost. If the first egg had been lost through predation, there is an increased probability the second would be lost to the same predator.

If single egg laying cycles are attributed to younger birds (speculation) and if the probability of successful hatching increases with experience as it has been shown to for some other birds (Coulson, 1966; Lehrman and Wortis, 1967), then inexperience and not the one-egg clutch per se would account for the lessened hatching success.

Eggshell Removal

Eggshell fragments were usually found in nests from which chicks hatched. Sometimes most of one shell and parts of another were there; at other times, only small chips were in the nests. Eggshell removal was seen on Mary Lake in 1971. One adult, which had been off the nest, returned, turned the egg, and sat. It then stood over the egg that had been broken when it sat on it, and returned to the water. From the water, it reached into the nest, took the eggshell in its bill, swam about 15 feet out from the nest, was joined by the mate, and together they billed and broke the shell and dropped it in the lake. The entire contents of the egg were left in the nest.

A crow and I raced for the egg; the crow won, but I did secure sufficient material for pesticide analyses, and did retrieve the shell from the bottom of the lake to measure its thickness. These results are given in the Toxic Chemical section, but were not significantly different than levels and thickness found in other loon eggs from the study area.

Eggshell removal has been described for Red-throated Loons (Keith, 1937; Nethersole-Thompson, 1942; Hall and

Arnold, 1966; and VonBraun, et al, 1968); and Sjölander, (1968) reported on removal by Arctic Loons. Nethersole-Thompson (1942) mentions that Lack and Dunlop said eggshells are not removed by Common Loons. Hall and Arnold (1966) noted that Red-throated Loon chicks remained in the nest for several days after hatching. Common Loons in my study area cared for the first chick both on and off the nest until the second was hatched, then both chicks left with the adults and did not return to the nest. This may explain why although loons do remove eggshells, single eggshells are often left on the nest. While it would be advantageous for the birds to remove the first eggshell, there would be no selective advantage to removing the second one.

Egg-laying

Description

Anyone who has seen a loon egg is apt to remember it first for its size. Any female loon who has ever laid an egg no doubt remembers it for the same reason.

On 14 May 1971 I was lucky enough to watch the female loon on Lost Lake lay an egg. The following description is from my field notes.

13:05-13:27	Female on nest, building.
13:27-14:02	Female sitting, no building.

14:02	Male approached nest, up to female, then swam slowly back and forth in front of her. He left.
14:02-14:08	Female raised body up and down 19 times. First 17 averaged 5 seconds each. 18th: 12 seconds 19th: 16 seconds Egg laid. Female stayed semi-upright, gave a tail-shake, moved tail up and down more than 15 times. She gripped the side of the nest with her toes and panted.
14:08-14:25	Female continued to grip side of nest with toes, panted, periodically opened and closed her eyes.
14:28	Female stopped panting.
14:29	Female pecked at vegetation, slid off nest, left. She swam away from the nest and was met by the male. They both engaged in Head Turning. The female dove, came up in front of the male, and swam past him using Crouch Swimming posture.

14:33	Male swam to nest, looked at it, returned to female, swam back to nest, returned to female, swam again to nest and climbed up on it.
14:34	Male stood on nest, rolled the egg over his feet, then rolled it forward, and repeated four times. He sat on the egg, pulled vegetation, and arranged nest material.
14:36	The female swam to the nest, dove in front of it.
14:39-14:42	Male moved to one side, off the egg, and continued to build. Female climbed on nest, both male and female engaged in nest-building.

Egg-laying appears to be divided into three parts. The first 35 minutes may be the time the egg is in the cloaca; six minutes, active voluntary expelling of the egg; the last 21 minutes the recovery period. Behavior during the first two divisions may be explained solely from a physiological standpoint; during the third, conditioning for the forthcoming incubation may act jointly with a physical recovery to compound the significance of this period.

These observations are quite different from those of Drury (1961) who watched a Red-throated Loon lay the first egg of a clutch in 15 minutes with "...no noticeable movement."

Time of Day

Very little is in the literature on the time of day of egg-laying. The exception is Drury's (1961) account of egg-laying by a Red-throated Loon from 16:40 to 16:55. I have data from three individuals, summarized here:

14:08	First egg of a first clutch.
13:08-17:15	Second egg of a first clutch.
16:30-07:15	First egg of 3rd clutch

The last example does permit considerable leeway, but indications as gathered from these are that loons lay their eggs in the afternoon. Further observations may show that egg-laying is quite variable.

Time of Year

Egg-laying began as early as 7 May and continued until the end of June. The latest I recorded was in 1974 when a replacement clutch of one egg was laid on June 28. Bee (1957) tells of collecting an incubating Yellow-billed Loon with ova as large as 6 mm. and 8 mm.., and of an Arctic Loon early in July with ova of 8 mm. Apparent readiness to nest throughout an extended period permits the renestings which accounted for the late June egg-laying mentioned above.

About half of all first nests were begun during the third week in May. Commencement of egg-laying did not show a fixed relationship to ice break-up. Most lakes in my study areas opened on the same day and loons arrived just a few days apart, yet initiation of egg-laying ranged from one to 4½ weeks after the birds' spring arrival. Egg-laying did not show any more synchrony on any single lake from year to year than in the same year from lake to lake. Nest-building to egg-laying time was but a few days in most cases, and one egg was found on 15 May 1972 with no nest. Caple (pers. comm.) recorded egg-laying by a loon that had been building its nest for more than a month.

There are many records in the literature citing the interval between spring arrival and nesting. Olson and Marshall (1952) found a minimum of two weeks in northern Minnesota; Sjölander and Ågren (1972) noted five days in Iceland; Drury (1961), one to two weeks for Red-throated Loons on Bylot Island; and Parmelee, et al, (1967) about one week for Yellow-billed and Arctic Loons on s.e. Victoria Island. Lehtonen (1970) found that 90% of all nesting of Arctic Loons in Finland began in May from five to 20 days after arrival on the breeding lakes. Late lake openings and early freeze-up in the Arctic and subarctic would select for rapid onset of nesting, but the same brevity of time between arrival and egg-laying did not occur in north central Minnesota where most lakes are open for nearly seven months every year.

Replacement Clutches

Loons are capable of re-nesting several times if nests are destroyed by predators or weather. Some laid four clutches, but no more than three laying cycles were recorded. Olson and Marshall (1952) also found three nest attempts in several instances.

Egg-laying was not immediately resumed upon loss of a clutch, although readiness to nest has been shown through prolonged follicular development, even during incubation (Bee, 1957). In four cases I was able to determine the interval between loss of a clutch and re-laying of another. In two cases there was a 12-day interval; in one, a 14-day span, and for the fourth, an 11-13 day interval. The 11-13 day interval occurred between a second and a third cycle; the others were between a first and a second. There were many instances of a lost nest after the first egg of a cycle had been laid; renesting and laying of the second egg occurred two days later. The usual laying interval of two days was retained for separate clutches that represented portions of a single laying-cycle.

None of the loons continued to lay at two-day intervals following the sequential loss of both eggs. This is longer than the intervals recorded by Olson and Marshall (1952), who found renesting occurred from five days to two weeks after a nest loss, with the average about 10 days.

Incubation

Study Methods

Times of observations were determined by day length and presence or absence of fog caused by mist rising from the lake. Two schedules were designed. Lost Lake loons were observed for 16-hour periods on two consecutive days every five days beginning with the third day after laying of the second egg (eight days of observations). Mary Lake loons were observed for 20 morning hours six days during the first two seeks of incubation, and for six-hour periods for 10 days during the last two weeks. Time during the last two weeks was rotated every third day: 04:00 to 10:00; 10:00 to 16:00, and 16:00 to 22:00. Early and late shifts were shorter as the study progressed as the day length shortened and very early and very late observations became impossible. Some mornings dense fog did not permit visibility as early as the scheduled observation period began.

The total time of monitoring was 219 hours and 26 minutes. Although covering only a short time, data are included because they were collected from an evenly distributed daily time pattern, they included only incubation following laying of both eggs and preceeding hatching, and they should provide a base line on which to formulate more detailed incubation studies.

Observations were made with a 40X spotting scope more than 300 yards from the nest. At no time did I sense the loons were aware of my presence and I believe there was no disturbance to the birds.

Observations of many other pairs of loons included egg-turning, nest relief, incubation during the presence and absence of fishermen, threat by potential predators, rain, storms, black fly infestations, and extreme heat. Quantitative results presented here, such as egg-turning frequency, and incubation constancy, are based solely on the data collected from the two nestings described on page 124. No human disturbances occurred to these two pairs; one was on a lake with no human access; the other nested behind a boundary prohibiting fishing.

Initiation

I watched the initiation of incubation following egg-laying as described on page 119. For the first two hours and 16 minutes the male and female each got on and off the nest nine times. They spent 31.6% on the egg, 11% away from the site, and the rest of the time building and maintaining the nest. It is doubtful that any functional incubation occurred. However, patterns of incubation behavior were used by both adults; egg-turning, nest relief with building activity, and settling on the egg. The flurry of activity by both adults may act to stimulate proper incubation behavior. Johnson and Johnson (1935) found that Red-throated Loons began to incubate with the first egg, but Lehtonen (1970) stated that Arctic Loons began incubation with the second, and that the male didn't begin to assist until 10 to 12 days after laying.

Postures

Incubation postures are shown in Appendix III. Head Tucked was used most of the time and is the same head position loons use when they are Drifting. Head Up was seen when the bird first was alerted to disturbance, such as noise or the arrival of an intruder. If the threat continued or increased, the Hang Over was employed. It is an intention movement to leave the nest, slide into the water, and reappear on the surface some distance from the nest site.

The Sprawl was used during the hottest portions of the day, usually in conjunction with panting and probably is a thermo-regulating posture.

Nest Relief

Ritualized nest relief using the same ordered components each time was not seen. Generally the off bird utilized Bill Dipping and Facing Away. The "mew" call usually was given, and some handling of nest materials occurred (agree, Hall and Arnold, 1966; Sjölander, 1968; Sjölander and Ågren, 1972), but were not essential to a nest exchange.

Although the preceeding describes the usual method of exchanging parental shifts, sometimes both loons were on the nest together before the bird which had just completed a bout left; and at other times, both adults met in the water, engaged in mutual Bill Dipping and Facing Away before the exchange occurred. Submissive posturing, such as Facing Away or Bill Dipping appeared to be a necessary component to a successful nest exchange.

Egg-turning

I always saw egg-turning done with the bill (Appendix III.) and Drury (1961) and Lehtonen (1970) report the same. However, Johnson and Johnson (1935) indicated the bird first attempted turning with the feet, and if that failed, used the bill. Frequency of egg-turning decreased and intervals between turnings increased as incubation progressed (Figure 32). The average time between turnings increased from 50 minutes during the first week to just under two hours by the beginning of the last week.

Nest Attentiveness

Nest attentiveness was 99.1% (Figure 33). The most frequent cause for a nest to be left unattended was for territory defense (79.9%). Feeding (5.6%) and nest relief when both adults were off the nest (14.5%) accounted for the remainder of the time neither adult was in attendance. However, they were not far from the

Figure 32. Frequency of egg-turning. Frequency indicates the number of times the eggs were turned within a time period correlated with the state of incubation such as,

$$F= \left[\frac{\text{egg-turnings}}{\text{minutes obs'd}} \right] \times 10^4$$

Intervals indicate the amount of time in minutes between egg-turnings.

There was a significant positive correlation between time intervals and the state of incubation, $P<.01$, and a significant negative correlation between turning frequency and state of incubation $P<.001$.

● Frequency

✱ Intervals

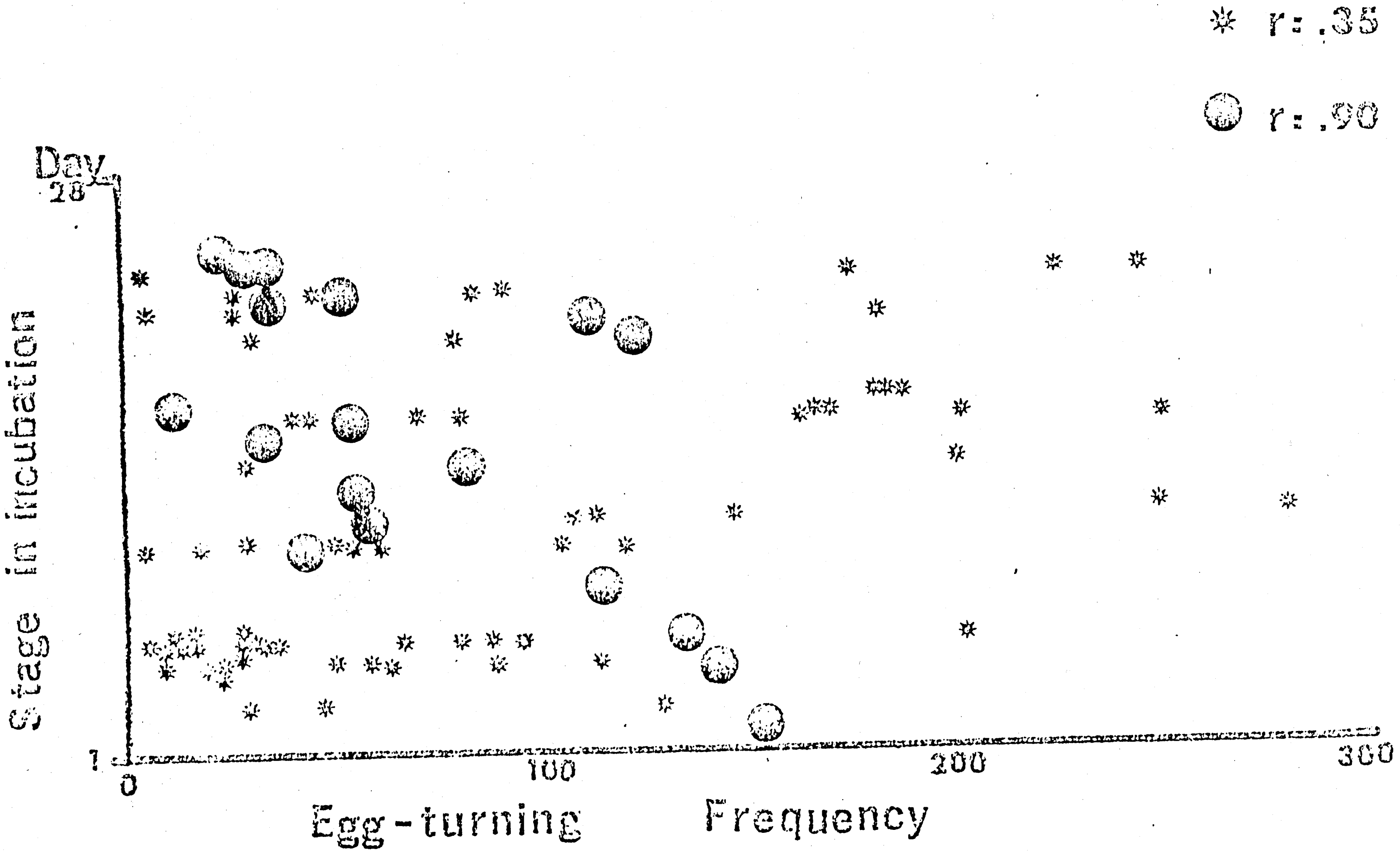
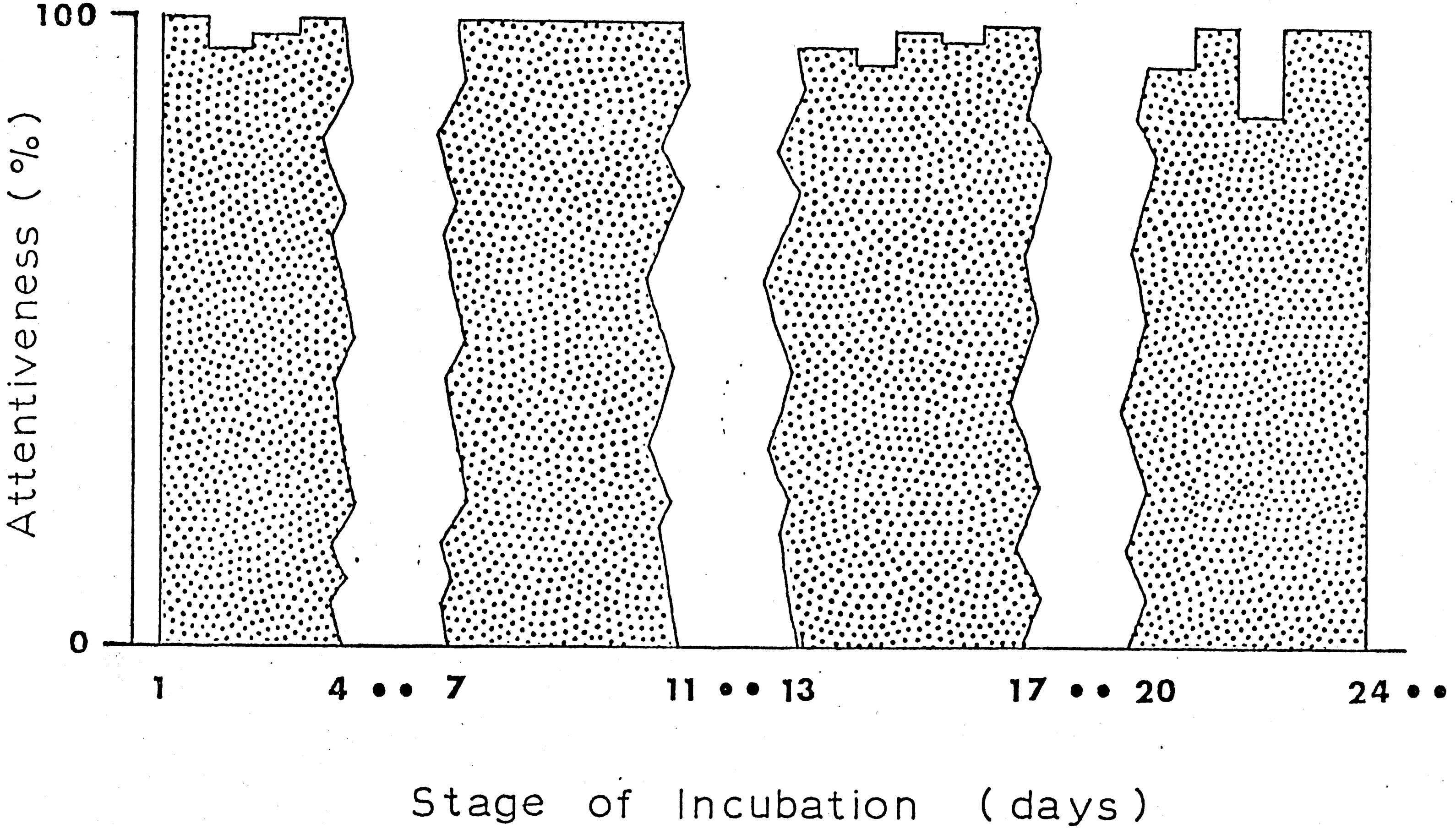

✲ r: .35
● r: .90
Day
28
1
Stage in incubation
0
100
200
300
Egg-turning Frequency

Figure 33. Nest attentiveness.


