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EFFECT OF FOOD, PREDATION AND CLIMATE ON
SELECTION OF BREEDING LOCATION BY
RED-THROATED LOONS (*Gavia stellata*)
IN THE HIGH ARCTIC

CHRISTINE EBERL

Thesis submitted to the
School of Graduate Studies and Research
University of Ottawa
in partial fulfillment of the requirements for the
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en vue de l'obtention de la maîtrise ès sciences à

L'Institut de biologie d'Ottawa-Carleton



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Abstract

The red-throated loon (*Gavia stellata*) is a circumpolar species ranging further north than any other loon species. The purpose of this study was to examine adaptations of this species to environmental conditions in the high arctic. I investigated the effects of food, predation, and climate on the selection of the breeding location by red-throated loons nesting on Bathurst Island, N.W.T.. I tested the following hypotheses: 1) Because loons forage in the ocean, flight distance to the foraging areas should influence selection of breeding habitat (habitat near the ocean should be preferred); 2) Because loons are unable to defend their eggs and chicks from many predator species, they should exhibit anti-predation tactics such as nesting in inaccessible locations, and/or camouflage through crypticity of nesting activities and spacing out of nests; 3) Finally, because open water is available for only a limited time during the summer and because small ponds presumably thaw sooner than large ponds in the spring, loons should prefer to nest on small ponds.

I first established differences in the breeding ecology of this population as compared to more southern populations. I found that the phenology of the loons in my study area was shorter than that of red-throated loons further south, and that this population tended to select nesting ponds much larger than in the south.

Next, I examined the effect of proximity to the foraging areas on the reproductive success and selection of breeding habitat of loons. I found that pairs nesting near the ocean (within 9.0 km) were able to rear larger broods (2 chicks vs 1 chick) than pairs nesting far from the ocean (9.0-13 km). Density of breeding pairs was higher near the

ocean than further from the ocean. These data suggest that proximity of nesting habitat to the ocean influences the habitat settlement of loons in this area.

A study of predation on artificial nests completed in the first year of the study, revealed that predation of unguarded nests in the study area was high. Consistent with this, most predation of loon offspring occurred during incubation. However, loon clutches were depredated only during the second and third year of the three year study, when 44% and 69% of all clutches were lost. Because loons can defend their clutches from the avian predators in this area (*Stercorarius parasiticus*, *S. pomarinus*, *Larus hyperboreus*), mammalian predators (*Alopex lagopus*, *Canus lupus*) pose the greater threat. In support of this, most loons (90%) selected nest sites on islands, with islands further from shore being preferred. Also, multiple logistic regression of four variables (pond depth, pond size, distance of the nesting island to the shore, and distance to the nearest nesting neighbour) indicated that increased distance of the island to shore decreased predation significantly. Predators were observed to use an area-specific search tactic when foraging; the uniform spacing of nests may serve to further reduce predation.

Finally, I examined the relative availability of open water in large and small ponds during spring thaw and fall freeze-over. I found that size did not influence melting rate but that large ponds took longer to freeze in the fall than small ponds. I also observed that 16% of loons moved their chick(s) to larger ponds either early in the season, or later, in the fall, when natal ponds began to freeze over. This supports the view that the use of large nesting ponds by these loons is an adaptation to the cold climate, where small ponds freeze over sooner in the fall.

Résumé

Le huart à gorge rousse (*Gavia stellata*) est l'espèce de huart qui niche la plus au nord. Le but de cette étude est d'examiner les adaptations de cette espèce aux conditions environnementales du Grand Nord. J'ai étudié l'effet de la nourriture, de la prédation et du climat sur le choix du site de nidification des huarts sur l'île de Bathurst dans les Territoires du Nord-Ouest. J'ai vérifié les hypothèses suivantes: 1) Comme les huarts trouvent leur nourriture dans l'océan, la distance de vol pour s'y rendre devrait influencer le choix de l'habitat pour la nidification: un habitat près de l'océan devrait être favorisé. 2) Les huarts ne peuvent pas défendre leurs oeufs et poussins efficacement contre les prédateurs, donc des tactiques anti-prédatrices comme le choix de sites inaccessibles, l'espacement des nids et le camouflage des nids, oeufs et poussins devrait être adoptées. 3) Enfin, comme les étendues d'eau sont libres de glace pendant une courte période de temps en été et comme les petits étangs dégèlent plus vite que les grands étangs, les huarts devraient préférer les petits étangs.

Premièrement, j'ai établi des différences entre l'écologie de notre population nicheuse et celle de populations plus au sud. J'ai trouvé que la phénologie des huarts à gorge rousse sur l'île Bathurst, T.N.O., était plus courte que celle des populations plus au sud et que cette population tend à choisir des étangs plus grands qu'au sud.

Ensuite, j'ai examiné l'importance de la proximité des aires d'alimentation sur le succès de la reproduction des huarts et leur choix d'un site de nidification. J'ai trouvé que les couples nichant près de l'océan (moins de 9,0 km) pouvaient élever des nichées plus grosses (deux poussins au lieu d'un seul) que les couples qui sont éloignés de

l'océan (entre 9,0 et 13 km). La densité des couples nicheurs était plus grande près de l'océan. Ces données suggèrent que, pour ce secteur, la proximité de l'océan devrait influencer la répartition des sites de nidification.

Une étude expérimentale sur la prédation utilisant des nids artificiels a été complétée lors de la première année d'étude, et a démontré que la prédation sur les nids laissés sans surveillance était élevée. De plus, la prédation sur les rejetons survient généralement pendant la période d'incubation. Des nichées de huart ont été perdues seulement pendant les deuxième et troisième année de l'étude quand 44% et 69% de toutes les nichées ont été perdues. Comme les huarts sont capables de se défendre contre les prédateurs ailés (*Stercorarius parasiticus*, *S. pomarinus*, *Larus hyperboreus*), ce sont les mammifères (*Alopex lagopus*, *Canis lupus*) qui représentent la plus grande menace. Une analyse par régression multiple logistique a indiqué que la distance de l'île de nidification à la berge de l'étang était la seule variable parmi quatre variables indépendantes (autres variables: profondeur de l'étang, taille de l'étang et distance du plus proche couple nicheur) qui expliquait une variation significative dans le taux de prédation. La plupart des huarts (90%) ont choisi des sites de nidification sur des îles, tout en favorisant celles qui sont éloignées des berges. L'espacement entre les nids semble aussi réduire l'importance de la prédation. Les nids avaient une distribution uniforme et les territoires incluaient plus d'un étang afin de fournir un étang pour se cacher les adultes et un étang pour la fuite des poussins qui survivent à l'attaque d'un prédateur.

Finalement, j'ai examiné la disponibilité relative de l'eau libre pour les étangs, petits et grands, au cours du dégel printannier et du gel automnal. J'ai trouvé que la taille de

l'étang n'influçait pas la vitesse du dégel mais que les grands étangs prenaient plus de temps pour geler à l'automne. J'ai aussi observé que 16% des huarts adultes avec une progéniture ont déplacé leur poussins vers des étangs plus grands tôt dans la saison ou tard à l'automne quand l'étang natal commençait à geler. Ceci appuie l'hypothèse que l'utilisation de grands étangs par ces huarts est une adaptation aux climats froids puisque les petits étangs gèlent plus vite en automne.

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Chapter I. General Introduction and Methods

Introduction

Optimal selection of a nesting location is vital to the reproductive success of birds and thus is an important component of parental investment (Morse 1980). This selection occurs in three stages: habitat selection, territory selection and nest-site selection (Lack 1968, Morse 1980).

Habitat selection entails mostly innate processes arising from behavioural and physical adaptations to elements of a habitat (Partridge 1978). Therefore animals are usually specialized to certain habitats. Competition for habitat (both intraspecific and occasionally interspecific) during settlement forces excess individuals to select similar habitats of lower quality (Fretwell and Lucas 1970, Fretwell 1972, Partridge 1978, Cody 1985). Quality gradients in the biotic and abiotic elements within and between habitats subsequently influence territory and nest-site selection.

Territory selection is generally influenced by food and nest-site availability in the habitat, and the intensity of competition for these resources among conspecifics (Davies 1978, Morse 1980). Subsequent ownership of the territory usually goes to the previous holder (priority effect; Dawkins and Krebs 1978, Morse 1980).

Individuals then select a nest-site within their territory. Selection of nest-site is based on both innate mechanisms and experience. Nest-site selection may be influenced by predation pressure in the habitat and tactics used to prevent predation, and by exposure of potential sites to the elements. Territory selection and nest-site selection are not necessarily independent, but I will deal with them separately.

Selection at each of these levels is based on differing criteria, each determined by the various constraints which influence reproductive success. These constraints are both biotic and abiotic in nature. To define the optimal nest location, these constraints must be identified and their mechanisms understood.

Selection of habitat and territory acquisition will be affected by the species density and sometimes by the presence of a competitively dominant species with similar habitat requirements (Fretwell and Lucas 1970, Fretwell 1972, Davis 1972, Morse 1974). Territory selection depends on the availability of sufficient food in or near the territory to feed adults and offspring. Susceptibility to predators influences the placement of territory and nest-site. Suitability of the abiotic environment (e.g. weather, stability of water levels) within the habitat will also affect selection of territory and nest-site. These factors are discussed in more detail in the following sections.