100
0
Attentiveness (%)
1
4 •• 7
11 •• 13
17 •• 20
24 ••
Stage of Incubation (days)

nest in the latter two cases, and unoccupied would be a better term than unattended.

Observations of lakes with recreational use indicated that loons left their nests when boats or canoes approached the nest site and many pairs didn't return to the nest for more than an hour after a disturbance. The two lakes being monitored were not subjected to human intrusion during the time the quantitative data were being recorded, so those factors cannot be included in this account of nest attentiveness.

Loon incubation should be monitored in situations where human disturbance is a factor so that data may be secured for comparison with the 99.1% attentiveness in undisturbed situations.

Division of Parental Duties

Both sexes incubate. Bisexual incubation is the more primitive strategy and is usually coupled with a simple nest (White and Kinney 1974). Intuitive as this may seem, loons were earlier reported to have a unisexual mode of incubation whereby only the female incubated (Van Oordt and Huxley, 1922). Later reports noted that both sexes incubated (all loon species, Drury, 1961; Sjölander, 1968; Lehtonen, 1970; Sjölander, in press). Lehtonen (1970) and Sjölander (1968) noted that female Arctic Loons did the major portion of incubating; and Common Loons have also been reported as having a female dominated incubation strategy (Yeates, 1950; Olson and

Marshall, 1952; Barr, pers. comm.). On the two lakes which I monitored, incubation was divided fairly evenly between males and females (Table 13.) Observations were not made for entire 24-hour periods, and bouts were recorded as complete (bounded by two nest exchanges), or incomplete (only one nest exchange occurring).

Females were usually on the nest early in the morning and at dusk (75% of the time). The same sex may not always incubate during the night, or both may, but it appears that females do most of the crepuscular incubating. Incomplete bouts would thus give a more accurate assessment of incubation sharing by sex, although the higher proportion of male incubation for complete bouts suggests that males do most of the diurnal incubating.

The duration of each sitting spell was longer for males than for females during the first week, but time was divided between the two quite evenly later (Table 14.). The times of day at which shifts occurred did not follow a daily pattern (Figure 34), neither was there a pattern as to which sex sat at what time. Taylor (1974) stated he found the shifts so regular he could "almost set a watch to their schedule" but he does not present evidence to support this. This apparent discrepancy may simply be due to individual differences.

Table 14. Bout length of incubating Common Loons.

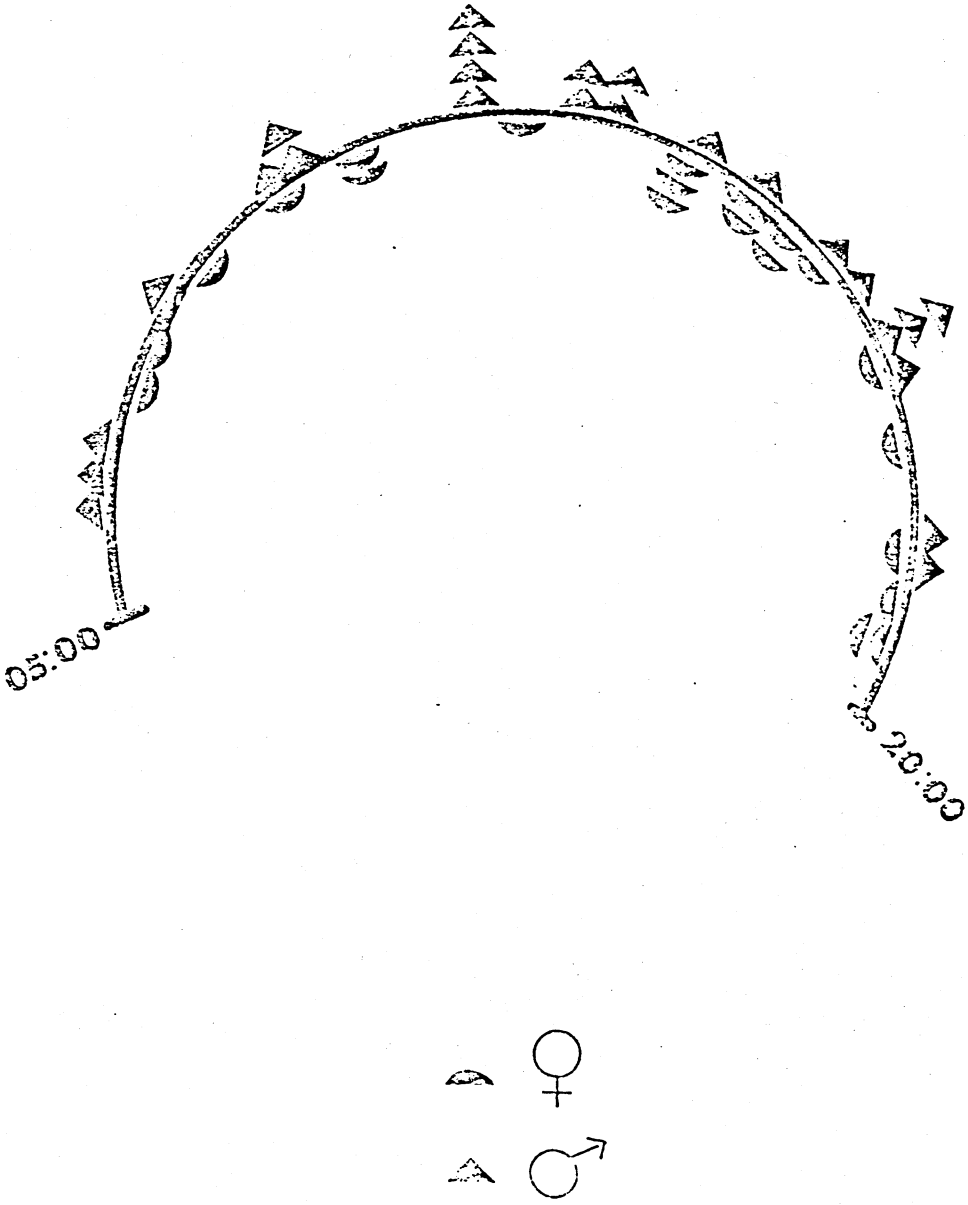
Stage in Incubation	Bout Length ($\bar{X}$ in minutes)	
	Female	Male
First week	114.5	173.0
Second week	96.0	94.8
Third week	120.8	137.8
Overall average	112.9	133.2

Figure 34. Incubation time partitionaing by males and females.

Each symbol represents one nest exchange and the sex of the loon beginning its shift. The arc corresponds to the time of day.

▲ Male begins shift

◠ Female begins shift


05:00
20:00
♀
♂

Beer (1972) has pointed out that kittiwake schedules differ from pair to pair, and the same variability may well exist among loons.

Nest Defense

Nests were defended against raccoons and crows, but no defense was directed to Great Blue Herons, deer, or beavers that were near the nest. Defense posture on the nest is the same as used in the water when defending young (see Appendix III, Penguin Dance.). The off bird was also seen defending the nest. During two incidents involving raccoons, the mate not on the nest ran across the water and up on land to chase away the intruders. I never saw a loon actively defend its nest against humans. Jakobs and Jakobs (1974) described a nest defense with Splash Dives engaged in by a Red-throated Loon and Common Loons also may go in the water away from the nest and present SplashDives to humans who approach the nest, especially if the eggs are close to hatching. Van Oordt and Huxley (1922) described an overt attack on humans directed from the nest by a Red-throated Loon but I have not encountered this behavior by Common Loons.

Length of Incubation

Incubation time varied. In general eggs were laid two days apart and hatched one day apart (agree, Olson and Marshall, 1952), although Yonge (pers. comm.) reports that loons he studied laid their eggs at various times, some as far apart as three days, yet they hatched one day apart. They may sometimes hatch simultaneously (Van der Heide, Yonge, Barr, pers. comm.) but I did not record it occur during this study.

Incubation durations that I could positively account for were for 26, 27, 26 and 31 days. Other incubation times for loons have been reported as 28 and 29 days (Common Loons, Olson and Marshall 1952; Bent, 1919; Sjölander and Ågren, 1972; Taylor, 1974); 27 days for Arctic Loons (Sjölander, 1968); and 26, 29, and 38-40 days for Red-throated Loons (Johnson and Johnson 1935; Keith, 1937; Drury, 1961).

Discussion

Nest attentiveness was nearly constant (99.1%). Drent (1970) concluded that the primary adaptation made by Herring Gulls to reduce predation is almost continuous attentiveness (97.6%). Island nesting and the cryptic coloration of nest and eggs are anti-predator strategies. So is high nest attentiveness which not only functions as a predator deterent, but assures that an adult will be in attendance to actively defend the nest.

The open nest site suggests that the incubating bird might absorb much heat from the sun, and panting and the Sprawl posture were commonly engaged in during hot weather. However, shading or additional wetting of the eggs was not seen.

Black flies are numerous during May, so numerous in fact that one method I used to locate loon nests both active and under construction was to look for hovering swarms of black flies. Black flies were collected from eight lakes and all were identified as <u>Simulium euryadminiculum</u>, a Simulid known to be host specific to the Common Loon (Lowther and Wood, 1964). Their time of emergence coincides with loon incubation and causes irritation as noted by the frequent Head Rubs and Head Shakes of the sitting bird. On 26 May 1971 I timed Head Shakes at 12:00, 14:00, and 17:30 of an incubating loon whose head could be seen to be crawling with black flies.

Head Shakes averaged one every 9.6 seconds. The bird did not leave the nest, and sat for more than nine hours.

Egg-turning frequency was greater during the first week of incubation than at any later time, although some short intervals also occurred into the fourth week. Bout length did not significantly lengthen as incubation proceeded, and although variable (the range was 25 minutes to more than six hours), the overall average was two hours, four minutes. Bout lengths and total incubation were longer for males than females. Nocturnal incubation could not be accounted for. More times females than males were on the nest when observations began early in the morning (70%:30%). However, when observations ended late at night (ca. 22:00), males were found to be on the nest 50% of the time. More data are needed to verify that there is no pattern of sexual regularity during the night, but those presented here indicate that males do most of the incubating during the day and both incubate at night.

Partitioning of incubation by sexes was different on my study lakes than other authors have reported. One obvious explanation is potential inaccuracy in sexing the birds. But there is another possibility. Other workers have studied loons on large lakes with many pairs and many territories. Territorial defense is primarily the responsibility of the male. If time is needed to defend boundaries, males have less time for nesting activities and females will be left with the major portion of the incubation duties. Early in the nesting period territorial disputes should arise more frequently, before boundaries are firmly established. This would account for the reports by others that the males' role is reduced early in incubation but increases as incubation proceeds.

My study lakes were small and intrusions were few. No intra-lake territorial boundaries existed; each pair claimed the entire lake for its territory. With less time required for territorial defense, more time could be spent by males in sharing incubation duties.

The Young

Success and Survival

Most clutches consisted of two eggs (69.4%) and these produced most of the chicks (81.8%) and fledged most of the juveniles (80.0%). In my study areas, more than half of the breeding pairs hatched at least one chick and almost all fledged (Table 15.). Reports from PLW for 309 broods indicated a fledging rate of 90.3%. The possibility exists that not all chicks were seen immediately after hatching so mortality of some very young chicks could have escaped detection, but fledging success in my study areas showed a similar survival rate (94.4%). Although I could have missed some early chick

Table 15. Hatching and fledging success.

HATCHING

Hatched Eggs	Pairs with Chicks	Unsuccessful Pairs
41.0%	57.7%	42.3%

Hatching Success:Clutch Size

	One-Egg Clutch			Two-Egg Clutch			
	0:1	1:1	1:unk.	0:2	1:2*	2:2	0:unk.
N	9	6	4	18	5	11	3

*One young collected.

FLEDGING

Fledging Success:Chicks in Brood

	One-Egg Clutch		Two-Egg Clutch		
	0:1	1:1	0:2	1:2	2:2
N	1	13	0	1	10

Fledged Young:Breeding Pair	Fledged:Hatched Chicks
0.77	94.4%

mortality too, the likelihood of that happening was reduced because nests had been monitored and clutch size known prior to hatching. It appears that fledging success in Minnesota may well be around 90%. Brood size from my study areas averaged 1.4 young per successful pair, and from the much larger sampling of PLW it was 1.53 (N=338 broods, Table 16.).

Sixty-six PLW lakes were monitored from two to three consecutive years and were used to assess whether there was an increase, decrease, or no change in reproductive success from year to year on the same lakes. Table 17. indicates there was no overall shift. Hatching success was close to 50% and nearly all hatched chicks fledged giving a fledging to breeding pair ratio of 0.77.

The critical time for young loons may be their first winter. From 1970 to 1973 we banded 9 juveniles, three of which were reported as mortalities during their first winter. None have been recovered as older birds. It is too early to report on four that were banded in 1974. Actual first winter loss may be much higher than reported numbers indicate because although loons are large, readily visible, and likely to be reported if found washed up on beaches, if they were shot, as many still are, it is questionable if they would be reported as readily as game birds because of their protected status.

Table 16. Brood size of Common Loons.

Location	Brood Size One Chick	Two Chicks	Three Chicks
My study areas	14 (58.3%)	10 (41.7%)	0
PLW reports	167 (49.4%)	165 (48.8%)	6 (1.8%)

Table 17. Reproductive success for lakes monitored from two to four years.

	Number	Percent
Increase	22	39.3%
Decrease	20	35.7%
No Change	14	25.0%

N = 66

The banding data present a small sample size from which to judge first year mortality, but because one-third of the banded birds were recovered (one shot, two died of natural causes) it prompts me to speculate that first winter mortality may be high.

<u>Weights and Measurements</u>

Some weights and measurements were taken (Table 18.) of young loons. This comprised a very small part of the study, but is reported so that they may be used for comparison. More complete data are given in Barr (1973).

"Dracula" was a hand-raised chick which died at 16 days; "Jesus" was its sibling and was raised in the wild by its parents. A comparison between the two indicated weights and measurements of captive young may be disimilar to those of wild individuals. It is possible this can be accounted for by individual variability, but other siblings did not show the same degree of variability (see Freeman and Nancy, Port and Starboard, Lost Lake #1 and #2 from 1974, and the 2 young from Baumgartner, 1971).

Young can be roughly aged from afar by the following formula:

Less than 1/3 size of adult: less than 10 days
1/3 to 2/3 size of adult: 10 days to 3 weeks
2/3 to full size: 3 weeks to fledging

Table 18. Weights and measurements of young Common Loons.

Age	Weight	Culmen (mm.)	Tarsus (mm.)	Skull (mm.)	Total	Longest Primary	Code or Status
0	—	13.2	30.6	20.7	143.5 mm.		Baumgartner 1970 1st chick
0	77 gms.				145.5 mm.		Big Rice 1970 1st in clutch
1	85.9 gms.	10.3	27.5	19.0			Dracula
1	79 gms.	11.5	21.8	20.0	181 mm.		Deming 1974
1	3.5 oz.						Lost Lake 1974 #1
1	86 gms.	14.2	30.9		7¼"		Lost Lake 1974 #2
2	95 gms.	14.2	35.1		7⅝"		Lost Lake 1974 #1
2	87 gms.	13.2		21.0	185 mm.		Deming 1974
3	98.9 gms.	11.9	29.5	20.0	190 mm.		Dracula
3	114 gms.	13.7	31.5	21.9	194 mm.		Deming 1974
4	124 gms.	15.5	31.4	22.8	204 mm.		Deming 1974
5	119.4 gms.						Dracula
6		14.0	32.0	20.5	215 mm.		Dracula
5–8	116.1 gms.				215 mm.		Gimmie
8	179.3 gms.	16.3	33.5	21.9	230 mm.		Dracula
11	223.3 gms.						Dracula
12		17.0	34.0	23.4	260 mm.		Dracula
13	9 oz. (255 gms.)	21.1	39.6		292 mm.		from Strettons
15–19	2# 0 oz.	26.1	54.0	30.1	15"		Baumgartner 1971
15–19	1# 9 oz.	25.5	53.5	30.4	14.5"		Baumgartner 1971
16	221.3 gms.						Dracula
16	589.6 gms.	27.3	43.1	28.0	385 mm.		Jesus
6 weeks 6 days		64.0	86.0		26⅝"	4¾"	Starboard
7 weeks 1 day		66.5	92.0			5¼"	Port
7 weeks 3 days	6# 13 oz.	63.2	89.9	43.8	27½"	174 mm.	Lost Lake 1972
7 weeks 6 days	5# 8 oz.	58.5	82.0	43.6	27½"	174 mm.	Deming 1974
8 weeks 0 days	6# 14 oz.	61.1	86.9	40.0	28½"		Jesus
9 weeks 3 days		61.9	90.0	40.0		6¼"	Baumgartner 1970
2 months	6# 1 oz.	63.0	87.1	44.3	730 mm.	210 mm.	Susie
2 months	5# 10 oz.	58.0	82.0	41.2		189.3 mm.	Nancy
2 months	6# 12 oz.	60.0	89.3	43.3		212.5 mm.	Freeman
3 months	5# 8 oz.	59.2	82.3	39.9	27¾"		Atherton

Behavior of the Chicks

Chicks usually remained on the nest for a day after hatching. One chick was seen leaving its nest only 36 hours after I had checked and found the egg unpipped. Another chick hatched 14 hours after pipping and left the nest 18 hours later. Sjölander and Ågren (1972) observed one young leaving 20 hours after hatching.

A pipped egg was collected and opened by hand. The chick had an attached yolk sac 3 cm. X 1 cm. which was mostly absorbed within four hours, and completely so within six hours. The chick was dry at that time, and able to swim within 12 hours of being hatched.

Chicks ate nest vegetation prior to leaving the nest. Three chicks were seen eating nest material; and the hand-reared bird eagerly ate nest material presented to it shortly after hatching, but refused to eat fish until 40 hours old.

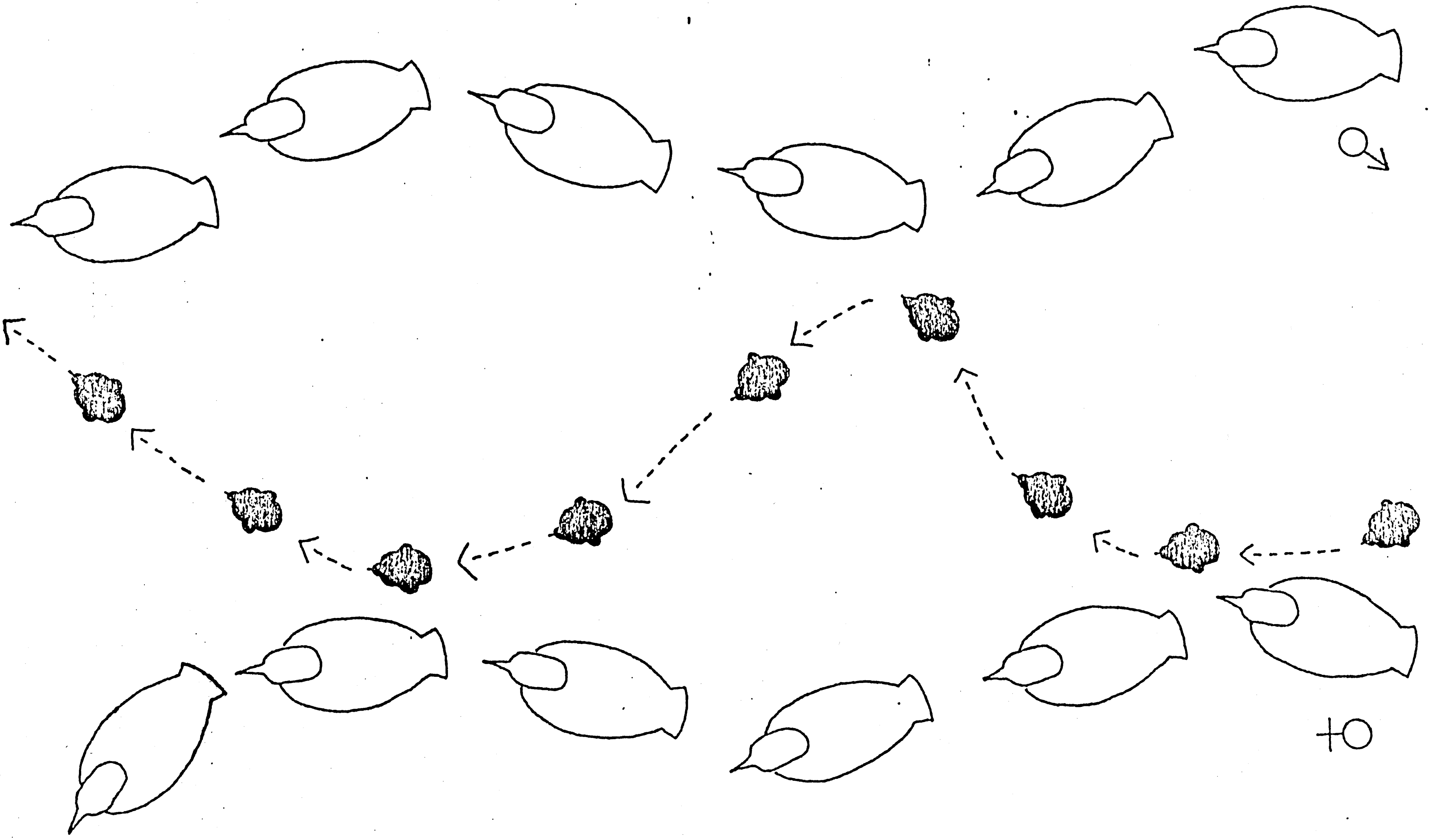
Chicks still on the nest spent most of their time being brooded or crawling over, under, and around the sitting adult. They crawled under the wing and over the back using the same technique they did later when riding on the adults' backs. It may be that post-hatching time spent on the nest provides opportunity to practise techniques for back-riding.

Sometimes the chicks left the nest initially if they were disturbed by people. But twice I was able to record nest-leaving under undisturbed conditions. In one case, a single chick was encouraged to leave the nest by both adults. The parents swam to and away from the nest and gave soft "mew" calls. When the peeping chick slid off the nest, it swam between the adults for 36 minutes before they permitted it to approach close enough to ride on the back of one (Figure 35).

The other nest-leaving episode that I recorded was of the first hatched chick from a brood of two. It slid off the nest, into the water, and was immediately taken on the back of a nearby adult while the other parent remained on the nest. The chick was dropped off seven minutes later and was left alone for 51 minutes, while the adult that had led it off defended its territory against two intruders. The chick did not return to the nest, but remained where it had been left until the parent returned. During the day, it left and returned to the nest four times. At 21:10, it, together with its sibling, left the nest, went to one of the adults, climbed on its back, left for the other side of the lake, and never returned to the nest site. No attempt was made by either adult to encourage following or to prevent back-riding.

Chicks left both in the morning and evening. Although I never saw any leaving during midday, it is possible they did so. When I checked hatched and hatch-chicks that were still in the nest, and the adult on the

Figure 35. Zig-zag following. Chick following the adults after being taken off the nest, Mary Lake, 18 June 1970.



nest quickly left, the chicks usually remained behind.

At nest-leaving time chicks could swim and make short dives of two to three seconds. By the time they were one week old, they exhibited all comfort movements. Initially, preening was done just with the bill. By the fourth day, chicks dipped their bills in the water before preening, and by the sixth day, they preened from the uropygial gland. Belly Preening was not observed in chicks younger than six days. When younger, they preened frequently under the wings, and during vigorous bouts, turned over on their backs. Perhaps Belly Preening originates from this rolling movement. Preening sequences ended with a Wing Flap, even though chicks had no remiges to be straightened.

Parental Care

Feeding

Parental feeding involved presenting the food item to the young in the adult's bill and the chick reaching for and taking it. Chicks begged by pecking at the base of the parent's bill, but did not gape, and the adult did not place food in the chick's mouth. If food was not taken on first presentation, the parent either presented it again or ate it itself. Adults fed their chicks small fish and crayfish and the young secured their own vegetation and grit. It seems likely this is related to the comparative ease of securing vegetation and gravel -- neither of which swim away.

Chicks began to secure some of their own fish when they were one to two weeks old. The hand-raised young began to secure some of its own fish at six days. Barr (1973) in a detailed study of the ontogeny of feeding found that although some feeding was done by very young chicks, capture efficiency was still only 3% for three-week old chicks.

When a chick dropped the fish being offered by the adult the adult retrieved and presented it again. Later, (Barr, 1973 determined the age was three weeks), dropping was reversed; the adult dropped the fish in front of the young and the young retrieved it.

Feedings on Mary Lake were recorded in 1971 (Table 19.). A feeding period was assigned as the time when no further presentations were made and both parents were engaged in other activities. The greatest increase in parental feeding intensity occurred in the first two weeks. Parental feedings continued until fledging. By the time the young were six to seven weeks old, the adults left the territory for longer and longer intervals, and eventually were with them only during the early part of the morning and again in the evening beginning about 18:00 to 20:00. Barr (1973) found the critical time for transition to independent foraging was eight weeks, which was later than I noted for the juveniles in my study areas.

During the nights spent shining to capture young during August (more than 200 hours), we found an adult present only once on a small lake, but on larger lakes we frequently encountered adults. Juveniles continued to beg when adults were present, and were sometimes fed by them until they left their natal lakes.

Table 19. Feedings by Mary Lake pair to a single young.

Age of Young In Days	Time Period (minutes)	Total Number of Fish Fed	Number Fed by Male	Number Fed by Female	Number Fed by Unknown	Feedings Per Minute
4	30	2	0	2		.067
6	15	4	0	4		.267
7	39	17	4	13		.436
11	53	16	7	9		.302
13	72	42	13	23	6	.583
18	36	3	1	2		.083
28	30	10	5	4		.333
40	11	17	4	5		.550

Back-riding

Chicks were carried on the backs of their parents until they were three weeks old. Both chicks rode on the back of the same parent, or one rode on the back of each adult. They rode both on the back and under the wing with the head facing to the front. Back-riding served several purposes. Large fish and turtles are potential predators on small chicks and riding was a safeguard against underwater attack from them. It permitted continued mobility of the adults while caring for the young, while at the same time prevented fatigue of the chicks.

It may also be a method of brooding. The area under the wing of an adult has only a few feathers, some exposed skin, and is a potential warming site. To see whether a chick's body temperature would fall if kept in the water for an extended time, I took temperatures of a chick at one day and four days of age with a telethermometer (Yellow Springs Instrument Company) by inserting a thermistor probe in the cloaca. The results are presented in Table 20.

The black down of the chick may act as a super-sun absorber and help maintain the chick's temperature. When placed in the shade, its temperature fell after 10 minutes. The rise of 2°C. can

Table 20. Temperatures of Loon Chick.

Age of Chick	Water Temperature	Chick's Temperature	Time Between Readings	Placement of Chick
1 day	25°C.	37°C.	initial	sun
			5 min.	
			10 min.	
			40 min.	
		32°C.	10 min.	shade
		34°C.	20 min.	
		37°C.	5 min.	sun
4 days	24°C.	33.5°C.	initial	shade
		35.5°C.	5 min.	
		34.0°C.	15 min.	
			20 min.	
		36.5°C.	2 min.	brooded

The chick was kept in the water, surrounded by a net so it could not escape and return to the adults. Brooded meant I held the chick next to my skin which was 34°C.

Temperature of adult loons has been reported as 39°C. (Dawson and Hudson, 1970).

be accounted for by behavioral regulation when the chick began shivering. Return to the sun caused an immediate rise to the original temperature. The second test indicated that a fairly even temperature could be maintained in the shade, although it was lower than when the chick was in the sun. The chick's temperature rose rapidly after being brooded against my skin.

I never saw young go to land after nest-leaving. This does not agree with the findings of Sjölander and Ågren (1972) who noted that Common Loons in Iceland frequently went ashore where they were brooded by the adults. They found the same to occur for Yellow-billed Loons, and for Red-throated Loons, as did von Braun _et al._, (1968).

Defense of the Young

Some adults did not defend the young, and left the general area, and in some cases the lake, upon the approach of humans. However, most loons showed strong defense behavior towards humans and other animals, and avoidance behavior with the Hunched posture when crows and Great Blue Herons flew over the chicks. The young dove or gave a Splash Dive and the adult attending the chick gave Splash Dives.

Defense behavior posturing included Penguin Dancing, Surface Rushes, and Splash Dives. The greatest intensity of defensive behavior was given just after hatching, but threat behavior continued until the juveniles ha~~ve~~d fledged. When the young were being defended, they did not ride the adult's back, but were taken to the side of the lake where they remained about 15 to 20 feet offshore in Hunched posture. When older, they were not taken inshore, but they dove and swam to the side by themselves, and both adults remained in the open lake.

Division of Parental Duties

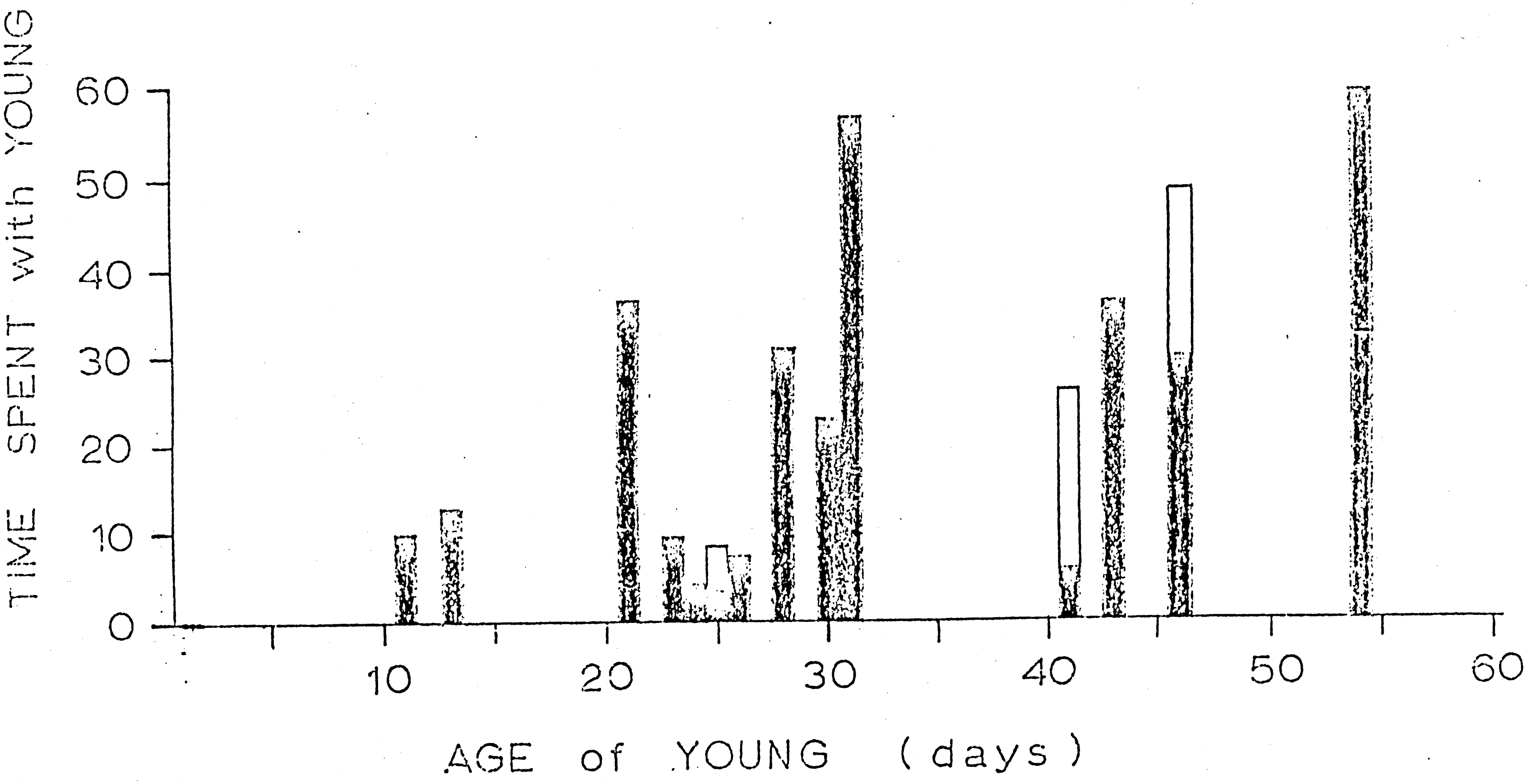
Both sexes share in the care of the young. The female did most of the feeding when the chick was young, but later when it was several weeks old, feedings were given primarily by the male. The male spent more time in carrying and otherwise attending the young in all respects except feeding for the first week. Both sexes defended the young although if both parents were in attendance, most of the defending was done by the male. The second adult remained with the chick and went to one side of the lake, while the other remained and gave tremolo calls and threat displays.