Interspecific competition

Interspecific competition reduces the ability of individuals of the subordinate species to occupy certain habitats or territories within the habitat (Cody 1978, Partridge 1978, Morse 1985, Terborgh 1985). In this way, interspecific competition decreases reproductive success by limiting choice by individuals to a narrower, potentially suboptimal, realized niche. Only in the absence of the competing species can a subordinate species utilize its entire fundamental niche (Cody 1974).

Foraging requirements

Food accessibility affects territory location. If food is predictable, territories may include areas specifically defended for foraging (Andersson and Wiklund 1978). However,

if food is unpredictable or distant from nest-sites, nesting individuals must travel away from the territory to secure food (i.e. Hunt 1972, Post 1974, Morse 1980).

The central place foraging theory is applicable to both all purpose territories and breeding territories. This theory deals with optimal foraging by foragers which must return, after acquiring food, to a 'central place' such as the nest, where young are located (Orians and Pearson 1979, Carlson and Moreno 1985, Eriksson et al. 1990).

The theory of central place foraging predicts that as the distance travelled from the nest increases (i.e. travel cost increases), the load of food items delivered should become larger (greater energy acquired; Orians and Pearson 1979). The upper limit to the size or number of prey items the individual can find, or transport back to the central place (the nest), places an upper limit on the distance the forager will travel to provision a given brood size.

A limit is also imposed on the central place forager by time (Martindale 1982). Energy expended in travel may be replaced by energy secured, but time lost in travel cannot be replaced in an energy equivalent, especially if offspring are left unguarded, and exposed to predators. Therefore, to maximize efficacy of foraging and guarding young, the territory should be near foraging areas.

Predation

Predators usually destroy an entire reproductive effort and hence present an important selective force affecting territory and nest-site selection (Kruuk 1964, Lack 1968, Ricklefs 1969). Anti-predator tactics used by nesting species may be active or passive. Active tactics involve aggression against foraging predators (Kruuk 1964).

Aggression is often enhanced by nesting colonially; mob attacks by a colony of birds may be more effective in repelling a predator than attacks by a single or pair of birds.

Passive anti-predator tactics involve the use of camouflage and/or avoidance of areas vulnerable to predators. Cryptic appearance and behaviour of adults and young, and camouflage of eggs, young and nesting activities all minimize success of predators in locating nests. Predation is further minimized through selection of well spaced territories (Tinbergen et al. 1967, Horn 1968, Krebs 1971), and placement of nest where a predator is least likely to find it (Page et al. 1983).

An alternative passive tactic is breeding at inaccessible nest-sites, such as cliffs, trees, cavities, or islands (Lack 1968, Duebbert et al. 1983). Coloniality may also occur if such sites are limited. Although not all predators may be effectively avoided using this tactic, coloniality may increase fitness due to dilution and predator saturation effects (Hamilton 1971), and thus be more beneficial to reproductive success than solitary nesting.

Both passive and active anti-predator tactics require optimal decisions in selection of territory (i.e. size and placement), and nest-site (i.e. location or access by predators least likely).

Abiotic environment

Successful reproduction also depends on relatively stable abiotic conditions during incubation and pre fledging. Abiotic factors which may decrease reproductive success include fluctuating water levels, as in tidal marsh habitats (Fair 1979, Post 1981, Frederick and Collopy 1989), or severe climatic regime, which can fluctuate in many geographic

areas (i.e. Perrins 1970). Birds nesting in tidal marshes must select a nest location safe from changing water levels. Extreme weather conditions, especially those of polar regions, often affect decisions about the timing of nesting and location of the nest. Adverse weather frequently delays breeding, which in turn diminishes reproductive success (Perrins 1970). This has been observed in arctic birds such as red-throated loons, *Gavia stellata* (Dickson 1987), red phalarope, *Phalaropus fulicarius* (Mayfield 1978), brant, *Branta bernicla*, and snow geese, *Chen caerulescens* (Cooch 1961, Barry 1962, Davies and Cooke 1983) and other species (see Mayfield 1983). In such an extreme habitat, selection of microhabitat for nest placement in the spring, must also minimize the effects of potentially extreme weather throughout the season.

General red-throated loon ecology

The red-throated loon is the smallest member of the Gaviidae family. Its range is circumpolar and extends further north than that of any other loon species (Godfrey 1966, Johnsgard 1987). It is a monogamous, long-lived aquatic bird which nests inland by fresh water ponds. Like other loons, it is piscivorous, but it is unique among loons in that it prefers to forage in marine waters during the breeding season (Davis 1972, Bergman and Derksen 1977, Gomersall et al. 1984, Reimchen and Douglas 1984). Because loons are relatively immobile on land, their habitat is restricted to areas with water bodies large enough to allow landing and take off (Palmer 1962).

After arrival in the breeding area, a nest-site is selected on a pond within a territory established or held the previous fall (Davis 1972). The nest is usually located on an island, although wet peninsulas or shallow areas of the ponds may sometimes be used

(Bergman and Derksen 1977). Two eggs are laid and incubated for 24-29 days by both parents (Davis 1972, Bundy 1976). Chicks are fed mostly fish throughout the 38-59 day pre fledging period (Davis 1972, Reimchen and Douglas 1984, Eriksson et al. 1990). Sibling rivalry is intense; asynchronous hatching of the eggs may promote an earlier resolution (Davis 1972, Neuchterlein 1981, Croskery 1989). Subsequently, the younger sibling may die of starvation if food is limiting, (Davis 1972, Reimchen and Douglas 1984, Eriksson et al. 1990). After fledging, care of young by the adults continues on the ocean (Bundy 1976, Okill and Wanless 1990).

Territory selection occurs in the fall, presumably to minimize time required for initiation of nesting in subsequent years (Davis 1972). This species, like all loons, is site tenacious (Palmer 1962, McIntyre 1974), and although territory boundaries may fluctuate (Davis 1972), the general placement of territories remains constant from year to year. Territories function solely for breeding; foraging occurs in the ocean or nearby lakes. Therefore, placement of territories within flying distance of foraging areas is important.

Few studies have been conducted on the red-throated loon in the high arctic (but see van Oordt and Huxley 1922, Keith 1937). Here, the time available for nesting is restricted to less than three months. However, the red-throated loon's main competitive dominant, the pacific loon, *Gavia arctica pacifica*, is absent, allowing greater flexibility in the red-throated loon's territory and nest-site selection. Nesting ecology of this species under these two conditions has not yet been described.

The main objectives of this study are to examine the selection of breeding location (habitat, territory and nest-site selection) by the red-throated loon in the high arctic and

determine how foraging requirements, predation, and climate may influence this selection. In Chapter II of this thesis, I describe the nesting ecology of the red-throated loon on Bathurst Island and characterize selection of nest ponds in the absence of the pacific loon. The effect of proximity to foraging areas on nesting success and breeding location is established in Chapter III. In Chapter IV, I present the results of experiments examining the various passive anti-predator tactics available to the nesting loon, and examine actual patterns of predation of the loon population over three years. Placement of territory and the nest may play a role in decreasing predation. In Chapter V, I examine how the severe climate and resultant melting/freeze-over patterns of ponds may affect success and nest-site selection of loons. Finally, in Chapter VI, I summarize the findings of Chapters II - V, and discuss the relative importance of the three factors affecting territory placement and nest-site selection.

Methods

The study area

The study was conducted on Bathurst Island, N.W.T., in the Polar Bear Pass National Wildlife Area (76° 44' N, 98° 25'W). The Canadian Museum of Nature's High Arctic Research Station was used as a base camp. The Pass includes a 26 kilometer band of wetlands which lies across a narrowing of the island and is bordered by ocean to the west (Bracebridge Inlet), and to the east (Goodsir Inlet). Red-throated loons forage in both of these marine inlets.

The dry rocky ridges to the north and south of the study area have little loon habitat. Such a boundary on the loon habitat makes this population of loons more or less

discrete, and complete surveys are possible. The area was subdivided into a main study area stretching 20 km inland from Bracebridge Inlet, in which most of the work was completed, and the less accessible eastern-most six kilometers of the Pass which was surveyed only twice in 1990.

The Polar Bear Pass wetland is typified by relatively lush growth dotted with permanent pools of water ranging in size from ponds a few meters in diameter to 27 hectares in size, and three lakes, 75-450 hectares in size. Pond depth generally does not exceed 1.5 meters, permitting complete freezing of these waters during the winter. There are, therefore, no fish in the ponds of the study area.

Vegetation of the wetland is dominated by *Sphagnum* mosses and low growing sedges such as *Eriophorum* and *Carex* spp. Emergent plants are sparse to absent in the ponds and generally do not exceed 10 cm in height. Substrate composition of the pond floors ranges from small pebbles in mud to 90% coverage in silty mud with a high organic content. A list of birds and mammals which regularly forage or nest in the wetland is given in the Polar Bear Pass management plan (Anonymous 1990).

Although Bathurst Island is not in the northernmost part of the red-throated loon range, Polar Bear Pass is one of the coldest regions in which this loon nests in North America. It is the coldest area used for study of this species, having a summer (July and August) average temperature of 1.5°C (low) to 8.0°C (high; see Appendix 1). It lies near the southern tip of a geographic triangle of low plant diversity known as the barren wedge, which extends south from west of Ellesmere Island and east of Melville and includes Axel Heiberg Island, part of the Grinnell Peninsula, Prince of Wales Island and

MacKenzie King Island (Savile 1961, Beschel 1969; as stated in Mayfield 1983). Spring arrives relatively late, with onset of melting from early to mid-June, and fall freeze-over terminating the reproductive season between late August and mid-September. Thus the effective window for completing the reproductive cycle may be little over two months in some years. Early laying and rapid rearing of young to fledging age are therefore essential for the reproductive success of the loon in this area.

General monitoring of nests

Loons nesting in the main study area were monitored during the summers of 1989, 1990 and 1991. All pairs were located, numbered, and their nests monitored roughly once to twice a week until mid-August in 1989, and until mid-September in 1990 and 1991, to determine hatching and fledging success. Specific details on monitoring are given in the chapters pertaining to the details.

In 1990 and 1991, to assist with recognition of pairs in the event of nest predation, I dyed all nesting loons in the main study area at their nests during the first nest visit. To accomplish this, I poured onto the rim of the nests, 30-50 cc of a picric acid solution containing a 1:2:8 mixture of picric acid, water, and ethanol. The white breast feathers of the loons were then effectively dyed during incubation bouts. Staining became progressively more intense during incubation; birds which lost clutches shortly after being marked, generally had a paler dye than birds which successfully incubated their eggs.

Pond surveys

I surveyed all breeding ponds and all potential nesting ponds (i.e. those with an island, and over 0.20 ha in size). I measured several parameters at each pond. Size

(ha) and distance of the pond from the ocean (km) was determined from a topographic map drawn from an aerial photograph of the area. In the case of large ponds, distance to the ocean was measured from the island. Pond depth at the deepest part of the pond (cm) and distance of the island from the shore (m) were respectively measured with a meter stick and by pacing. Percent of pond bottom comprised of rock, moss, and mud (including dead organic material) was visually estimated, as was shoreline slope of islands (1=shallow to 4=vertical, measured in tenths of shoreline). An estimate of whether the bottom was easily stirred up with a walking stick, (important to chicks hiding from predators) was ranked from 0, 1 or 2. Also recorded were number of islands, height of islands (cm), and substrate of islands (moss or soil base, estimated percentages). Only nesting islands, or islands most suitable for nesting were included for analyses.

Experimental procedure

I dyed the chicken eggs used in the egg predation experiments to be more camouflaged. A mixture of diluted india ink, green food colouring and tea leaves was used to create a mottled green-brown colour. The eggs were then further concealed by draping modest amounts of vegetation over the edges of the eggs to mask the shape. Further details of experimental setup and design are given in Chapter IV.

Statistical analyses

Statistical procedures used were obtained from Zar (1984) unless indicated otherwise. The software package used for all parametric and some non-parametric analyses was Statistical Analysis Software (SAS; SAS 1983, 1985).

Other details not discussed here are elaborated in relevant Chapters.

Chapter II. Nesting Ecology of the Red-throated Loon (*Gavia stellata*) In the High Arctic

Introduction

Much research has been done on the nesting ecology of the red-throated loon (Davis 1972, Peterson 1976, Bundy 1976, 1978, Gomersall 1986, Dickson 1987, 1992, Douglas and Reimchen 1988a, 1988b). Most of these studies have concentrated on populations of this species occurring in more southerly parts of its range, more specifically on the Shetland Islands (Bundy 1976, 1978, Merrie 1978, Gomersall et al. 1984, Gomersall 1986, Okill and Wanless 1990) and on the Queen Charlotte Islands (Reimchen and Douglas 1984, 1985, Douglas and Reimchen 1988a, 1988b). Both areas border the southern extent of the red-throated loon's range, where its key competitor, the pacific loon (*Gavia arctica pacifica*) does not occur. Studies from the low Arctic regions of North America, where the red-throated and the pacific loon are sympatric, include north-western mainland populations (Peterson 1976, Bergman and Derksen 1977, Dickson 1987) as well as populations in the Hudson Bay region and the north shore of the St. Lawrence (Davis 1972). Several studies also originate from the Scandinavian arctic (Lindberg 1968, von Braun et al. 1968, Sjolander 1977, and Eriksson et al. 1988, 1990, 1991).

There is however a paucity of detailed research on high arctic populations. The present study, located in the high arctic, will provide a useful contrast to other studies. Because of local weather patterns, it is among the coldest regions of its range, resulting in a very condensed breeding season. Furthermore, it borders the northern limit of the red-throated loon's range, and is outside the range of the pacific loon.

In this Chapter, I examine the nesting ecology of this high arctic population and compare it to populations breeding further south, particularly those on the Queen Charlotte Islands and on the Shetland Islands. I also address two questions in this chapter. First, is the high arctic population of loons physiologically adapted to the condensed breeding time? Physiological adaptation could include either capacity to lay immediately on spring arrival, or shortening of the incubation and/or pre fledging period. Secondly, is survival of this population, given the short season, made possible by modified habitat or nest-site selection? In this case, pond use by loons would be restricted to small ponds, which open up earliest in the spring (Davis 1972, Irving 1972).

Methods

Monitoring of nests

During the summers of 1989, 1990 and 1991, I located and monitored all nesting loon pairs one to two times a week until mid-August in 1989, and until mid-September in 1990 and 1991. Details of success during incubation and raising of chicks were recorded. I determined laying dates for as many pairs as possible (1990: n=21; 1991: n=22) by flushing adults from their nests to establish clutch status during the laying season. Adults were dyed using picric acid placed on the rim of the nests during these visits (see Chapter I, Methods). In all years, I determined hatching dates of as many broods as possible.

Because the 1989 field season terminated before most chicks fledged, and the fledging success in the 1990 season could not be determined due to adverse weather, I defined success of chicks as the survival of chicks until the last day of observation, or

until the end of the minimum 38 day pre fledging period.

Pond surveys

I surveyed all ponds and lakes in the study area which were used by nesting red-throated loons and all ponds which I considered potential nesting ponds (i.e. had an island, and were over 0.2 ha in size). Sixty-nine ponds (26 nesting ponds, and 43 non-nesting ponds) were surveyed in 1989. The remaining 89 ponds were surveyed in 1990 and 1991. Details of the parameters measured at each pond are given in Chapter I.

To avoid disturbing loons with eggs or young chicks, I commenced surveys of nesting ponds only after the first week of August or after chicks were over 1.5-2 weeks of age. Non-nesting ponds were surveyed mostly in July (80%) and August (20%), and thus were, on average, surveyed 26 days sooner than the nesting ponds. This may have created a bias making nesting ponds appear shallower than non-nesting ponds.

To determine which of the pond parameters accounted for the most variation between nesting and non-nesting ponds, I used logistic regression (SAS 1983). I tested each variable individually against pond use, and then used multiple logistic regression (stepwise), with significance level of 0.15 (Hosmer and Lemeshow 1989), to establish which variables best accounted for variation in pond use.

Results

General ecology. Details of laying phenology for the three years of study are given in Figure 2.1. This laying period lasted between 15 and 19 days. In 1990 and 1991, most of the late nesting pairs (71.4%, n=7), were unsuccessful, and in three cases occupied territories not used the previous year. Incubation period per egg ranged between 24 and

Figure 2.1. Laying phenology of red-throated loons on Bathurst Island, 1989-1991.

Laying Phenology

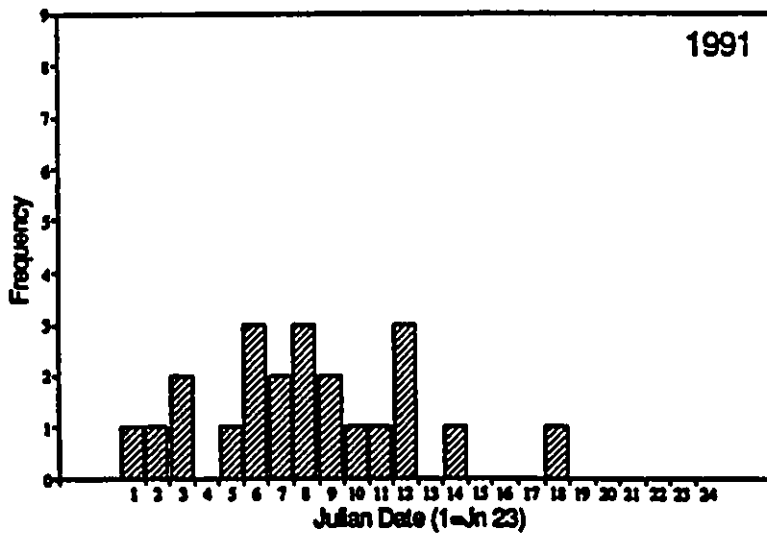
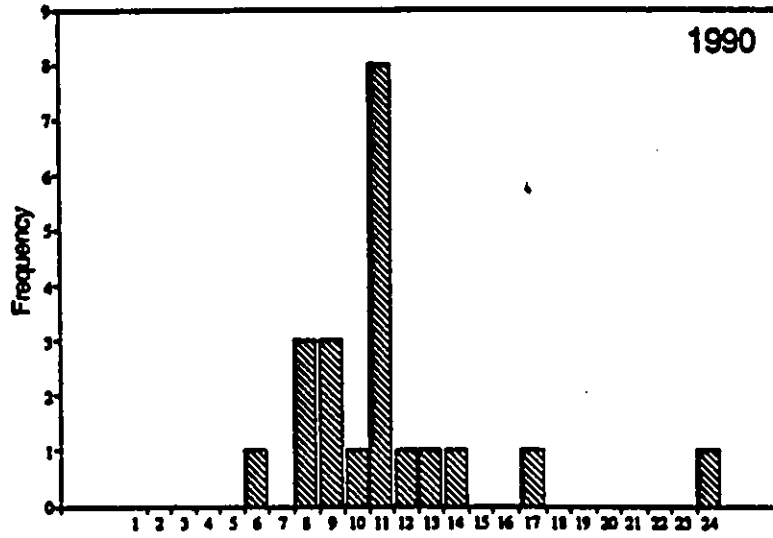
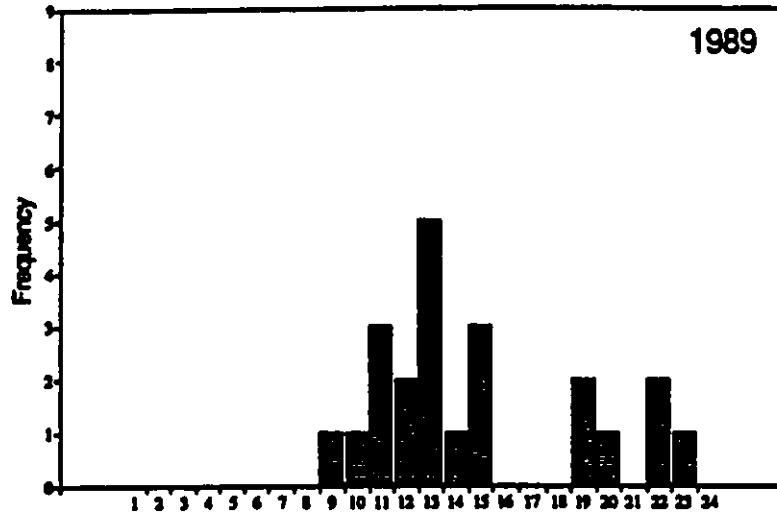