Figure 36. shows that when one adult was left alone with the young it was usually the male.

Figure 36. Amount of time spent by each adult alone with the chick, Mary Lake 1971.

■ Male

□ Female


TIME SPENT with YOUNG (%)
60
50
40
30
20
10
0
10
20
30
40
50
60
AGE of YOUNG (days)

Fledglings

Juveniles left their small natal lakes when they were 11 to 13 weeks old. It has been suspected they may move to larger lakes, and my data support this. On Lake Itasca in 1973 I rediscovered a pair of siblings which I had banded and wing-tagged on another lake a month earlier. In 1974 two other marked young were found on Lake Itasca in the fall (Figure 37). Additional evidence comes from survey data of Lake Itasca. In 1973 there were 12 adults but no young during the summer. On 16 September, there were only six adults but 11 young present. The number of young remained nearly constant until they migrated.

In 1974 there were 11 territorial adults and two young. On 1 September one marked young flew to Lake Itasca; by mid-October there were six young on the lake. The age of the young was the major factor which determined when the shift occurred. Although most young changed lakes early in September, there were two late hatches in 1974 from which young did not leave until mid-October when they were 11 and 13 weeks old. Departure dates for 23 young showed their age to be 11-14 weeks, except for the two young raised on Lake Itasca which did not leave until they were more than five months old.

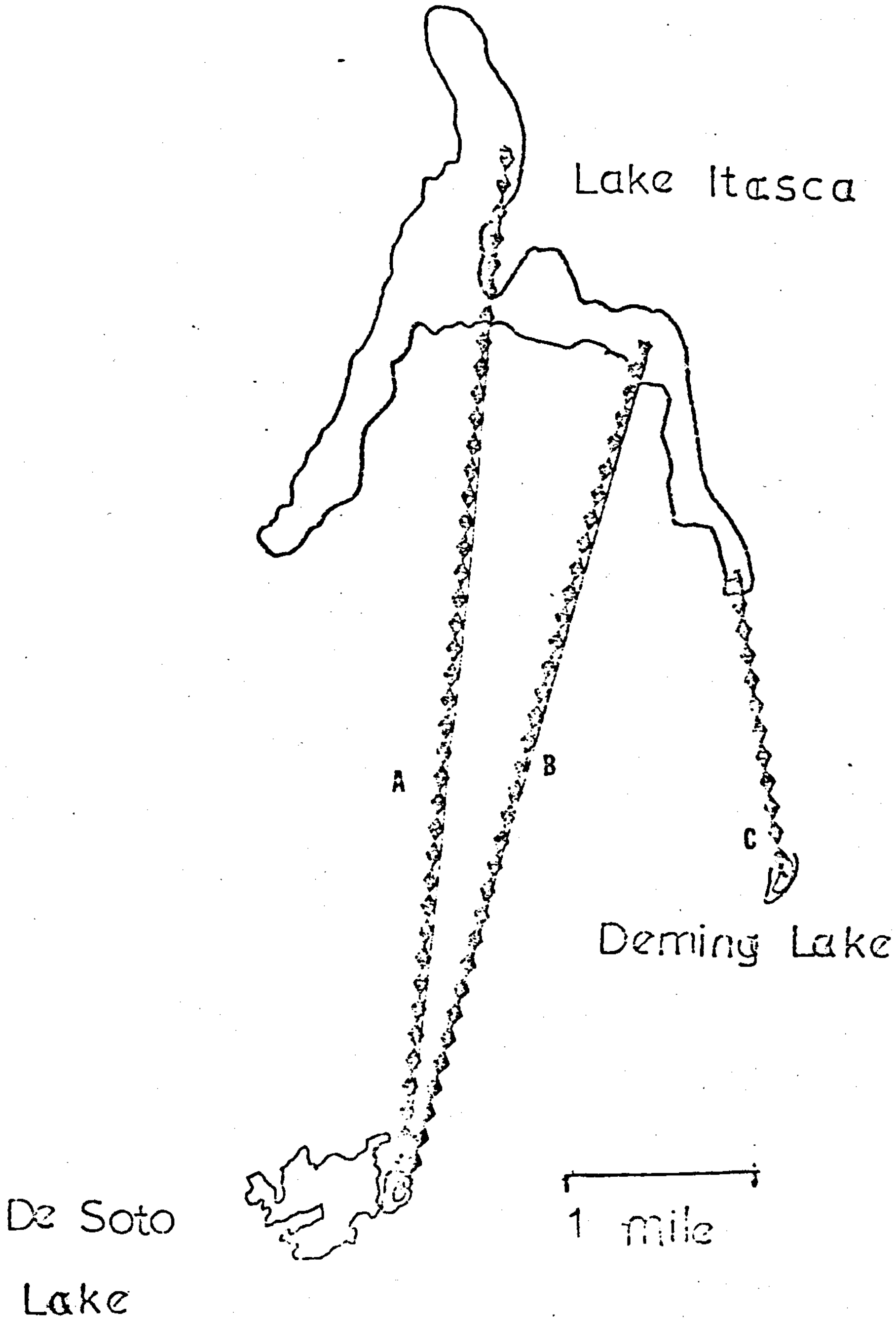
At seven weeks of age some young weighed nearly

Figure 37. Movements of banded young from their natal lakes to Lake Itasca.

A. One juvenile, 1974

B. Two siblings, 1973

C. One juvenile, 1974


Lake Itasca
A
B
C
Deming Lake
De Soto
Lake
1 mile

seven pounds, although there was a range from five to eight pounds. Immatures collected in mid-November and mid-January during several seasons had weights of six to seven pounds, which compares favorably with weights of small adults. Length of the primaries at two months is nearly as great as found in adults, thus flight should be possible. However, I have no data confirming flight prior to 11 weeks.

Activity patterns of young during the two months preceeding migration varied throughout the day. From 07:15 until 10:00 feeding was the major activity. At dawn, young from the center of the lake swam to the shore and fed on vegetation, primarily Scirpus sp., but also on identified submergent vegetation. Small pebbles were taken at the same time and the birds continued by feeding on crayfish. Young fed alone or in small groups of two or six birds from 10 feet to 40 feet offshore in shallow water. After about 09:00 they moved away from the shore and/or from each other and continued feeding on both fish and shellfish. The marked pair of siblings subdivided their bay and were consistently found to spend the balance of most days each in its own portion (Figure 38).

Towards mid-October some flights from one part of the lake to another occurred. Calling began about the same time, first a few soft talking calls, then wails and

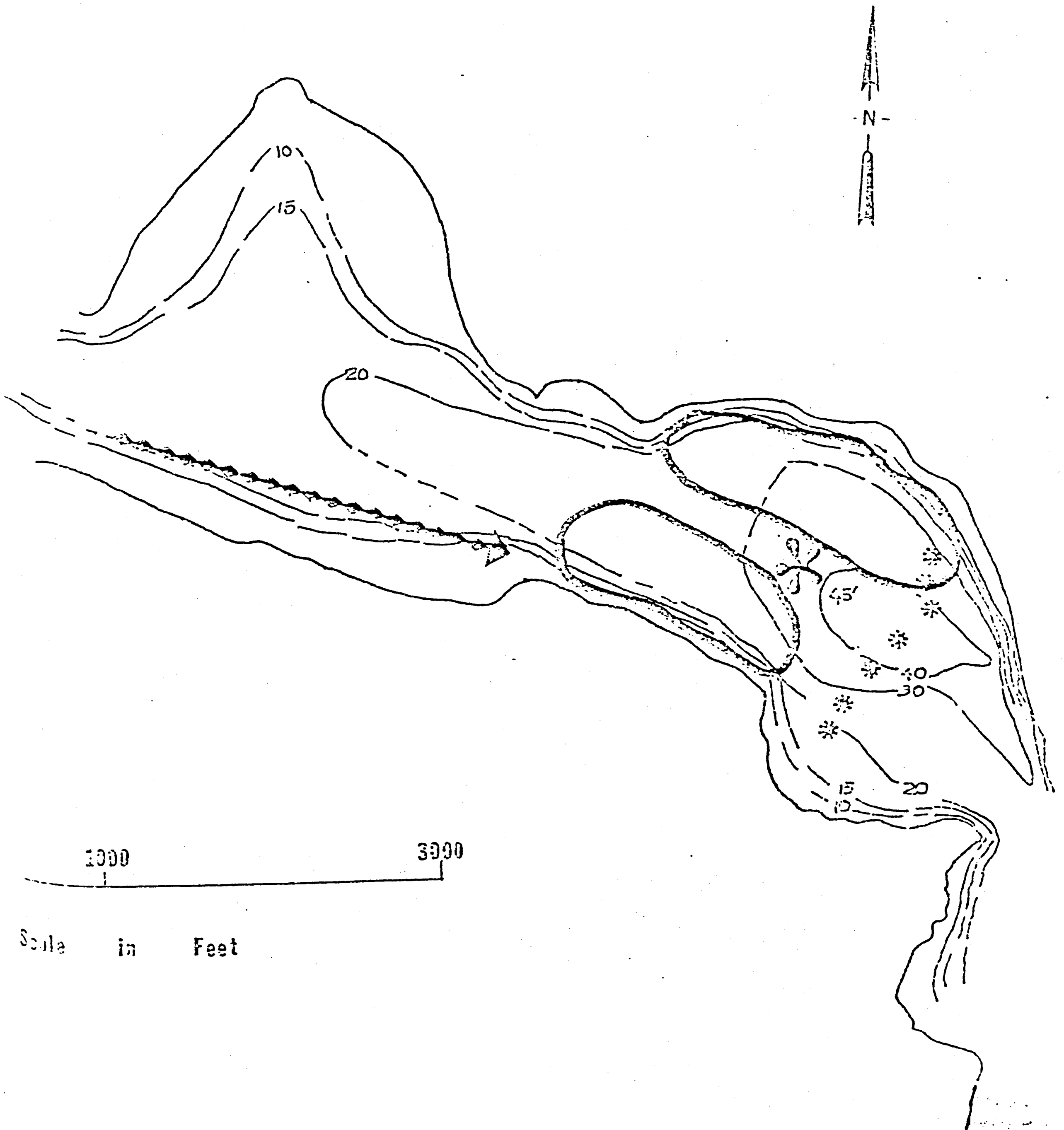
Figure 38. Subdivision of bay by marked siblings and the location of their nightly rafting.

⬭ Subdivision boundaries

✻ Site of nightly rafting

◆◆◆◆➤ Path of migrating juveniles into the bay

✱ ✱ ✱ Line-up of juveniles prior to migration take-off.


N
10
15
20
45'
40
30
20
15
10
1000
3000
Scale in Feet

semiyodels with increasing intensity. Vocalizations occurred from the third week in October until departure.

Morning activities were monitored for 13 days. Midday activity was also observed and on 5 October 1973 all behavior of one marked loon was recorded from 10:10 until 14:00. Both siblings had been observed since dawn that day and the previously described feeding behavior predominated. Midday activity showed 28.3% feeding, 32.6% maintenance, primarily preening, and 39.1% drifting. Feeding increased late in the afternoons, and evening behavior was mainly preening maintenance. By dusk the birds drifted away from shore. The marked young spent each night in the center of the bay (Figure 38).

At times during the early morning two or three young fed together near the shore but did not exhibit coordinated, ritualized, or aggressive behavior. However, young which came in contact later (from about 08:30 to 9:30) did interact with tremolo calling, running, and diving. Young loons chased others from their feeding area with underwater pursuit. The intruder ran, and the sequence ended when the pursued bird left the feeding area of the initial occupant. Ritualized Social Gatherings were never seen among juveniles.

The bay used by the marked pair (Figure 38) had not been occupied by a territorial pair during the summer.

These siblings were monitored for 31 days after they were first sighted and 29 times they were found in the same bay and within the same subdivision.

In 1974 a similar division of feeding areas was seen between members of the sibling pair that hatched on Lake Itasca. They fed together throughout the parental territory initially, but by August had separated into two feeding zones. The separate areas increased in size throughout late summer and fall.

A single loon occupied the southeast bay of Lake Itasca in which the Deming Lake young took up residence in the fall of 1974, but the bay had been unoccupied for several weeks prior to the arrival of the juvenile.

Young-adult encounters were observed on several occasions. Behavior was similar to that described for parent-young interactions. The adults were not marked and their identity was unknown, but it is possible these were meetings between parent and offspring. Juveniles were never seen exhibiting aggressive posturings towards adults.

At 08:00 on 2 November 1973, 13 young were sighted swimming in single file toward the bay (Figure 38). They joined the marked pair, lined up across the bay and faced west. They all took off within eight minutes of each other, flew west, and turned to the north. The barometer which had been 29.70 the day before, registered 30.05 and steady that morning. It snowed and was calm at 07:00 but later the sky was clear and the wind was NNW at 9 mph. There was one adult on the bay when the group of 13 swam in, but it did not fly when the juveniles did. There were scattered individuals after that on Lake Itasca, but neither the marked pair nor other groups of young were seen. The lake froze on 10 November.

Discussion

The day post-hatching spent on the nest serves several functions. Drying of the feathers is essential before chicks can swim. Only nest vegetation is eaten for the first day and access to a different food source is unnecessary.

Zig-zag following appeared to be a technique to promote imprinting. I found that a captive chick did not imprint until between the second and third day, and the added day on the nest allows time for imprinting readiness. Parts of the on again-off again sequence as described for the second example were seen in other families, but the entire process was only recorded once. This method also serves to stimulate the following response. More examples must be recorded before a conclusion can be drawn, but it appears that there may be differences in taking off a single chick, the first of a pair, or the second of a pair. Loons are more vulnerable on the nest than in the water and speed of taking off the second chick is advantageous.

On small lakes where there is but one pair, the need for early parental recognition is not immediately apparent. However, intruder loons land on lakes of all sizes during the time the chicks are small. On larger lakes where there are many loon territories, there is a selective advantage for the chick to recognize and follow its parent. A chick which I presented to a pair with young was not rejected by the adults (although it was by the young, and was pecked, harassed, and deserted). But I also collected a chick two weeks old which was killed when an adult loon, intruder in its parents' territory, impaled it. Recognition-acceptance experiments need to be done to accurately assess the extent to and age at which it occurs, and the functions it confers. Data presented here are sufficient to indicate more work on this would be fruitful.

Fish dropped in front of the young provided them with a partially immobilized prey which they could use to practise capture techniques. Barr (1973) discussed this in far greater detail, and showed that capture techniques develop over several weeks, competence not occurring until the young are nearly 11 weeks old.

A pilot study which I did in 1968 showed that a pair with no young left their territorial lake frequently during late summer and that the time each was away varied according to sex. The female was absent 89.5% of the time from 22 June until 27 August, while the male was absent 22.1% for the same period. Perhaps the results of Figure 36 are just coincidental with the greater amount of time females spend away from the territory. Barr (1973) found parental care was primarily by the female. If territorial defense and/or affinity is invoked, the difference in our findings is reconciled. His observations were made on a large lake with several breeding pairs, and territorial boundaries had to be maintained, defended, and surveyed by the male pair member. Time spent defending territory lessened available time for care of the young. My lakes were small, and territorial disputes arose only when an intruder flew in. Males stayed on their territories more than females did, but with little time spent in territory defense, more time was available for care of the young.