Table 2.1. Incubation periods for red-throated loon clutches. The assumption that there are two days between laying and one day between hatch of first and second egg stands. Note that only the first two categories are precise within one day.

	Incubation range for 2nd and 1st eggs (days)				
	24&25	25&26	24&25 or 25&26	25&26 or 26&27	26&27 or 27&28
Clutch frequency	4	2	4	3	1

27 or 28 days (Table 2.1). This estimate, determined from incubation length for each egg in a clutch, assumes a two day laying interval and one day hatching difference, unless observed otherwise (3.7%, n=27). The mean for twelve precisely measured incubation periods is 25.2 (± 0.75 SD) days for the first and 24.3 (± 0.52 SD) for the second laid egg.

Breeding success varied between years (Figure 2.2), and was highest in 1989 (97% of clutches laid were successful, n=32), and lowest in 1991 (30.6% of clutches were successful, n=36). As failure increased, the ratio of one:two chick broods also increased (Figure 2.2). However, this increased ratio corresponds with high nest loss in areas producing mostly two chick broods (see Chapter III). The number of chicks raised by each pair in successful years does not vary significantly (Table 2.2, $G=12.63$ $p<0.001$).

Only three of the total of 42 failures resulted from inviable eggs. Two of these failures occurred over two years on the same territory. The eggs of this nest were depredated in the third year. One failure may have been due to destruction of the nest by wave action and drift ice. Except for two nests (lost due to observer interference), all other failures involved sudden disappearance of eggs, or occasionally young, and were presumably due to predation.

Pairs which lost their clutches or chicks remained on their territory for the remainder of the season. In cases of clutch loss, 73% of 15 pairs were known to relay (Table 2.3), usually within 12 days of loss. Eleven losses occurred less than 1 week after laying. In 12 cases of clutch loss (3 from 1990 and 9 from 1991) it was unclear whether replacement clutches were laid. Only 4 of 15 pairs losing clutches did not relay, and replacement clutches were not laid following loss of chicks.

Figure 2.2. Frequency of failure, one chick broods and two chick broods in 1989, 1990 and 1991.