The spectacular threat display given in defense of the young is that which many fishermen and other midsummer lake-users report as loon "dancing" or "playing". Because young are quietly hunched near the shore, they are frequently not noticed. Adults do not return to them while the intruders are present, but wait until they have left and then retrieve them by swimming near the shore and giving the "mew" call. Chicks wait until the adults are directly in front of them before moving, so it often happens that adults swim around the lake for

20 to 30 minutes before securing the chicks.

Chicks are particularly vulnerable to predation during the times when left alone. Underwater predators have free access to them, as do other loons, gulls, and in the northern part of their range, jaegers. Although the period of parental care extends several weeks beyond the time when the young can secure some of their own food, Barr (1973) found that self feeding by chicks was insufficient for the first 11 weeks. The 11-13 week age at independence which occurred during this study concurs with his evidence.

On Lake Itasca, the parents remained with their young until October and on the smaller lakes the parents began to leave for a part of each day by August. Lake Itasca has an abundant fish resource, but some of the smaller lakes have primarily mudminnows and sticklebacks. If young are left alone, they become the sole predators on the available fish resource. This offers the maximum food supply to the young, and at the same time, permits adults to secure a readily available supply for themselves. If they are moving into non-territorial portions of other lakes, they may also be feeding in areas where the fish have not been acclimitized to hunting pressures. Barr (1973) found that naive fish provided the most readily captured prey.

Establishment of a separate autumn "territory" by juveniles confers several benefits. The young become familiar with the area, and gain maximal feeding efficiency, and security from interference by other loons. Observations of marked juveniles confirms that they move to the nearest large lake with a good food supply, retain a distinct feeding range, and migrate in the company of other juveniles.

During the fall, juveniles spent most of their time feeding. Even during midday, when maintenance and resting occupied much of their time, one-third was devoted to feeding. Regular groups of young did not occur until mid-October, after most juveniles had been on Lake Itasca for a month. These factors indicate that the major advantage for the move is food related. There may also be a secondary advantage in group migration by the young. Most adults left their small territorial lakes prior to juvenile departure which permitted all available food to go to the young. Although it appeared that most adults migrated before the young did, which gave total food resources to the young, some mixed groups of three or four adults and young were seen at Mille Lacs Lake in mid-October 1973. There may not be a consistent pattern of adult-adult and juvenile-juvenile migrating groups.

TOXIC CHEMICALS

Introduction

There has been a wealth of literature concerning the effects of toxic chemicals on birds ever since a study in the early 1950's provided experimental evidence implicating chlorinated hydrocarbon insecticides as deterrants to normal reproduction on quail and pheasants (DeWitt, 1955). Primary among these have been studies involving the aquatic habitat. Water is the final resting place of pesticides, and the aquatic food chain is a depository for toxic chemicals (Hickey _et al_., 1966; Keith, 1966).

In the course of this study, loon eggs were analyzed for pesticide residues and eggshell thicknesses were measured. Materials for pesticide analyses were frozen after being collected, and no preservatives were used. Relationships were assessed between pesticide levels and eggshell thickness among samples from New Hampshire, Saskatchewan, Alberta, and Minnesota, and between eggs I collected and those which had been collected prior to 1946 (Anderson _et al_, 1970).

Methods

Each egg was thoroughly mixed in a Virtis blender. Separations were made according to the techniques of Porter and Burke, (1973); Mills _et al_., (1972); and Armour and Burke, (1970). Determinations of pesticide levels were done by electron capture gas chromatography on columns of 10% DC-200 80/100 gas Chrom Q.

Eggshells were measured with a micrometer. For entire shells, (those with only a hole drilled to remove the contents), four measurements were taken 7 mm. from the edge of the hole as described by Hickey and Anderson (1968). For broken shells, four different shell fragments were measured. For both, the four measurements averaged to the nearest 0.01 mm. were used as the shell thickness.

Most measurements included membrane and cuticle, but a few shells had no fragments with either intact. Where possible, four measurements with and four without the membrane were made, the difference calculated, and averaged ($\overline{X}$=0.1247 mm., N=49 shells). For those with no membrane (N=7), 0.1247 mm. was added to the shell measurement to determine the total shell thickness.

Results

Toxic chemical residue analyses are given in Table 21. Residues reported from the BWCA (Ream, 1968) were made prior to experimental evidence that separation of the DDT's from the PCB's is necessary to most accurately assess contribution by each. Our first tests were made using material both before and after separation; results from pre-separation samples were used to compare with those from the BWCA. There was not a significant difference between eggs collected during these two studies (Mann-Whitney test, U=11).

Minnesota eggs had a slightly lower pesticide content than eggs from Saskatchewan, but it was not significant (DDE, Mann-Whitney test, U=14; PCB, Mann-Whitney test, U-27). Alberta loon eggs (Vermeer, 1973) had a significantly lower residue level, both

Table 21. Results of pesticide residue analyses in Common Loon eggs. All values given in ppm. wet weight.

$\bar{X}$ = geometric mean ± S. E.

Locality	Before Separation DDE	p-p' DDE	p-p' DDD	p-p' DDT	o-p' DDT	After Separation PCB's as AROCHLOR 1254	Dieldrin	Endrin	Heptachlor Epoxide	Source
Minnesota North Central										
1.	21.736	NC	0.88	1.49	NC	16.77	ND	NC	0.033	this study
2.	12.465	4.66	1.09	1.12		9.93	0.29		ND	
3.	8.373	4.34	0.52	0.18		7.51	0.17			
4.	19.284	7.31	0.91	0.38		18.33	0.65			
5.	15.193	10.47	1.89	0.39		21.12	0.49			
6.	22.171	1.78	1.471	ND		26.07	ND			
7.	11.426	ND	0.507	1.139		10.48	0.320			
8.	10.179	4.09	0.361	0.857		12.16	0.026			
9.	NC	6.91	NC	0.31	1.20	5.17	0.28	0.03	0.06	
	$\bar{X}$=14.3±1.1	$\bar{X}$=4.99±0.8	$\bar{X}$=1.28	$\bar{X}$=0.51		$\bar{X}$=12.7±1.2	$\bar{X}$=0.29			
[illegible]										
1.	14.20									Ream (1968)
2.	23.40									
3.	21.82									
4.	17.20									
5.	16.20									
	$\bar{X}$=18.2±1.1									
New Hampshire										
1.	NC	4.42	NC	0.12	1.17	10.86	0.48	0.02	0.14	this study
2.		5.49		0.29	0.23	45.02	0.32	Tr	0.15	
3.		4.50		0.14	0.25	5.30	0.05	0.02	0.05	
		$\bar{X}$=4.78±0.14		$\bar{X}$=0.17	$\bar{X}$=0.55	$\bar{X}$=20.39±12.4	$\bar{X}$=0.26	$\bar{X}$=0.02	$\bar{X}$=0.11	
Saskatchewan										
1.	NC	4.79	NC	0.38	0.17	9.02	0.10	0.04	0.06	this study
2.		4.06		0.33	0.39	10.63	0.24	0.03	0.08	
3.		47.62		1.55	8.77	160.61	3.09	0.31	0.97	
4.		7.41		0.96	0.65	18.48	0.46	0.06	0.18	
5.		5.59		0.97	0.12	14.87	0.45	0.03	0.31	
6.		0.15		0.09	0.13	0.13	1.91	0.09	ND	
7.		9.87		1.56	1.21	34.43	0.86	0.04	0.24	
		$\bar{X}$=6.28±1.6		$\bar{X}$=0.99	$\bar{X}$=1.49	$\bar{X}$=14.7±1.7	$\bar{X}$=1.40	$\bar{X}$=0.13	$\bar{X}$=0.33	
[illegible]										
		$\bar{X}$=1.7±0.01				$\bar{X}$=1.2±0.4				Vermeer (1973)

NC = not checked　　ND = not detected　　Tr = trace for DDE and PCB (Mann-Whitney test, $U=7$, $P < .02$ for DDE; and t-test, $t=2.315$, $df=22$, $P < .05$ for PCB's). Three eggs from New Hampshire were tested, and were not significantly different from Minnesota eggs.

Eggshell thicknesses were compared with measurements of eggs collected prior to 1946 (Anderson et al, 1970), (Table 22.) Shell-thickness from those I collected ranged from 0.465 mm. to 0.655 mm., and 20% were as thick or thicker than the mean for the pre-1946 eggs. Nevertheless, Minnesota shells from 1970-1974 were significantly thinner-shelled than pre-1946 ones (t-test, $t=2.33$, $df=92$, $.01 < P > .025$). Shell thickness from this study was nearly the same as that reported from Alberta (Vermeer, 1973), ($t=0.52$, $df=65$). Shells from eggs which hatched were compared to those which were infertile and/or deserted and were found to be slightly thinner but not significantly so (Mann-Whitney, $U=65.5$). Eggs from known first clutches and subsequent nestings were compared, and there was virtually no difference between them. It appears that the difference is too small to implicate eggshell thickness as a causal agent to subsequent hatching success.

On 20 May 1971 I watched a loon sit on its egg and break it. It removed the shells, but I retrieved them from the bottom of the lake and collected the contents from the nest for analysis. The shell was thinner than the average for this study but not significantly so, and toxic chemical residues were lower than the average (4.09 ppm DDE and 12.16 ppm PCB).

Table 22. Eggshell thickness of Common Loons.

Locality of Condition	Thickness in mm. $\overline{X}$	$\pm$S.E.	N	Source
Minnesota	0.55	.013	55	This study
Minnesota, Michigan, Wisconsin, Ontario (Geographical Region No. 4)	0.61	.02	39	Anderson *et al.* 1970
Alberta	0.572	.01	15	Vermeer, 1973
Infertile or deserted	0.567	.019	10	This study
Hatched	0.532	.015	19	This study
First clutches	0.557	.01	19	This study
Re-nests	0.552	.004	14	This study

Eggshell thickness and toxic chemicals (DDE and PCB) were correlated (Figure 39). Neither correlation was significant (DDE, r=0.38; PCB, r=0.01). However, if the sample with PCB value of 26.07 ppm. and eggshell thickness of 0.615 is ignored, there is a significant inverse correlation (r=0.8, P <.05). Vermeer (1973a) did not find a significant correlation between DDE and eggshell thickness either and he suggested that the sample size may have been too small or the DDE levels too low. The results of my testing, especially PCB data, indicate that testing of a larger sampling should be done.

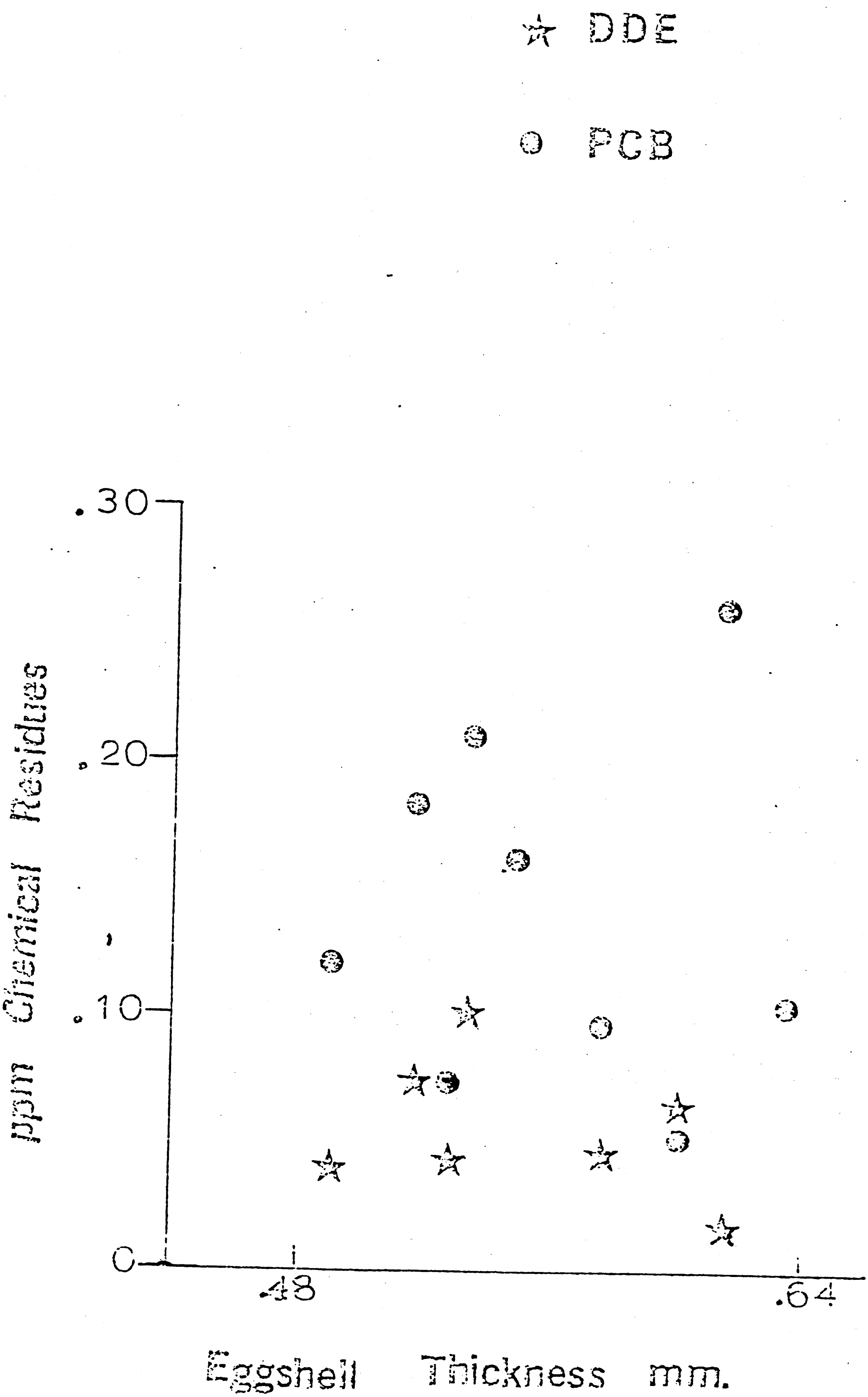
Discussion

Eggshell thinning has not occurred in loon eggs as extensively as in eggs of some other birds (see summaries by Ratcliffe, 1967; Peakall, 1970). Loons feed primarily on small fish; Barr (1973) found the most frequently taken prey items were from 11 to 70 grams. These fish may be representative of small species which, although carnivores, are not at the end of a food chain; or they may be young individuals of larger species. Loons do not feed on carrion as Bald Eagles and gulls do, nor are they able to take fish as large as ospreys and Bald Eagles do.

Belted Kingfishers occupy a similar niche in the food web and similar changes in their eggshell thickness should be expected. In a recent report, Fox (1974) found there was a small, but significant, change in thickness between pre- and post-1946 kingfisher eggs (P <.05).

Indications from this study are that pesticide residue levels do not vary greatly in Common Loon eggs from different geographical

Figure 39. Correlation of eggshell thickness and DDE and PCB values. Eggshell thickness is given in mm., pesticide values are presented in ppm.


☆ DDE
○ PCB
.30
.20
.10
0
.48
.64
ppm Chemical Residues
Eggshell Thickness mm.

regions. The lower levels reported from northern Alberta may be the result of less use of pesticides in Alberta, a difference in the food on the wintering grounds, implying the populations winter in discrete areas, or may only appear lower due to the small sample size.

At this time it does not appear certain that the DDT complex is having an adverse effect on loon productivity. Eggshells are just significantly thinner, but apparently not sufficiently so to affect hatchability. Those eggs which hatched did not have thicker shells than those which did not, (infertile or deserted). Johnston's (1974) report on the lessening of DDT residues in recent years is also encouraging for loons. However, PCB levels bear continuing analyses. The indication of potential inverse correlation with eggshell thickness, and the fact that loons winter off coastal areas in waters where PCB's are major pollutants, suggest that loon eggs should be analyzed annually from several areas throughout their breeding range.

POPULATION SURVEYS

Description of the Survey Areas

Survey figures from six areas were used for comparison (Table 23.).

1. Burntside Lake

Burntside Lake is north of Ely, Minnesota in the Superior National Forest, just outside the southern border of the Boundary Waters Canoe Area (BWCA). It is a large oligotrophic lake with 189 islands, 40% of them developed for homesites. All islands are subject to some use as stopping places or picnic sites by lake users. There is much boating, fishing, water-skiing, and other recreational activity, and the lake is also used by float planes.

I surveyed it 30 and 31 July 1974. Each portion of the lake was traversed at least twice to verify numbers and locations of the birds. Although it is possible that some were there in June and not present when the survey was made, I have found from my earlier studies that emmigrations rarely occur before August. The opportunity to survey this lake was for only a single time due to its distance from my study areas, and I opted to take the census when nesting was past and the young half-grown. Hatching to fledging success has been over 90% in other areas (Yonge, pers. comm. and this study), occurring before the chicks were two weeks old, so I felt

Table 23. Densities and productivity of six loon populations.