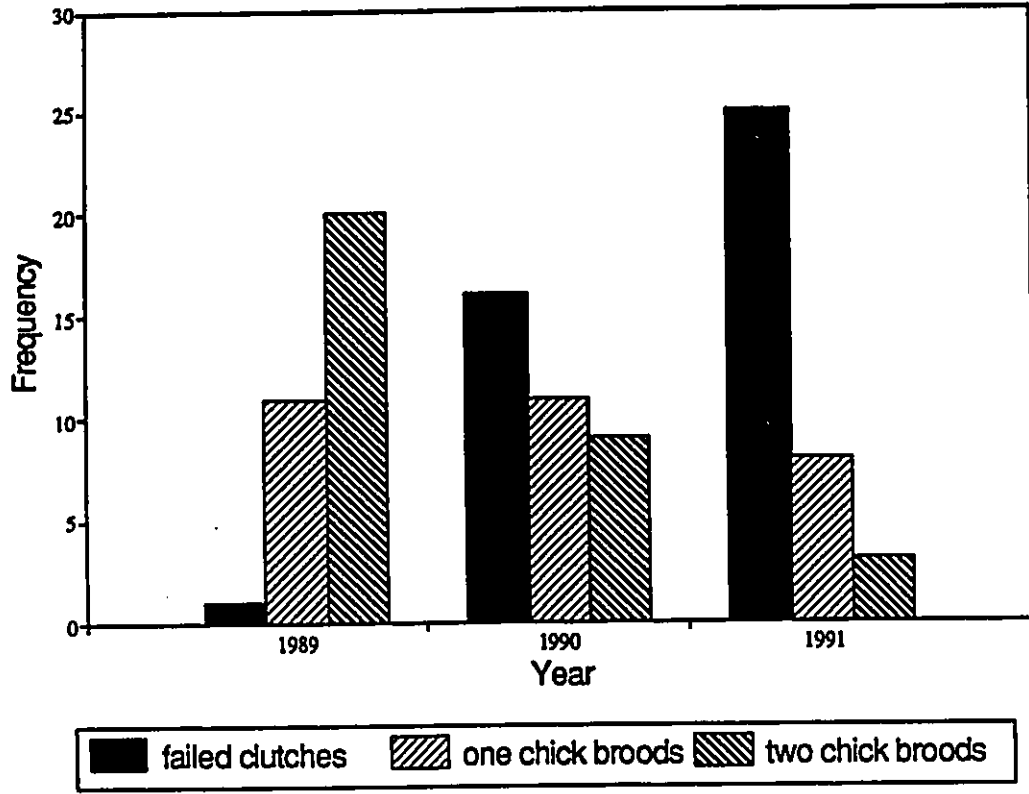


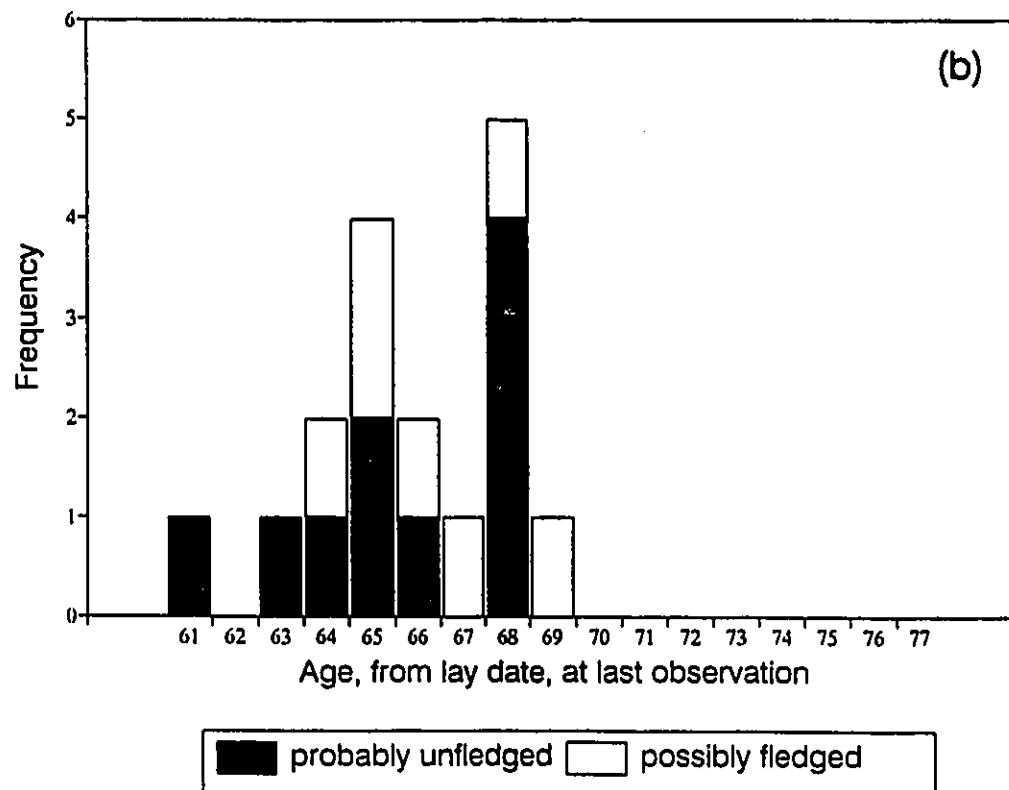
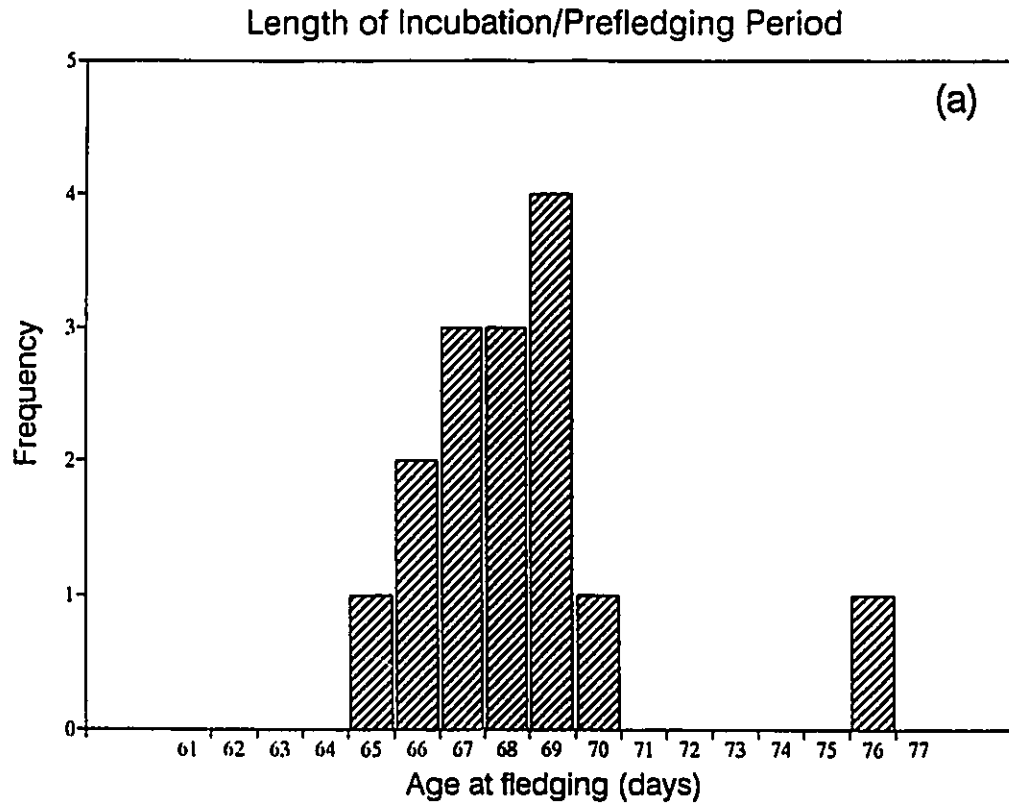
Table 2.2. Repeatability of brood size of each pair nesting successfully in two successive years. ($G=12.63$, $p<0.001$).

		Year 1	
		One chick	Two chicks
Year 2	One chick	13	5
	Two chicks	1	11

Table 2.3. Timing of reproductive failures, and frequency of relaying attempts.

Re-lay category	Age of lost clutches				Other losses	
	1 - 7 days	8 - 14 days	15 - 21 days	Age not known	Either egg or chick	Chick loss
Yes	6	0	1	4	-	0
No	1	1	2	-	-	5
Unknown	4	0	1	7	4	0

Figure 2.3. Length of incubation/prefledging period of (a) successfully fledged chicks and (b) chicks at last observation in 1990.



Two renestings resulted from nest loss from wave/ice action early in the season. One of these produced the only chick from a relay to survive until the end of the field season. Two other renest attempts resulted in a chick which hatched late in the season but disappeared after a few days. Two of the 3 replacement clutches producing chicks were established over 12 days after loss of the first nest.

All other renest attempts failed within a few days of re-lay, presumably due to predation of the clutch. Although third clutches may have been laid in 2-3 cases, none were confirmed.

The period between date of lay and fledging was determined for one chick in 1990, and for 14 chicks in 1991 (Figure 2.3a, $x=68.27 \pm SD$). Because chicks could not be watched continuously, fledging was defined as the time when a chick flew from its pond to another body of water over 1 km away. Fledging by this definition occurred on the day the chick flew to the ocean in all but one case. Douglas and Reimchen (1988b) defined fledging as the first flight sustained for at least one minute. In my study, this often occurred a day or two before chicks left the pond. However, in at least one case, the chick's first sustained flight took the chick 2.5 km to another body of water. This occurred at a time when most ponds were frozen (Sept 13, 1991).

Observation of fledging in 1990 was hampered by weather and nightfall. As a result, only one definite fledging was observed (see above). The fate of 15 other chicks is unknown, but their ages at last observation are given in Figure 2.3b. Six of these may have fledged judging from behaviour at last observation, but the others were likely depredated in their diminishing ponds.

Table 2.4. Means and ranges of parameters of non-nesting and nesting ponds, and statistic obtained from logistic regressions of individual variables against pond use.

Parameter	Non-nesting ponds (n=113)		Nesting ponds (n=45)		Logistic regression Wald χ^2 (P)
	Mean \pm st.dev.	Range	Mean \pm st.dev.	Range	
Distance of island to shore (m)	11.9 \pm 8.75	2 - 60	24.4 \pm 21.36	0 - 100	16.86 (0.0001)
Depth of pond (cm)	42.2 \pm 10.42	20 - 70	50.1 \pm 11.10	25 - 75	14.69 (0.0001)
Size of pond (ha)	1.7 \pm 2.98	0.2 - 19.7	54.3 \pm 116.68*	0.3 - 445.3	8.67 (0.0032)
Moss and mud on pond floor (%)	80.7 \pm 19.90	30 - 100	72.6 \pm 18.05	50 - 100	5.33 (0.0210)
Distance of pond to ocean (km)	8.7 \pm 3.09	2.3 - 13.1	7.5 \pm 3.18	2.6 - 13.1	4.82 (0.0280)
Looseness of pond floor (0-2)	1.2 \pm 0.68	(0 - 2)	1.1 \pm 0.50	(0 - 2)	0.75 (0.3880)

* - mean obtained by including multi-pair ponds only once.

Selection of nest ponds

Many ponds had more than one island, and hence many distance-to-shore (DTS) values. To determine which DTS to include in the logistic regression, I examined which island, in nesting ponds with more than one island, was typically selected for nesting on. A Wilcoxon paired sample test comparing DTS of nesting islands and non-nesting islands in the same nesting ponds revealed a significant difference between DTS of the two groups; nesting islands are generally further from shore than non-nesting islands ($W=388.5$, $p<0.0001$, $n=51$). Based on this, I selected, in non-nesting ponds with multiple islands, the island with the greatest DTS for the following logistic regression analysis, providing it had adequate access points for nesting loons.

Variables of nest and non-nest ponds are characterized in Table 2.4. Simple logistic regression of individual pond variables with pond use indicates that DTS, pond depth, pond size, percent of moss cover on the pond floor, and distance of the pond to the ocean (DTO) each contribute to variation in pond use. Multiple logistic regression however, excludes DTO as a contributing factor (Table 2.5). Variables contributing significantly to variation in pond use are, in order of importance, DTS, pond size, pond depth and percent of moss cover on the pond floor (Table 2.5).

Discussion

Nesting phenology

The study population occurs in one of the coldest extremes of the species' range. Because members of the loon family rely on open water to take flight and land, the time available to lay eggs and raise offspring is limited to the period in which the breeding

Table 2.5. Wald Chi-square values calculated using maximum likelihood estimates for variables included in the multiple logistic regression model.

	Wald Chi-square	Probability
Distance of island to shore	4.69	0.03
Depth of pond	3.15	0.07
Size of pond	2.85	0.09
Percent of moss cover on pond floor	2.17	0.14

waters remain open. The reproductive phenology of the red-throated loon generally includes a period of pond occupation before laying (up to 2 months, Bundy 1976, Douglas and Reimchen 1988b), laying and incubation (up to 31 days), and a period of parental feeding of chicks on territory (up to 58 days, Petersen 1976), followed by a period of parental care of chicks on the ocean after fledging (Okill and Wanless 1990). The time spent on the breeding waters is of interest here. The maximum duration of 90+ days is clearly much greater than the durations of pond availability (Appendix 1 shows temperature regime; see also Chapter V). A minimization of time spent for each activity may be a necessary adaptation for successful reproduction. Thus we must compare phenology of this population to that of other populations.

In general, the first loons arrive at Polar Bear Pass 1 or 2 weeks before laying begins. No loons were sighted flying over the study area before June 15th (1988, June 21; 1989, \leq June 19; 1990, June 17; 1991, June 16), and nesting usually begins in the last week of June or the first week of July. This is in contrast with the loons of the Shetlands which may occupy their territories two months before laying begins (Bundy 1976). In the Queen Charlotte Island population, arrival on territory is one month before nesting begins (Douglas and Reimchen 1988b).

In spite of this, the mean date of lay at Bathurst Island occurs more than one month later than in southern populations. Even the MacKenzie Delta population ($\sim 68^\circ\text{N}$, Dickson 1987) may begin laying up to two weeks before that on Bathurst Island population (June 10-June 26 compared to June 23-July 1, $n=3$ years). Ponds of my area are not available sooner and loons often wait on territory until ponds are open enough to begin nesting. Pairs do not necessarily delay nesting until ponds are ice-free; pairs may

nest when entire pond surface is melted, though the bottom may still be frozen (see Chapter V). This behaviour has also been observed in other loon species (Parmelee et al. 1967, North and Ryan 1988, 1989).