Location	Total Area (square miles)	Water (acres)	Percent Water	Recreational Use	Source	Year of Survey
1.	16	10,236	100.0	9	This study	1974
2. a.	16	10,184	100.0	0	Yonge	1973
b.			100.0	0	Yonge	1974
3.	32	1665 (626)	8.1	variable (0-8)	This study	1970-74
4.	6	826	21.5	2	This study	1973
5. a.	34.3	2309	10.5	variable (0-7)	Krause and Chambers, 1957	1957
b.	34.8	2344	10.5	variable (0-7)	Chambers, 1958	1958
c.	35	2352	10.5	variable (0-7)	Eberly and Dunstan, 1968	1968
d.	43	2880	10.5	variable (0-7)	This study	1972
6. a.	60	12,173	31.7	4	Olson, 1951	1950
b.	51	10,117	31.0	4	Magnus	1964
c.	51	10,117	31.0	4	Magnus	1965
d.	51	10,117	31.0	4	Magnus	1966
e.	51	10,117	31.0	4	Magnus	1967

Table 23. (cont.)

	LOONS						
	Adults				Young		
Location	N	N per Square Mile	Acres Per Loon	Pairs	N	Ratio, Adults:Young	Ratio, Young:Pair
1.	36	2.25	284	14	13	2.7	0.93
2. a.	194	12.1	52.5	96	48	4.0	0.50
b.	206	12.9	49.4	104	58	3.5	0.56
3.	18	0.56	52 (92)*	25	20	2.5	0.80
4.	19	3.17	43.5	9	2	9.5	0.22
5. a.	33	1.17	70	11	4	8.25	0.36
b.	30	1.05	78	11	2	10	0.25
c.	33	1.06	71.2	15	10	3.3	0.63
d.	59	1.7	48.8	26	7	8.0	0.29
6. a.	112**	1.8	108	52	21	5.0	0.40
b.	112**	1.8	108	45	19	4.7	0.42
c.	112**	1.8	108	31	10	6.2	0.32
d.	112**	1.8	108	21	2	21.0	0.10
e.	112**	1.8	108	24	6	8	0.25

Table 23. (cont.)

Survey locations:

1. Burntside Lake
2. Hanson Lake
3. Chippewa National Forest, Blackduck Ranger District
4. Wolf Lake Camp
5. Itasca State Park
6. Superior National Forest, Knife Lake Region

* The figure in () represents the entire 32 square mile area including the larger lakes. The rest of this column is the combined figures from 5 years of the 11 small study lakes.

**Estimated population was 105 to 120 each year. The figure of 112 was used as the average for the purpose of calculating the ratios.

this survey gave an accurate account of fledged young.

Although surveys were taken throughout both days, all areas were checked at least once in the mid-portion of the day to reduce the probability that birds counted were not on territory, but engaged in the packing activities so common in early mornings and late afternoons in July and August.

2. Hanson Lake

Hanson Lake is nearly the same size as Burntside, is located in east-central Saskatchewan, and has been studied for the past several years by Yonge (in prep.), who has graciously given me permission to use his data for comparative purposes.

It is an oligotrophic lake with 239 islands, none of them developed for homesites or used by campers. There is almost no fishing and no other recreational use. The entire lake is best described as undisturbed habitat.

3. Blackduck

This area is described in the earlier description of the study areas. In Table 23., the 626 acres represents the water area of the study lakes. The 1665 acres includes two larger lakes within the 32 square mile area which were not included in the study, but lake surveys were made for them, hence the additional three pairs (six individuals) included in the N value for adults, and for loons per square mile. The acres per loon column includes both the smaller study lakes only (626 acres, 52 acres per loon) and the total areas (1665 acres, 92 acres per loon).

Recreational use varied from lake to lake; public campgrounds and water skiing occurred on some, and on others, there was no human disturbance during the time the loons were using the lake.

The area was surveyed several times each summer from May to September, 1970 to 1974.

4. Wolf Lake Camp

Privately owned and in the same family for the past 80 years, the area is undisturbed. Lakes are used occasionally for canoeing and fishing by the family, but boat motors are not used. There are only three homes on the entire estate. I surveyed the area on 2 August 1973 and checked my findings with those of the owners from the earlier part of the summer.

5. Itasca State Park

This area is described earlier under the descriptions of the study areas. Loons were surveyed in connection with student projects at the University of Minnesota Forestry and Biology Field Station in 1957, 1958, and 1968 (Krause and Chambers, 1957; Chambers, 1958; and Eberly and Dunstan, 1968). I surveyed the population throughout the summer of 1972. The entire park was never surveyed at once, hence the different sizes shown in

Table 23. In 1974 I censused the southwest corner of the park, the only area not monitored in 1972, where all lakes were shallow and less than 10 acres. There were no loons present in the area.

6. Superior National Forest

The Knife Lake Region of the BWCA, at the U. S.-Canadian border, was the study area that formed the basis of the paper by Olson and Marshall (1952). It was censused by the U. S. Forest Service each year from 1964 to 1967 as follows:

1964	27 July to 1 August
1965	22 July to 27 July
1966	11 July to 15 July
1967	20 July to 25 July

These reports denote which territories of the original study were checked, which territories did not have pairs in the 1960's and what new territories had been established. The total population was considered to be the same in 1950 (Magnus, pers. comm.).

Lakes in both areas were subject to heavy canoe travel and overnight island occupancy by campers, but most had no permanent residences and were not sites of motorized boats, water skiing, or similar recreational pursuits.

Population Density

Population densities of Burntside and Hanson Lakes were different. Loon territories in Hanson Lake were centered around islands (Yonge, in prep). Locations of loons, both pairs and singles, on Burntside Lake indicate that islands also provided the focal point for each territory. Burntside Lake is noted among sportsmen for its excellent fishing, and the high rate of fledging success suggests the lake has an abundant food resource for loons.

Forty per cent of the islands were developed for summer homes. About 113 were left as "available nest sites". Islands in these lakes rarely lie alone, but are in groups, so that territorial spacing determines that only a portion can feasibly be used for territorial delineations. On Hanson Lake, 41% of the islands provided all nest sites. If this figure is extrapolated to potential territory numbers on Burntside Lake, about 46 territories should be expected, assuming there is sufficient food in both lakes. There were only half that number, 22 territories, and only 14 pairs. Lower density may well be due to increased human disturbance. Disturbance on one island may cause an adjacent island to also be rejected as a nest site and so compound the effects of development.

Density in Wolf Lake Camp was greater than for Blackduck both in terms of loons per square mile~~s~~ and amount of water surface required per loon. Fledging success was greater in the Blackduck area. The population remained stable for the five years it was monitored.

Total population was reported to be about the same in the Knife Lake Region from 1950 to 1967 (Magnus, per. comm.) based on the surveys; however, the number of breeding pairs holding territories declined.

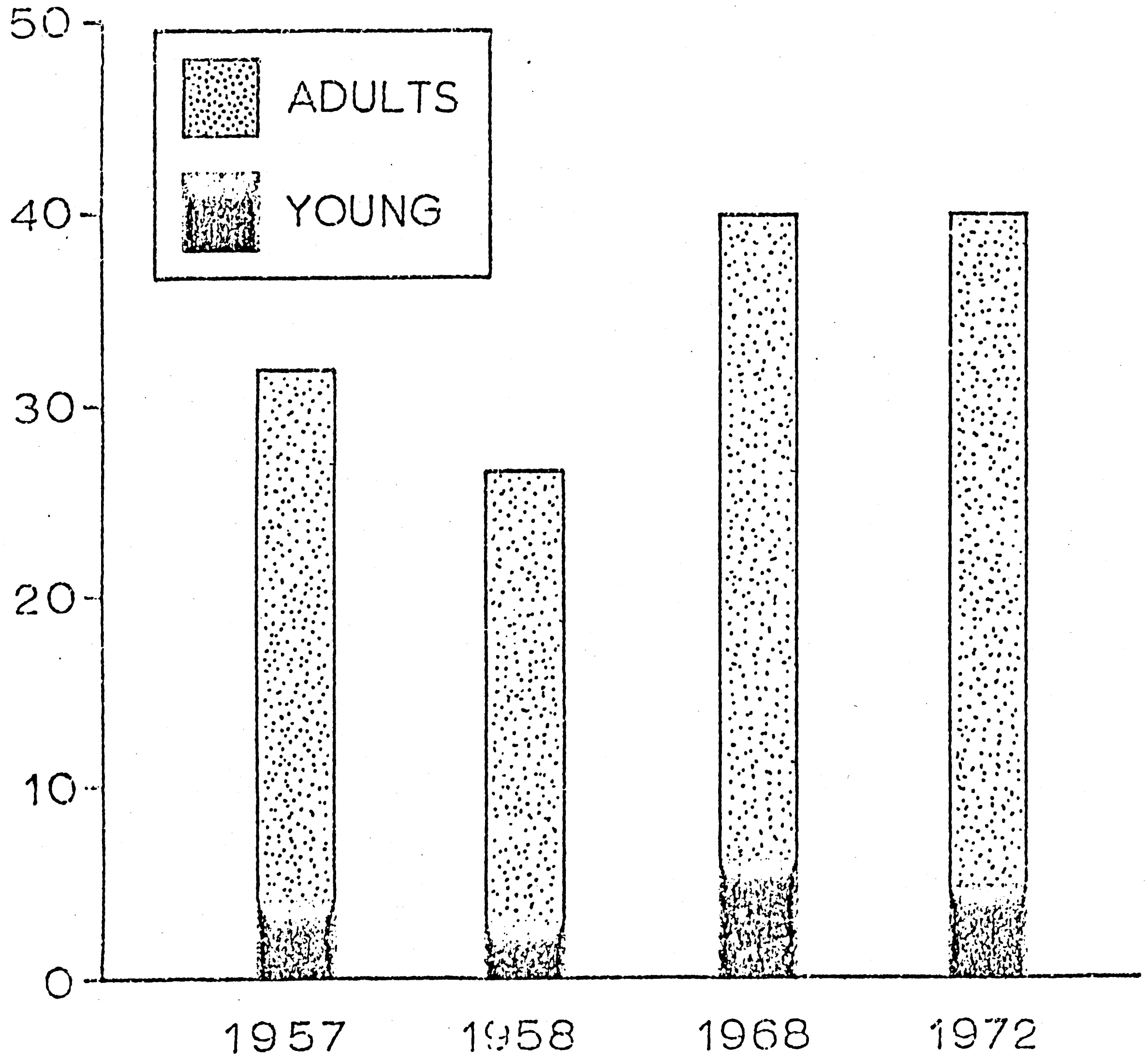
Nineteen lakes in Itasca State Park were monitored each of the four years surveys were taken. These were compared and there was found to be a slight increase from 1957 to 1972 (Figure 40).

Spacing, even in areas of dense population or in those areas where most loons utilized small lakes, indicated a requirement of 100 to 200 acres per pair. Many of the pairs occupying small lakes used an adjacent small lake for supplementary feeding. Although they were never seen defending the second lake, it was possible the second lake was part of the territory.

Single Loons

Single loons were present in all areas although this is not indicated in Table 23. for the Blackduck area. Because of the distance between lakes and the mobility of the birds, it was not possible to determine an exact number of non-breeding birds. Some single birds were seen again and again on the same lake and it was estimated there were two or three singles in the area during most summers.

Figure 40. Results of population surveys in Itasca State Park, 1957, 1958, 1968, 1972.


50
40
30
20
10
0
ADULTS
YOUNG
1957
1958
1968
1972

The number of single birds as a percent of the total population in each area was plotted against water acres per loon to assess the relative proportion of singles compared with density (Figure 41). There was not a significant correlation coefficient, $r = .515$, $t = 2.40$, $P < 0.2$), but other than the results from Itasca State Park, there was evidence that more unmated loons were found in areas of low density.

High density populations may result in reduced food supply per individual, increased time spent in territorial defense, and consequent reduced productivity. To see if this was occurring in the areas surveyed, fledged rates and population density were averaged for each of the six areas and a correlation coefficient made (Figure 42).

If a P value less than 0.05 is accepted as significant there was not a significant correlation ($P < 0.2$), but these results indicated that high density may have some effect on limiting annual reproduction and that low population density may permit some recovery.

Figure 41. The proportion of single loons in a population as related to the population density.

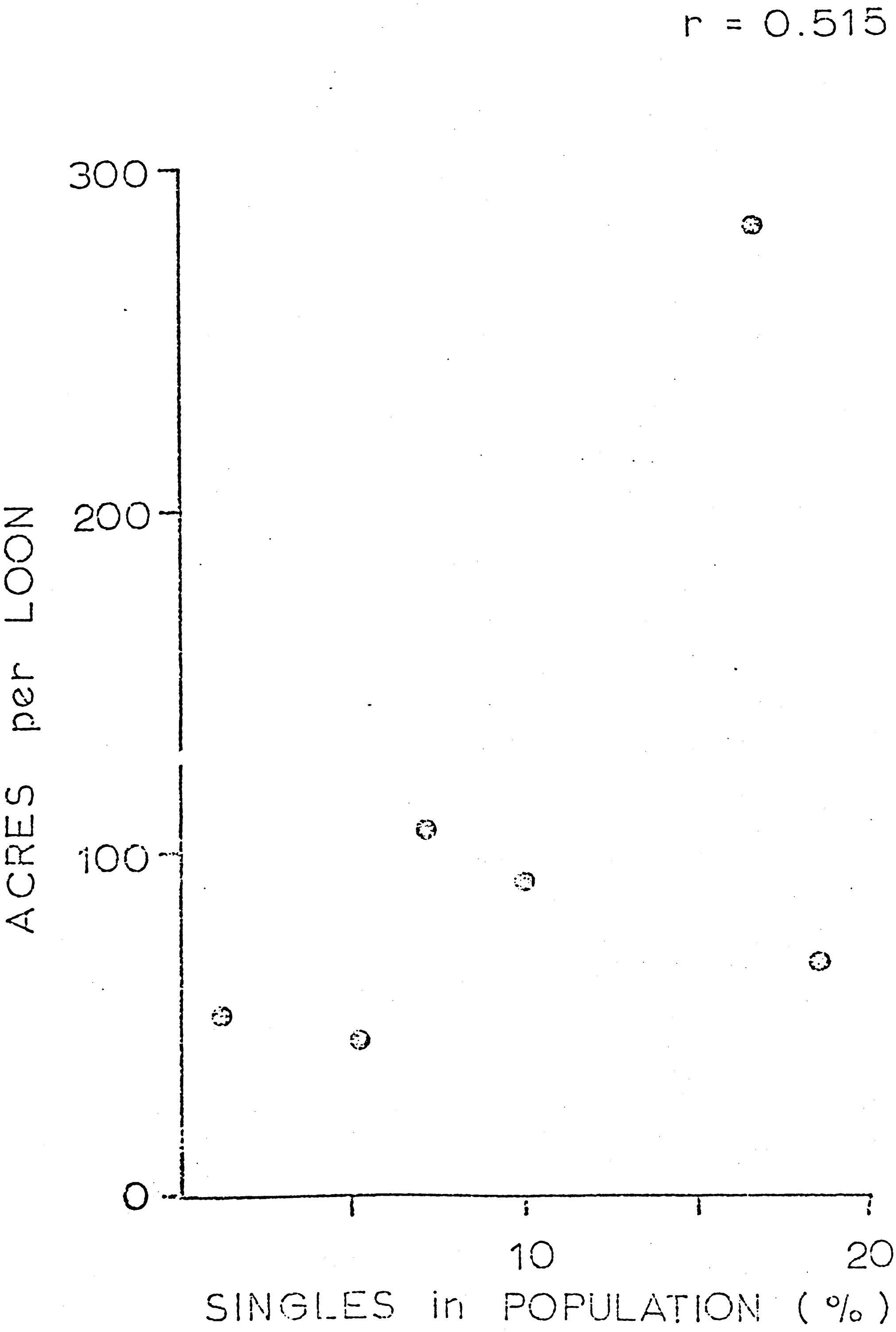
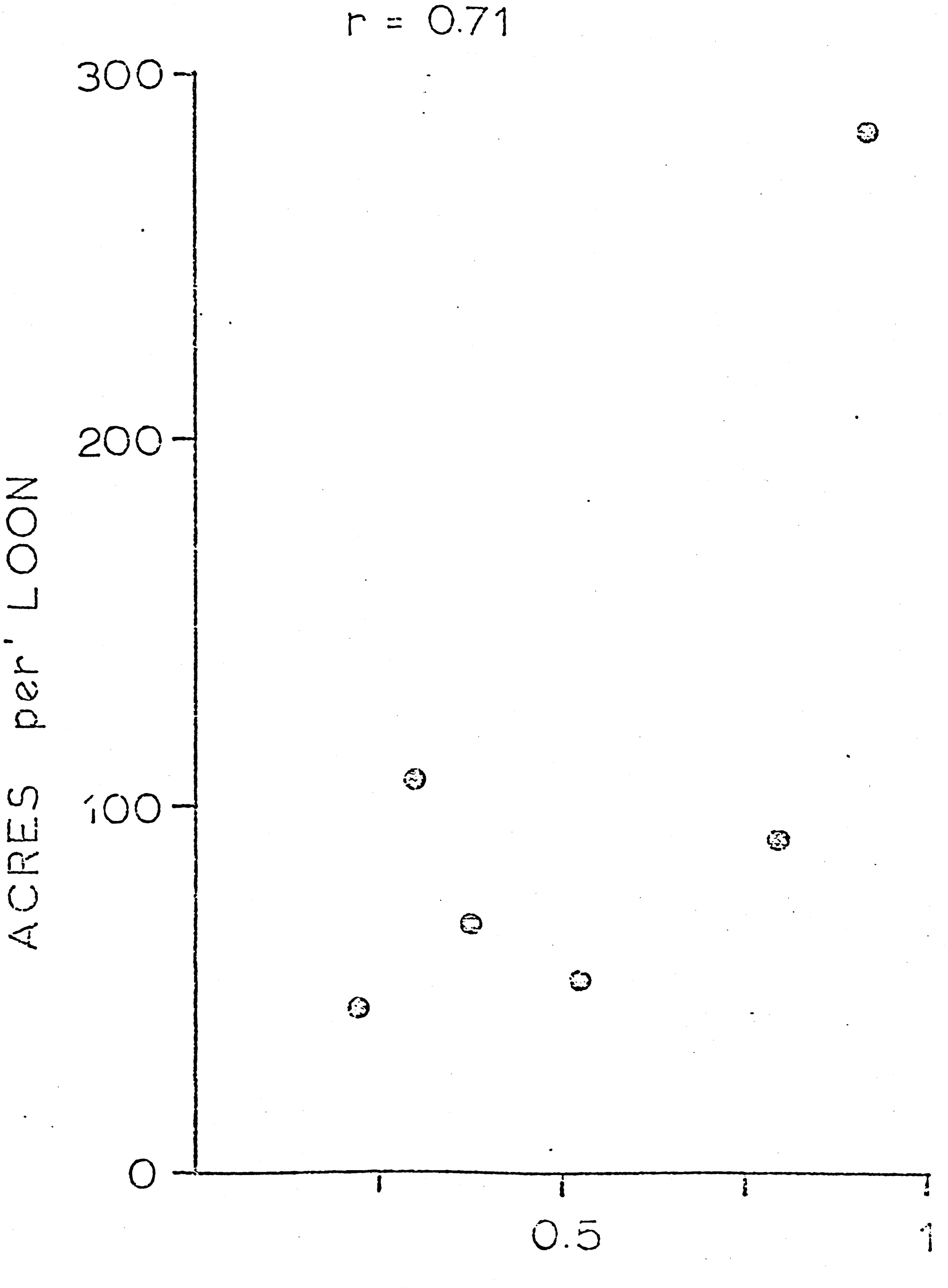

r = 0.515
300
200
100
0
ACRES per LOON
10
20
SINGLES in POPULATION (%)

Figure 42. The rate of fledging in relation to population density.


r = 0.71
300
200
100
0
ACRES per' LOON
0.5
1
FLEDG~~L~~ING RATE

DISCUSSION

INTRODUCTION

During the last 20 years there has been an increasing awareness of hazards and threats to wildlife habitat as a result of human alterations to the environment. Conflict of interest has polarized industry and environmentalists, green revolutionists and green conservationists, farmers and wildlife managers, and on and on. The issues are too well known to warrant their being itemized further. As urbanization increases, there is a corresponding increase in the number of people spending a part of their year engaged in outdoor recreation, wilderness camping, or "at the lake." Several changes to loon habitat are occurring with people pressure.

The effects of toxic chemicals have been investigated intensely for more than a decade. Although their use is not a direct result of increased human intrusion into northern lake country, the proclivity of chlorinated hydrocarbons ultimately to move to aquatic habitats (Keith, 1966; Hickey, Keith, and Coon, 1966), and the use of mercury in pulp processing plants with resultant release to river systems, make their consideration here essential. Increased use of lake areas, both as regards recreational lake use and lakeshore and homesite development is another potential hazard for loons.

Solitude, isolation, and wilderness are invoked as the essentials of preferred loon habitat in every popular article. Some studies have implicated human disturbance as a major component of reduced productivity or altered behavior (Ream, 1968; Dunker, 1973; Vermeer, 1973a). This discussion will assess the possible consequences of environmental changes and will estimate the potential effects of increased mortality and reduced fertility on the population of Common Loons.

BEHAVIORAL PLASTICITY

Wintering

Winter requirements are restricted by the advantages of a marine habitat. They need an area of unrestricted space so they may be mobile during their molt period. From January to March they need an abundant food supply for the requirements of molt and hyperphagia. Coastal areas, especially bays and coves are preferred because they confer the double benefit of shelter and the most efficient water depth for securing bottom dwelling prey items.

Migration

Loons are probably opportunistic with regard to spring stopovers, staying on whatever open water they can find. Because their arrival on the breeding grounds closely follows ice break-up, rivers, and lakes with river inlets and outlets are important. Crowding does not appear to stress the birds, although during layovers they spread out and feed during the day, and congregate at dark. Availability of open water from sources such as power plant outflow could be advantageous, providing there is food available at the site. Fall stopping sites are traditional, and the availability of specific lakes may be more important to loons than the availability of only certain lakes in the spring.

Breeding Biology

Loons are flexible in many of their requirements. They can use lakes as small as 14 acres to successfully raise young. Water clarity is limiting in the choice of deep lakes, although shallow turbid ones may provide good habitat.

Although all my study lakes contained fish, other studies showed that loons nest successfully on lakes with none, and will take mollusks, aquatic insects, or will fly to another lake for fish (Munro, 1945; Dunker, 1973). They utilize a variety of substrate for their nests, varying nest construction to suit their needs. Mottled and varied coloration causes their eggs to blend with a wide range of vegetative materials.

Island sites are preferred. If there are none, or if those that are available are being used by campers, as homesites, or for any human activity, the chance for reproductive success is significantly lowered.

Loons are capable of scrambling up inclines. Instances have been recorded where nesting has been started when water levels were high, and nest fidelity assured continued incubation despite the relative inaccessibility of the nest. Flooding or raising of the water level after incubation has begun, probably poses a more severe hazard, as there is no way loons can rescue eggs that float away.

Loons lay replacement clutches and have been known to go through three laying cycles in a season. However, while loons are competent to re-nest, a change of site is vital to ultimate success. The availability of only one good nest site could jeopardize successful nesting.

Constancy of nest attentiveness is the major strategy employed for nest protection. Disturbance by humans is responded to by nest-leaving and the eggs are vulnerable to predation. The normal clutch size is two eggs, and although there have been occasional reports of three eggs or three young, it has never been confirmed that these are all products of the same female. Two should be considered as the annual normal maximum clutch size.

Both parents share in the three months of parental duties. Chicks are vulnerable during the first two weeks to underwater and avian predators, require parental feedings for the first eight weeks, and need a local food supply until they are nearly three months old. During times of human disturbance, chicks are dropped off the adult's back, and are left near the shore, where they may be vulnerable to predation. They are capable of being captured by curious humans when they are very small, and are easily subject to fatigue, with consequent mortality. Adults will not re-nest if chicks are lost.

Large lakes with more than a single pair of loons have territorial boundaries which need defending from neighbors, and are used by more non-breeding pairs and single loons than are small lakes. Common Loons have a flexible system of parental care whereby both adults can care for the young on lakes with little interference from other loons but one adult is capable of providing most of the parental care on those with competition for resources from other loons and which consequently need more defense. On lakes where food availability may be less than optimum but the probability of intruders is lessened, dual sharing of responsibility increases the possibility that young will be raised.

Juveniles from small lakes require space on larger lakes for one to two months prior to migration. Early migration by non-breeding adults might reduce competition for the young and might also be advantageous for the adults if food is more readily available at some of the major areas of concentration, such as Mille Lacs Lake or the Great Lakes; or if migration with extended feeding stops is more energetically advantageous. Juveniles migrate together in small groups, and the necessity for large lakes where they can concentrate prior to migration may be as important to them as is the necessity for an abundant food supply.

TOXIC CHEMICALS

Wintering areas of loons may be subject to the largest concentration of PCB's if located near industrial centers. There has been a significant eggshell thinning since 1946, but it does not approach the magnitude of birds such as Brown Pelicans or Peregrine Falcons that have been threatened by thinning sufficient to cause breakage. Hazards from DDE and PCB accumulation may affect mortality as well as reduced fertility. Implications for mercury build-ups also imply increased mortality. For ~~a~~ long-lived birds, like ~~the~~ Common Loons, mortality factors have potentially far greater consequences than decreased fertility, and in the last section I will discuss these implications further.

LOON DEMOGRAPHY

In order to present a complete description of the demography of any population of birds the following factors must be examined: 1) the number of eggs per clutch; 2) frequency that clutches are laid; 3) survivorship of the young; 4) age at first breeding; 5) longevity (Ricklefs, 1972).

There is not sufficient information concerning the life history of Common Loons to formulate a thorough appraisal of a life expectancy table. Although there has been some banding over the past 40 years, most was done as a consequence of other activity and birds banded were adults of unknown age. Of these, a large proportion were caught in fish nets, injured, iced in, or were secured for banding in some way other than as normal, healthy birds, so that there was acute sampling bias.

I have wild-captured and banded wild, healthy loons of known age, but the sample size is small (N=15) and the duration of banding is short (since 1970). Three of the juveniles I banded through 1973 were reported dead during their first winter, indicating that first winter mortality may be high. But even this is speculative with such a tiny sample.

In earlier portions of the thesis, data concerning the first three factors are presented, and there are some indications as to the probable situation for the other two. Each is summarized here:

1. Fecundity

   There is no verification that loons are capable of raising more than two chicks, nor is there verification that all eggs from three-egg clutches were laid by the same female.

2. Frequency with which clutches are laid

Loons are not multiple-brooded. Although they lay replacement clutches in the event of nest loss, loss of chicks does not result in re-nesting. Annual breeding occurs.

3. Survivorship of young

Fledging success in my study areas was 0.77 young per pair. As shown in Table 23, fledging rate was highly variable from population to population (0.1 to 0.93) and this variability will be discussed further.

4. Age at first breeding

Unknown, but probably Common Loons do not breed for the first time until they are over four years old. Rationale for this is as follows: they do not attain nuptial plumage in their second year, and although they may in their third, this has not been verified.

There are non-breeding birds in the population and most populations have at least some single birds in nuptial plumage, as well as some non-breeding pairs. When Barr (1973) collected loons, he noted that territories with loons removed were immediately filled, and when single pair members remained, they too acquired new mates, both males and females (Barr, pers. comm.). Single birds collected were smaller than members of breeding pairs, and were judged to be younger individuals.

In Itasca Park in 1973 the territory of a breeding pair that died during the summer was later claimed by another pair. There are single loons throughout the summer in all areas I have investigated, although their numbers vary considerably. Many entire small lakes and parts of larger ones are occupied throughout the summer by single loons, and this seems to confirm they are resident birds and not transients.

For the following discussion I am assuming the singles and non-breeding pairs are younger birds, but it should be acknowledged they *may* be unsuccessful older birds that are reproductively dead (Ricklefs, 1972).

5. Longevity

This is unknown. Common Loons may live for 15 to 30 years. Schüz (1957) has several recoveries of Arctic Loons that were over 16 to 22 years old. There are very few recoveries for banded Common Loons, but several of those we do have are for birds banded as unknown age adults before being recovered six to eight years later.

POTENTIAL FOR REPRODUCTIVE ADAPTATIONS

It has been 25 years since Dobzhansky (1950) said that natural selection functions in different ways for temperate and tropical species to maximize reproduction. He presented evidence to show that tropical species selected for excellence of competitive ability while those in temperate areas selected for rapid breeding. This he argued was due to the frequency of genetically independent catastrophic mortality in the temperate regions as opposed to the relative stability of the tropics.

Later, MacArthur and Wilson (1967) discussed this concept calling it "r-selection" and "K-selection". The terms were derived from the logistic equation for population growth,

$$\frac{dN}{dt} = \frac{rN\ (K-N)}{K}$$

where "r" refers to the maximal intrinsic rate of natural increase and "K" refers to the carrying capacity of the environment. Pianka (1970) summarized some correlates of "r" and "K" selection and stated that each organism had its position along the r-K continuum.

Some relatively short-lived organisms have selected for high fecundity, rapid breeding, semelparity, rapid development and short generation time. Other organisms are long-lived, iteroparous, have a low annual rate of reproduction, a long period of development, and put most of their energy into evolving efficiency in utilizing a limited resource. The first is r-selection; the latter K-selection, and there is a gradient between the two.

King and Anderson (1971) discussed the mechanisms by which genetic components of r- versus K- strategy change during population growth with regard to changing pressures as a space becomes "filled" and a shift from r- to K- occurs. Gill (1974) summarized the implications of α -selection, or interference competition, and showed that α -selection, not K-selection, is the factor responsible for ability to out-compete.

For purposes of this discussion, I have regarded loons as being primarily K-selected. Although α-selection has undoubtedly been a factor in the evolutionary history of loons, the question here involves their ability to adapt to projected habitat changes, and so does not involve competition as much as their ability to maximize available resources.

Dobzhansky (1950) generalized for tropical versus temperate organisms, and Brown (1974) stated that migratory species are most likely not K-selected. There are exceptions among them, such as Whooping Cranes and loons.

Migratory behavior has been selected for as an adaptation for maximizing available habitat on a seasonal basis, thus providing some degree of annual stability in temperate regions not found by species remaining within the same range throughout the year. On the other hand, the glacial lakes that provide breeding habitat for loons are ephemeral, and many are shallow. Natural climatic variability, most strikingly exemplified by the droughts of the 1930's, drastically and abruptly change lakes from oligotrophic to eutrophic, or can dry them to ponds. At other times, heavy spring rains cause raised lake levels and flooding. Because loons are long-lived and have extended iteroparity, it is possible these fluctations may occur within the life of the individual bird. They must have evolved some degree of flexibility in breeding adaptations while at the same time a low annual reproductive rate, long life, and iteroparity were selected for adjusting to permit these changes.

Their plasticity has been discussed and they are considerably more flexible than popular accounts would lead us to believe, but there is some limit to their behavioral adaptability. The normal clutch size of two limits their annual reproductive rate and shortening of reproductive seasons either by delayed onset of breeding or increased mortality poses a more severe threat to population stability than decreased fertility for iteroparous species with overlapping generations (Mertz, 1971). Insidious toxic chemical effects that delay breeding or cause premature death will have a greater long range effect than thin eggshells and increased embryonic mortality.

Continued loss of nesting islands and shoreline to development will cause a permanent decline. Mortality through fishing net drownings has a particular negative impact, especially during spring sets, such as those in March off the Atlantic coast or the May-June fish harvest in northern Canada (Vermeer, 1973a) when losses of breeding adults are sure to be high. The loon shooting that occurred on the east coast of the United States early in this century may have decimated that population beyond recovery.

Common Loons selected for a low reproductive rate and delayed breeding in a climate where hastening the period of growth and development of the young is advantageous because lakes are ice-free for only four to seven months during the summer. In that time adults must lay eggs and hatch them, and young must reach migratory readiness. Because loons are predators and need to develop fishing skills for efficient foraging, a long period of parental care for no more than two young optimizes the chance that young can grow and develop fast enough to be ready to migrate before lakes freeze. Delayed breeding assures sufficient time to develop fishing skills adequate for feeding young; additional delay of singles and non-breeding pairs in the area of marginal habitat may prevent breeding where insufficient food, nest sites, or other factors would assure unsuccessful breeding. As a beneficial corollary, continual flights to occupied lakes by non-breeding loons permits ~~continual~~ reassessment of good habitat, and optimizes chances to "move in" if a territory is vacated. A decline in this activity during late June and early July may signify decline of gonadal hormones and ultimately prevent breeding after a "breeding deadline" has passed.

Later gatherings of loons may offer the opportunity to acquire territories for the following year (Davis, 1972) or may represent a pre-migratory build-up.

Common Loons are capable of limited behavioral modification during the winter, some adaptability in their breeding strategy, but are restricted in their potential for increased annual productivity following catastrophic mortality. Their numbers have remained stable in Minnesota during the past 20 years aided by the availability of additional small lakes in central and north central Minnesota since the end of the droughts of the 1930's. The Common Loon's selection for extended iteroparity, laying of replacement clutches, and ability to raise young on many different kinds of lakes, including those with human recreational use, permit expectation of the maintenance of a stable Minnesota population if nest sites are left undisturbed and the release of toxic chemicals to the environment is curtailed.

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Appendix I. Eskimo names for Loons.