The phenomenon of later nesting at higher latitudes has been documented for several bird species in Finland (Slagsvold 1975). A comparison of mean laying dates between the various study areas indicates a delay in mean laying date of 1-3 days per progressive degree latitude. This is in agreement with the range of 1.5-2 days per degree given by Slagsvold (1975). Variation in spring temperature regimes between years (see Appendix 1) likely accounts for the broader range observed by Slagsvold.

The laying period observed here is also less protracted than that further south. Bundy (1976, 1978) and Douglas and Reimchen (1988b), report a laying spread of one to two months, while Dickson (1987) reports for a more northern population a less protracted spread of 18 to 25 days (n=3 yrs). I observed a spread of 15-19 days (n=3 yrs).

The average incubation period still falls within the normal range of 24-29 days, but is marginally less than the average incubations reported elsewhere. Both Bundy (1976) and Douglas and Reimchen (1988b) report an average incubation of 27 days, while Dickson (1987) specifies incubation for the first egg at 26 days (n=7), and the second egg at 25 days (n=6). This latter is still almost one day longer than the average incubation period of six precisely measured clutches in the high arctic study area (24.3-25.3 days for second and first eggs, respectively). No reference to decreased incubation within a species over a latitudinal range was found although member species of the Anatidae

family have decreased incubation times with increased latitude (Lack 1968).

The pre fledging period is within the lower range of periods recorded elsewhere, ($x=42 \pm 1.86SD$ days, $n=6$); no chicks remained unfledged for longer than 45 days. Dickson's report (1987), describes fledging by some chicks at more than 48 days (average=44 days, $n=24$). Reimchen and Douglas (1984) report chicks fledging at between 49 and 51 days, ($n=2$) while Petersen (1976), in an Alaskan study, observed a chick fledging at 58 days.

I also examined the entire period between egg-laying and fledging, as it is this entire time which must be minimized to ensure fledging before freeze-over. No chicks in this study required more than 76 days from the time of egg-laying, to fledge. Douglas and Reimchen (1988b) record an average of 75 days from laying to first one minute flight (which is usually shorter, by 1-2 days, than the fledging time of my definition). In contrast, the average time required from egg-lay to flight away from territorial pond in my study area is 68 days ($n=15$). No such measurement was made by Dickson (1987), but addition of the recorded average incubation and pre fledging results in a pre fledging period of 69 and 70 days for second and first chick.

The data suggest that the Bathurst Island population has adapted to the short season by minimizing the time required for successful raising of chicks. They have adapted by eliminating much of the pre-nesting time observed in most other populations. They have also adapted by reducing the time required by an egg to become a fully fledged chick, by minimizing both the incubation period and pre fledging periods. Although the differences found between the populations of Dickson's report (1987), and those of

Bathurst Island are small, they are consistent in direction: the Bathurst loons accomplish each activity, from settlement on territory through to chick fledging, between one to two days more rapidly. In total, the Bathurst Island loons may produce fledged chicks in a shorter time period following settlement on territory, and require at least a week less than those of the MacKenzie Delta region (Dickson 1987) and up to 1.5 months less than those of the Shetland Islands (Bundy 1976).

Shortened phenology with increasing latitude has also been noted in common loons (*G. immer*, Yonge 1981) in northern Saskatchewan, and yellow-billed loons (*G. adamsii*, North and Ryan 1988) in Alaska. In northern populations of both species, the prenesting period was reduced, while the incubation and prefledging periods remained similar to that of southern populations. In other avian species, shortened phenology with increasing latitude has been attributed to a decrease in the prenesting and prefledging periods (Irving and Krog 1956, Williamson and Emison 1971, Morton 1976, as cited in Carey 1986). However, shortened incubation has not been documented by these authors. Likewise, in this study, the incubation period is not shorter than reported elsewhere. However it does fall within the short end of the known range for red-throated loons.

Nest pond characteristics

Red-throated loons of the high arctic may have also adapted to the short breeding season by selecting the first available ponds on which to nest. The use by this species of small ponds, which open sooner than larger ponds in the spring, has been cited as an adaptation to the severe arctic conditions experienced during the species' evolution in the

Pleistocene (Davis 1972, Irving 1972). Therefore, red-throated loons should always prefer small ponds, regardless of the availability of large ponds.

However, in my area, loons were breeding on ponds significantly larger (Davis 1972, Bundy 1976, 1978, Bergman and Derksen 1977, Gomersall 1986, Okill and Wanless 1990), as well as deeper (Bergman and Derksen 1977) than those used elsewhere. Figure 2.4 shows the ponds of three size classes used by loons from the Shetland Islands, versus the ponds of the same size classes used by the Bathurst loons. Ponds less than one hectare were most frequently used in the Shetlands. It has been suggested that the Shetland Islands do not have many large ponds, and those which are large are used for fishing and other human activities which decrease loon reproductive success (Gomersall 1986, Okill and Wanless 1990). This may discourage use of these ponds by loons.

A re-examination of the Shetland data (Bundy 1976, Gomersall 1986; see Reimchen and Douglas 1984) shows that ponds are used in proportion to occurrence. This is also observed in the ponds used by the Queen Charlotte Islands population (Douglas and Reimchen 1988a, Figure 2.5). Absence of pacific loons in both these regions allows the use of large ponds, but small ponds are also utilized. Because climate is not limiting in this area (i.e. the summer is more than 100 days in length in the Queen Charlotte Islands: Douglas and Reimchen 1988b), there is no pressure to select small ponds.

It is therefore unclear, in terms of competitive release (Cody 1974, Yeaton and

Figure 2.4. Numbers of loons nesting at ponds of three size classes (<1 ha =small, 1-5 ha =medium, >5 ha =large), in the Shetland Islands and on Bathurst Island.

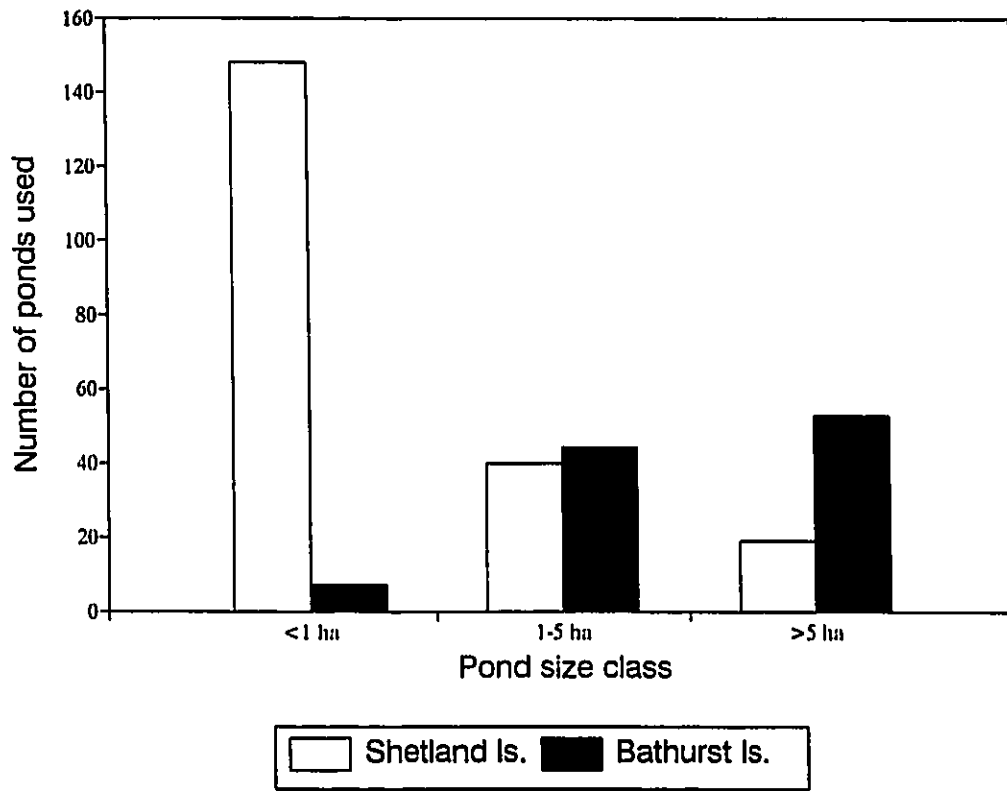
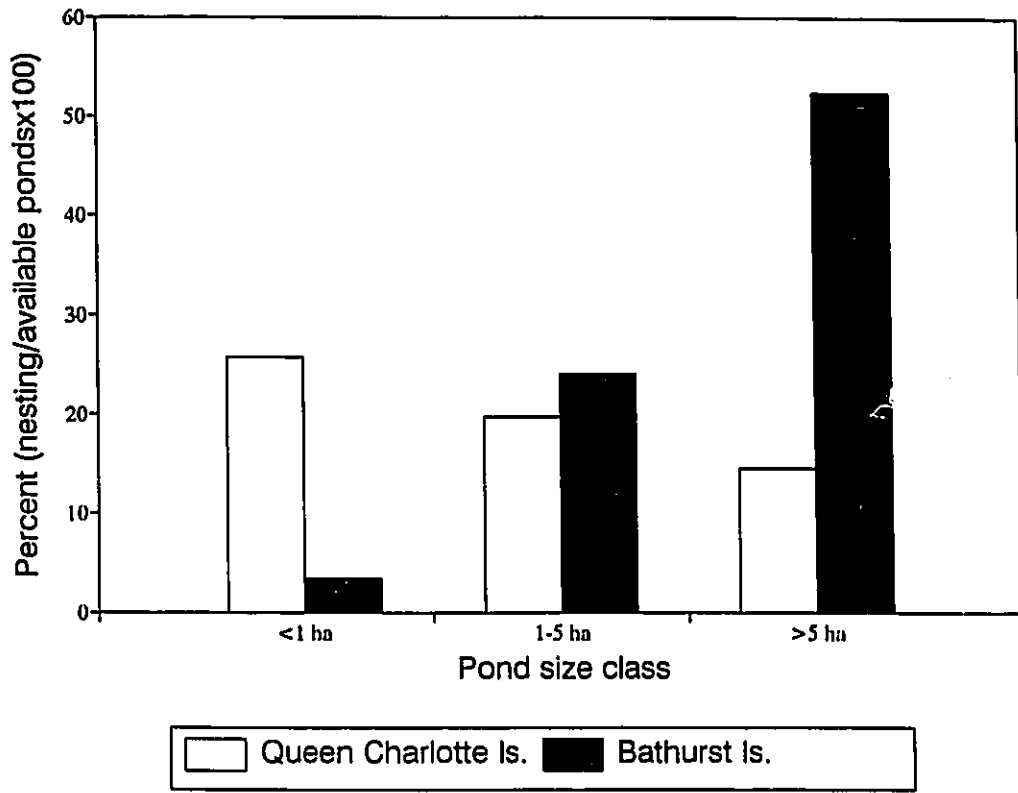