Name	Locality	Species
Moke	Barren Ground and Davis Inlet	*G. immer*
Tood-lik	Perry River	*G. immer*
Too-lick	Hooper Bay	*G. immer*
Tuhlik Tarsineq	Mackenzie Delta (the Tuhlik with the black bill)	*G. immer*
Tudlik	Leaf Bay, Baffin Island, and Keewatin, NWT	*G. immer*
Tullik	Leaf Bay and Baffin Island	*G. immer*
Tuu'lik	Keewatin, NWT	*G. immer*
Tuhlik	Mackenzie Delta	*G. adamsi*
Too-lik	Hooper Bay	*G. adamsi*
Ren-nuch-chlick	Hooper Bay, Igiak Bay	*G. arctica*
Malare	Mackenzie Delta	*G. arctica*
Mal-ar-ek	Perry River	*G. arctica*
Kudloulik	Southhampton Island	*G. arctica*
Kudlulik	Leaf Bay, Baffin Island	*G. arctica*
Koo-chew-nik	Hooper Bay	*G. stellata*
Gahaurauk	Mackenzie Delta	*G. stellata*
Gahuralukpik	Mackenzie Delta	*G. stellata*
Kaa-raak	Perry River	*G. stellata*
Kokshouk	Southhampton Island	*G. stellata*
Kaksau	Southhampton Island	*G. stellata*
Hoksowk	Leaf Bay	*G. stellata*
Kokson	Baffin Island	*G. stellata*

Appendix II. Scientific names of plants and animals mentioned in the text.

PLANTS

Red Pine	*Pinus resinosa*
White Pine	*Pinus strobus*
Balsam Fir	*Abies balsamea*
Aspen	*Populus tremuloides*
Birch	*Betula papyfera*

ANIMALS

Fish

Alewives	*Alosa pseudoharengus*
Herring	*Clupea harengus*
Mackerel	*Scomber scombus*

Birds

Horned Grebe	*Podiceps auritus*
Cormorants	*Phalacrocorax* sp.
Great Blue Heron	*Ardea herodias*
Brant	*Branta bernicla*
Greater Snow Goose	*Chen hyperborea*
Ring-necked Duck	*Aythya collaris*
Common Goldeneye	*Bucephala clangula*
Bufflehead	*Bucephala albeola*
Oldsquaw	*Clangula hyemalis*
Scoters	*Melanitta* sp.
Ruddy Duck	*Oxyura jamaicensis*
Red-breasted Merganser	*Mergus serrator*
Bald Eagle	*Haliaeetus leucocephalus*
Osprey	*Pandion haliaetus*
Whooping Crane	*Grus americana*
Herring Gull	*Larus argentatus*
Kittiwake	*Rissa tridactyla*
Belted Kingfisher	*Megacyrcle alcyon*
Common Crow	*Corvus brachyrhynchos*

Mammals

Beaver	*Castor canadensis*
Muskrat	*Ondatra zibethicus*
Raccoon	*Procyon lotor*
Striped Skunk	*Mephitis mephitis*
Mink	*Mustela vison*
White-tailed Deer	*Odocoileus virginianus*

Appendix III. Pictorial glossary of behavioral terms for the Common Loon.

The posturings represented here are divided into three sections: Displays, posturings that communicate; Maintenance Behavior, movements with no signal function; and Incubation Postures. Each is briefly described (Illustrations follow copy).

DISPLAYS

Descriptions are given from bottom to top and represent signals from submissive posturing with a high degree of escape components to overt aggression.

Hunched

The body is flattened and held low in the water with the shoulders brought forward. The term is borrowed from gull terminology (Tinbergen, 1960).

Pelican Posture

The head is directed forward with the bill held straight down. When seen from the front, both the bill and white throat patch are hidden.

Facing Away

The head is turned to one side with the bill held down and towards the side. It is similar to Head-Flagging in gulls, a posture also called Facing Away. The latter term was chosen for loons because the head is not moved back and forth as "flagging" indicates, but is held still.

Upright

The head is carried high with neck elongated. The terms "Aggressive Upright" and "Anxiety Upright" are borrowed from gull descriptions (Tinbergen, 1960). The bill is tilted up in Anxiety Upright and slightly down in the Aggressive Upright Posture.

Bill Dipping

The bill is dipped in and out of the water. This can be done quite rapidly and is usually accompanied by turning the head slightly to one side after raising the bill.

Circling

Two or more birds swim in a small circle, alternately looking forward and peering, then to one side and back. May be accompanied by Bill Dipping.

Splash Dive

Before diving, the loon splashes water with its feet which makes a loud noise and sends up a spray of water. This dive is most commonly given at the end of a running sequence.

Jerk Dive

The head is jerked forward on a straight plane two or three times before diving.

Penguin Dance

This is an upright posture with the wings partially or fully outstretched. The bird may tread water or move forward during this display and it is usually accompanied by the tremolo call. The term is used by Dunker (1975) for Arctic Loons, and is a description of posturing termed "Fencing" by Sjölander and Ågren (1974).

Surface Rush

The bird runs across the water with head low, bill down, and wings flapping. The tremolo call is given during this display.

This behavior has been seen during physical encounters and the chased bird is attacked from the rear by downward thrusts of the pursuer's bill.

COMFORT MOVEMENTS

Wing Flap

At the end of a preening sequence or after diving, the Wing Flap is used to straighten the remiges.

Foot Waggle

The foot is extended and shaken, then placed under the wing. This is used before drifting when the bird maintains its position with the aid of one foot.

Head Rub

Oil is taken from the uropygial gland, rubbed over the back feathers, then to oil the top of the head, the head is rubbed over the back.

Belly Preening

The body is rolled to one side with the foot extended and the belly feathers are preened.

Swimming

This is the posture most commonly seen used by swimming loons. The neck is held higher than during drifting.

Drifting

The neck is relaxed and the head held low.

Dozing

The head is placed over the back with the bill between the wings. This posture is the same as used when sleeping, but because it is also used when the bird is awake, the term dozing (Dunker, 1975) has been assigned.

Peering

The head is lowered into the water above eye level. Used before feeding to locate fish.

INCUBATION POSTURES

Egg-turning

The bird stands over the eggs, and with its bill open, rolls the eggs towards itself, pushing them with the underside of the lower mandible.

Head Tucked

The posture is similar to the Drifting Posture when the bird is in the water.

Head Up

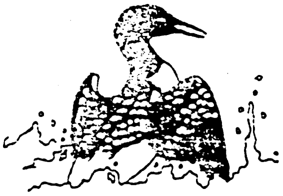
Corresponds to the normal Swimming Posture when the bird is in the water.

Sprawl

Used when the bird is hot, it is a thermoregulatory position. The wings are spread and the bird usually pants.

Hang Over

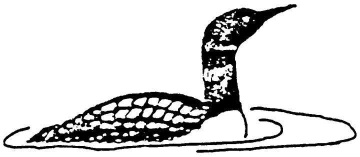
The bird assumes this when disturbed but not surprised at the nest. If it leaves the nest from this position, it can do so by sliding directly off the nest into the water. It is an intention movement to leave.



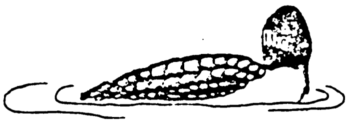
Penguin Dance

Splash Dive

Bill Dipping

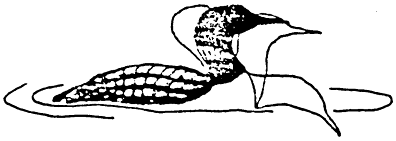


Anxiety Upright

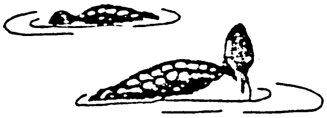


Pelican Posture

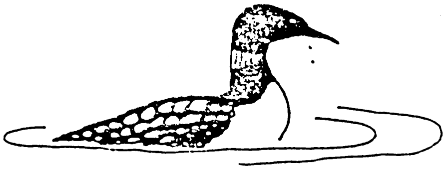
Surface Rush



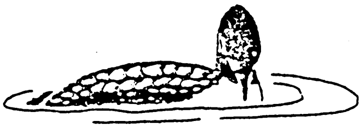
Jerk Dive



Circling

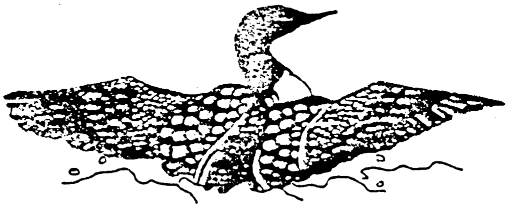


Aggressive Upright

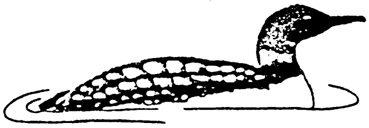


Facing Away

Hunched

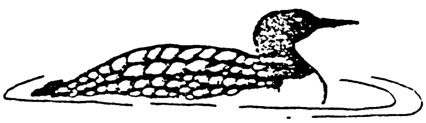


Wing Flap

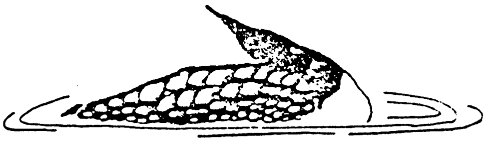


Swimming

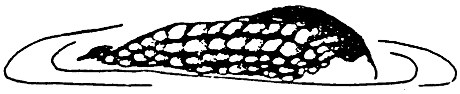
Foot Waggle



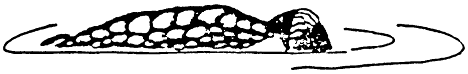
Drifting



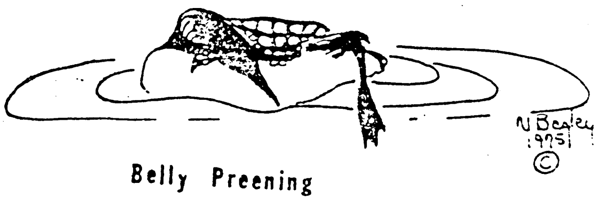
Head Rub



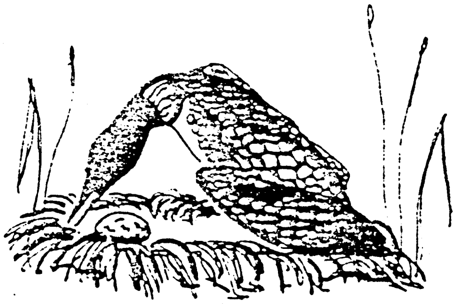
Dozing



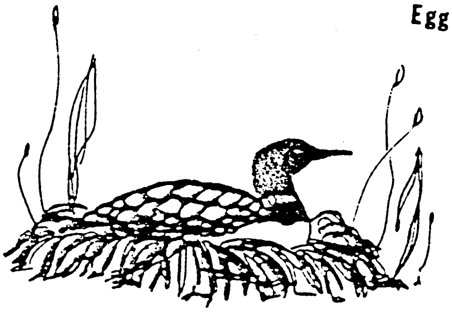
Peering



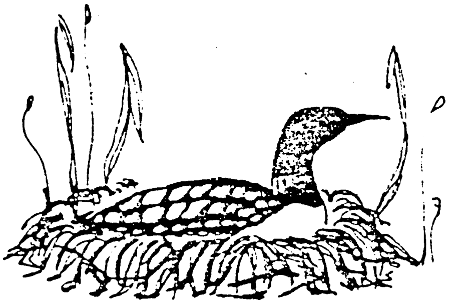
Belly Preening



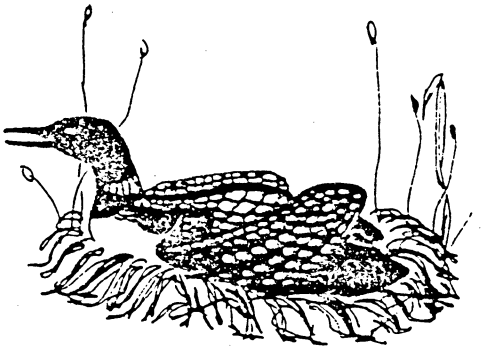
Egg-Turning



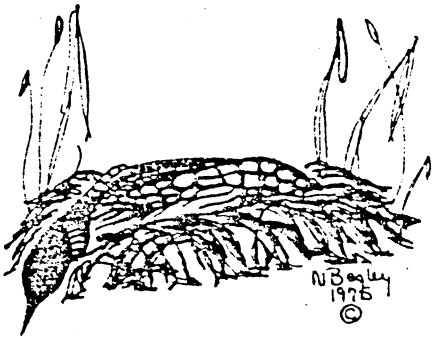
Head Tucked



Head Up



Sprawl



Hang Over

Appendix IV. Building of artificial islands.

A. Squares of sedge mat are cut with a hay saw. The preferred thickness is from 15" to 18", and the squares are about five to seven feet square.

B. Logs are placed on the sides. Either three or four may be used, Black Spruce or Tamarack are good, but any logs about 3" to 4" in diameter that are not too heavy are all right to use. The length should be about six feet. The logs are wired together at the corners and on diagonally opposing corners, concrete block anchors are affixed.

C. Completed island. The islands have lasted on many lakes for three and four years, but on other lakes, especially when placed in non-protected locations, they have blown to shore during the spring or fall and may have to be pulled back out or replaced.

A.

B.

C.

Appendix V. Predator Track Traps.

A. A wet mixture of sand and clay was placed and flattened around an old loon nest or around a structure made to resemble a loon nest. It was smoothed out, and an egg, dyed to resemble a loon egg, was placed in it. I used double-yolked turkey eggs when I could secure them, but chicken eggs were also used.

B. Tracks left in the sand-clay mixture identified the predator, as shown here by the raccoon footprint.

A.

B.

Appendix VI. Nest Descriptions for Yellow-billed, Arctic, and Red-throated Loons.

	Location	Source	Nest Description
G. adamsii	Victoria Island	Parmelee *et al.*, 1967	turf, grass removed, but covered with small pellets of grass and peat; wet peat, wreathed with fresh green willows; unlined depression in turf
	Sweden	Lindberg, 1968	no nest; scrape, or not even scrape; vegetative nest
	Fort Yukon	Davie, 1898	no nest
G. arctica	Victoria Island	Parmelee *et al.*, 1967	scrape in wet turf; large structure of peat, moss, plant stems and decomposed aquatic vegetation
	Finland	Lehtonen, 1970	on sand or turf; among rushes and sedges, with a path to the water
	Sweden	England, 1955, 1957	built up on pile of rocks, 10" above water; mass of weeds and peat
	England	Rankin, 1947	flattened rushes (*Juncus communis*)
	Jenny Lind Island	Parmelee *et al.*, 1967	muddy structure of moss and decomposed aquatic vegetation
	Bylot Island NWT, Canada	Drury, 1961	muddy moss, gathered from pond bottom
	Gulf of St. Lawrence, Quebec	Johnson and Johnson, 1935	Sphagnum moss, crowberry vine, and reindeer moss
G. stellata	Spitsbergen	Huxley, 1923	mud and moss
	Spitsbergen	Keith, 1937	moss
	Spitsbergen	Van Oordt and Huxley, 1922	flat heap of mud and vegetable remains
	Alaska	Davie, 1898	no nest; hollow on ground
	Newfoundland	Peters and Burleigh, 1951	vegetation, lined with vegetation
	Quebec	Dionne, 1906	bare scrape
	Shetland	Rankin, 1947	rushes, lined with moss; bulky nest

Appendix VII. Common Loon Nests

Nests described as masses of vegetation, usually at least partially rotted, and consisting of reed, bulrush (Scirpus sp.), cattail (Typha sp.) and approximately two feet in diameter.

Maine, Bent, 1919; Sim, 1923; Palmer, 1949
Massachusetts, Forbush, 1925
Minnesota, Olson 1951; Olson and Marshall, 1952; Roberts, 1932
Newfoundland, Peters and Burleigh, 1951
Nova Scotia, Tufts, 1961
Northwest Canada, Raine, 1892
Western Canada, Taverner, 1926, Munro, 1945

Nests described as a hollowed-out space, a depression to about 3" in depth, placed at the top of old muskrat houses.

Alaska, Gabrielson and Lincoln, 1959
British Columbia, Munro, 1945
Alberta, Salt and Wilk, 1958
Massachusetts, Forbush, 1925
Minnesota, Roberts, 1932; Olson and Marshall, 1952
Michigan, Manville, 1952
Ontario, Snyder, 1951

Nests described as bare or nearly bare; a scrape on sand or rock.

Maine, Palmer, 1949
Newfoundland, Bent, 1919
Alaska, Gabrielson and Lincoln, 1959
British Columbia, Munro, 1945
Iceland, Yeates, 1950
Minnesota, Roberts, 1932; Olson, 1951
Massachusetts, Forbush, 1925
Adirondack Mountains, Davie, 1898
Michigan, Manville, 1952
Nova Scotia, Tufts, 1961
Ontario, Raine, 1898
Alberta, Salt and Wilk, 1958
Quebec, Dionne, 1906

Moss only

Ungava Peninsula, Harper, 1958

Lily leaves, grasses, and rushes

New Brunswick, Raine, 1892

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