Figure 2.5. Percent of nesting ponds over ponds available for nesting in the Queen Charlotte Islands and on Bathurst Island.



Cody 1974), why loons of Polar Bear Pass select ponds which are significantly larger than those used elsewhere. Competitive release may explain the use of large ponds, but it cannot explain the relative absence of loons on small ponds, especially as ponds provide no other resource than a place to land and take-off from.

It is evident that another factor is influencing selection of ponds. As discussed in Chapter I, predators, food availability, and climate may all have an affect on nest pond selection by red-throated loons in the following ways. 1) The apparent selection of large ponds may be influenced, not by the decision of loons to nest on large ponds or on islands with a large DTS, but by the decision to nest near the foraging waters where the largest ponds occur. In this case, pond selection is determined by their availability, and use of large ponds is a result of a greater availability in otherwise higher quality habitat. 2) Predators may be less able to access nests located on ponds which are large, deep or have islands located further from shore, three variables which determine much of the variation between nesting and non-nesting ponds. 3) Finally, loons may select ponds which remain open longest in the season, rather than select ponds which open earliest. This may explain the use of large ponds. These possibilities will be examined in greater detail in the following chapters.

Chapter III. The Effect of Distance to Foraging Areas on Reproductive Success and Nesting Location: (a) The Effect of Nest Site Location on the Reproductive Success of Red-throated Loons (*Gavia stellata*).

Introduction

Reproductive success of birds is usually determined by the availability of food and the intensity of predation (Kruuk 1964, Horn 1968, Ricklefs 1969, Hunt 1972). These factors, in turn, play a dominant role in shaping reproductive strategies involved in habitat selection, nest site selection, and mate choice. An adequate amount of food is a prerequisite for successful reproduction. If food is abundant and predictable in time and space, birds generally establish all-purpose territories. However, if food is unpredictable and is not economically defensible, colonial nesting optimizes foraging efficacy of birds (i.e. Horn 1968). The type and intensity of predation, however, also plays an important role in shaping the reproductive strategies by either favoring active anti-predator tactics improving nest defense, or by selecting for predator avoidance tactics such as camouflage through nest concealment or by choosing nesting sites at safe places.

Some avian species, such as seabirds, forage in a habitat where there are no opportunities for nesting. When feeding and nesting habitats are separated, birds must frequently fly great distances to feed. Because the costs of travelling are generally high, there should be selection on birds foraging some distance from their breeding territories to choose nesting sites as close as possible to their foraging ground. However, limited availability of high quality nesting sites which are safe from predators and close to the foraging grounds may force some individuals to breed further away, in spite of increased

travel-related costs to the breeding individuals and their offspring. Some birds may thus have to compromise and this should be reflected in their reproductive success (Martindale 1982, Fagerström et al. 1983). Therefore, when one examines reproductive success of individuals in any given population, one has to address all these problems dealing with the role of food distribution and predation.

The red-throated loon, *Gavia stellata*, is a monogamous species with circumpolar distribution. It nests by freshwater ponds; females lay two eggs in a shore-line nest, usually on an island. Predation of eggs and young is often high (Davis 1972, Bundy 1976, 1978, Bergman and Derksen 1977, Gomersall 1986). Predator avoidance tactics include low densities of breeding pairs, nesting on islands, and the inclusion of several 'escape' ponds in nesting territories (Davis 1972). Adults also actively defend eggs and chicks from smaller predators.

Although nesting territories usually contain more than one pond, adults leave the territory to forage, preferentially in marine waters (Weller et al. 1969, Davis 1972, Bundy 1976, Bergman and Derksen 1977, Reimchen and Douglas 1984, Eriksson et al. 1988). They deliver only a single fish to their chicks from each foraging trip (e.g. Norberg and Norberg 1976, Eriksson et al. 1990). Because many fish (7-14) are fed to each chick daily (Reimchen and Douglas 1985, Dickson 1987, 1992, Eriksson et al. 1990), foraging flights are frequent, making them costly in time and energy (Norberg and Norberg 1971, 1976, Davis 1972). Often only one of the two chicks is raised to fledging.

Davis (1972) found that the incidence of nesting failure increased with distance from the coast, and suggested that distance to the food source affects survival of chicks.

In addition, he observed that only 3 of 22 successful pairs reared 2 chicks, and all 3 pairs were in the coastal region. However, no detailed examination of how distance to foraging waters affects reproductive success has been made. Lack of other evidence concerning the effects of this variable on success may stem from the paucity of studies in areas more than 9 km from foraging waters (7.0 km, Bergman and Derksen 1977; 8.0 km, Merrie 1978; <5.0 km, Gomersall 1986; 8.6 km, Douglas and Reimchen 1988a; 7.7 km, Eriksson et al. 1990; but see Davis 1972, 35 km). However, Douglas and Reimchen (1988a) suggested that distance should limit the number of foraging flights per day and increase time adults are absent from nests.

In this chapter, I focus on the effect of distance from foraging waters on reproductive success. Increased distance of pairs from foraging waters could decrease incubation success by increasing foraging time, and decreasing time both adults are on and protecting their territory (usually, at least one is on territory). Predation on eggs could thus increase with increasing distance of a nest from the ocean. Distance from the ocean may also decrease the survival of chicks in two ways. First, foraging adults may not be capable of delivering enough fish to both young, resulting in starvation-related mortality of chicks. Second, adults may maintain an adequate feeding frequency at the expense of time spent guarding and defending chicks from predators, increasing predator success (Fagerström et al. 1983, Reimchen and Douglas 1985).

In addition to the potential benefit of nesting near the foraging areas, success is enhanced by early date of laying in many species (Perrins 1970), including loons (Bundy 1976, Gomersall 1986). Pairs nesting in those areas available earliest in the season

should be more successful in their reproductive effort. This may have special significance in the Arctic, where nesting may begin at a date by which populations further south have completed egg-laying (Bundy 1976, 1978, Gomersall 1986), and where the season ends relatively early. Initiation of nesting may also be influenced by microclimatic conditions affecting relative rates of thawing (Chernov 1988) within the nesting area.

Thus the objective of this chapter was two-fold. First, I investigated if distance from foraging waters influences reproductive success of red-throated loons. To achieve this, I examined success in each reproductive stage and established which factors effect differential success in each stage. Second, I investigated the effect of microclimatic gradient on breeding success. Information on these aspects of breeding ecology of red-throated loons should in turn improve our understanding of territory selection and nest-site preferences of this species.

Methods

Study area. Loons occur throughout the study area, and forage either to the east in Goodsir Inlet, or to the west in Bracebridge Inlet, whichever is closer to the nest. All pairs nest within 13 km of a coastal area. As all ponds are shallow (less than 1.5 m in depth), they freeze to the bottom in winter, preventing the survival of fresh-water fish. Loons in this area can thus forage in marine waters only.

Nesting ecology. I monitored all loons nesting within the study area in 1989 and 1990 bi-weekly from mid-June until 28 August in 1989 and until 10 September in 1990. Loons were observed from a distance of 200+ m with binoculars, except when I determined date of lay or hatch, when I flushed the birds from their nests. I selected a boundary of 9.0

km from the ocean to distinguish between pairs nesting near to and pairs nesting far from the ocean, and examined reproductive performance of 'Near' and 'Far' pairs by comparing date of laying and/or hatching, and success at each reproductive stage. The lack of published differences in success of pairs breeding at different distance categories within 9.0 km of foraging areas and the need to maintain adequate sample size in the resulting categories, determined the selection of 9.0 km as a boundary. Reproductive success was defined as the survival of at least one chick at the end of the field season (1989), or immediately before the fall freeze-over of ponds (1990). The assumption that date of laying influences reproductive success was tested by comparing hatching and pre fledging success to date of lay (1990) or hatch (1989). Finally, I compared pairs within 1.5 km of the base of the southern ridges to those more northerly to examine the effect of south/north position of pairs on date of lay and breeding success. I used non-parametric statistics (two-tailed Mann-Whitney U-test, Fisher's exact probability; Zar 1984, and G-test of independence with William's correction; Sokal and Rohlf 1981) to test for differences between pairs within the different spatial classes.

Nesting pond is defined to be the pond within a territory used by a pair for incubation. Because large ponds are frequently used by more than one pair, the term pond-site denotes the location within a given pair's territory which is used for nesting.

Allocation of parental investment. In 1990, I selected six pairs of loons for observation based on distance from the ocean, ease of access for observation, and the successful hatch of both eggs. Selection was independent of success the previous year. The three Far pairs and the three Near pairs were 10.6, 11.0, 12.9 km and 3.4, 4.0, and 4.1 km

from the nearest coast, respectively. Blinds were placed within 150 m of the nests during incubation and used for observations initiated when the first chick hatched. At this time the brood was considered a two-chick brood in case a pipping sibling had a competitive effect on the feeding of a hatched chick. Observations were made between 8:30 and 18:30, and were five hours in duration. Two observation periods of less than five hours (3 and 4 hrs), were included by extrapolating activity to a five hour period. Each pair was observed 1-3 times per week.

During each observation period, I recorded number of chicks, the duration of attendance by adults, the foraging frequency, and the success of each feeding event (if observed). Time allocated to foraging for chicks could not be measured directly, but a minimum was estimated from the number of feeding trips, distance to the ocean and flight speed (70 km/hr, Norberg and Norberg 1971, Davis 1971). Time spent on the ocean foraging was unknown and therefore excluded from the analysis.

To determine if quantity of fish delivered to chicks per unit of time is similar regardless of distance to the foraging waters, I compared the number of fish delivered per observation by Near and Far pairs. Minimum flight time required for foraging by Near and Far pairs was compared to examine whether proximity to foraging waters may affect the ability of adults to guard and protect chicks. The effect of distance (Near vs Far) and brood size (one vs two) on the dependent variables, feeding frequency and minimum flight time, was tested using a nested two-way ANOVA (Sokal and Rohlf 1981, SAS 1985). Two additional variables were included to control 1) for interaction between the main effects (distance x brood size), and 2) for behavioural variations between pairs (pair

nested in the distance x brood size).

Results

General reproductive success

In 1989, I located 32 breeding pairs. Except for three shore-line nests, all nests were on islands. Because predation was low in 1989, all but a single infertile pair succeeded in hatching eggs and subsequently rearing at least one chick. Of 30 pairs that hatched both eggs, 21 reared both chicks until the 28th of August, at which time chicks ranged in age between 19 and 36 days. One of these pairs lost a 3.5 week old chick to predation by pomarine jaegers (*Stercorarius pomarinus*). Brood reduction in all other cases (n=8) occurred within the first week of hatch.

In 1990, I located 36 pairs of loons with at least 38 nests, including second nesting attempts. All but five nests were on islands. Only 1 single-egg clutch was found; this plus 1 other clutch (2 eggs, same pair as in 1989) were infertile. Nest losses were high; 15 pairs (43%) failed to rear any chicks. Most losses occurred during incubation (n=12), while one of the 3 brood losses was caused by observer interference. Between 2 and 4 pairs re-laid, but only one replacement egg hatched. Of 20 pairs that hatched both eggs and successfully reared young, 9 reared both chicks until the 5th of September, when ponds began to freeze over. At this time, chicks ranged in age between 34 and 42 days.

Effect of distance on reproductive ecology and success

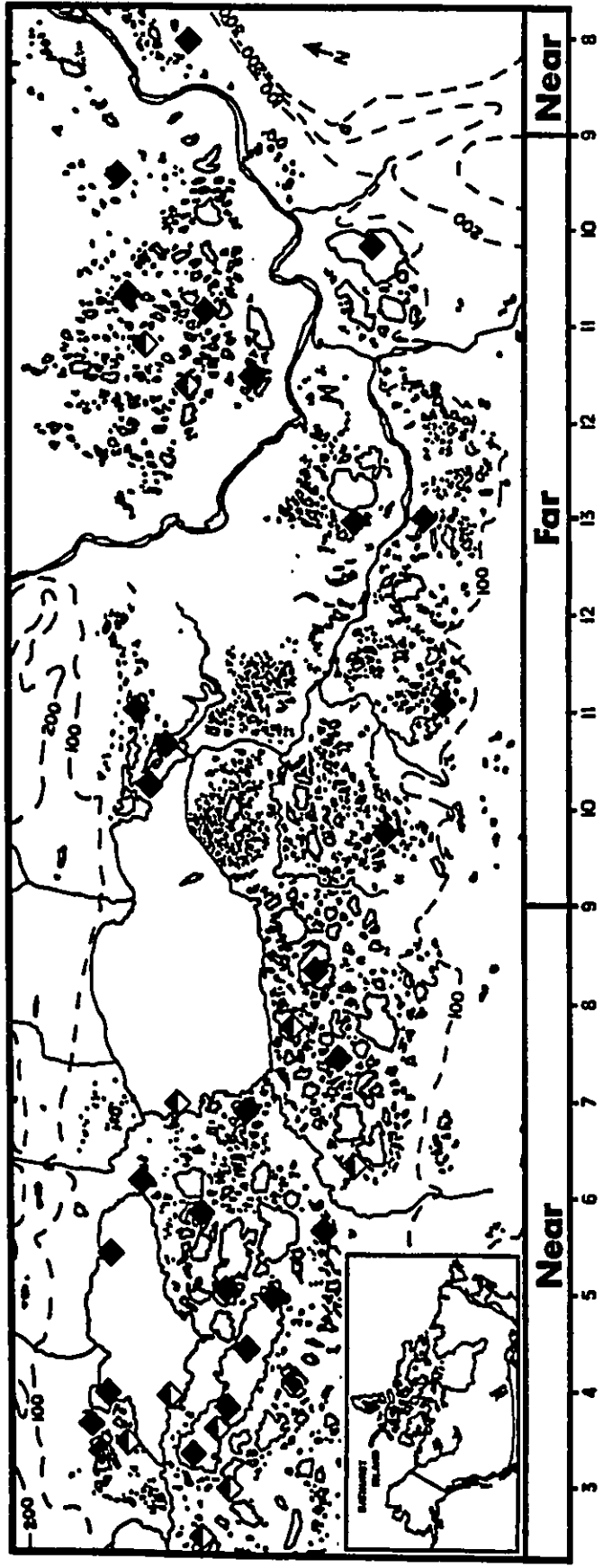
The average distance to the ocean for Near pairs was 5.3 km and for Far pairs was 11.3 km. Distance had an effect on density of loons and on success of loons in

raising both chicks until the end of the season. The density of nesting pairs in the Near region was between 1.4 and 1.7 times that of the Far region (Near: 0.90 and 1.09 pair/km², in 1989 and 1990 respectively; Far: 0.63 pair/km², both years; Figure 3.1). Although a comparison of the nearest neighbour distances for each year does not reveal a significant difference between Near and Far for either year (1989: $U=126$, $p>0.1$; 1990: $U=207.5$, $0.1>p>0.05$), pooling the data from the two years does (Near: range 0.26-1.58 km, $n=42$; Far: range 0.4-1.79 km, $n=26$; $U=726$, $p<0.05$). Furthermore, density was highest within the western most 3 km of wetland habitat, within 5.5 km of the ocean (in 1989: 1.58 pair/km² of wetland, $n=12$, and in 1990: 1.71 pair/km², $n=13$).

During the study, 17 Near pond-sites (89.5% of 1989 nests) and 12 Far sites (92.3% of 1989 nests) were used both years ($G=0.06$, $p>0.5$). Pond-sites used for the first time in 1990, when the nesting population was larger, were more numerous in the Near region ($n=6$), than in the Far region ($n=1$), suggesting a preference to establish new territories in the Near region.

Loss of eggs did not occur in 1989. All pairs with fertile eggs (31 of 32 pairs) raised at least one chick until the end of August. In 1990, 14 of 34 pairs lost all offspring either during incubation or prior to fledging. There was no relationship between distance and nesting failure (Table 3.1). Far broods from clutches in which both eggs hatched were more often reduced to one chick by the end of the season than were Near broods (Table 3.1). Seventy percent of all one-chick broods were from Far territories, and 79.3% of two-chick broods were from Near territories (pooled).

Figure 3.1. The study site at Polar Bear Pass, Bathurst Island. Insert shows location of Bathurst Island in Canada. 'Near' and 'Far' refer to distance categories relative to the ocean. Filled diamonds (n=29) show nesting sites used both years; half-filled diamonds (n=10) show nesting sites used only one year.



Distance from the Ocean (km)

Table 3.1. Nesting success and brood size as a function of distance from the ocean. Far locations are defined as >9.0 km from the ocean: Near locations <9.0 km from the ocean.

Comparison	Year	Category	Distance Class		p*
			Near	Far	
Nest Success	1989	Successful	18	13	0.59**
		Failed	1	0	
	1990	Successful	13	8	>0.50
		Failed	9	5	
Brood size	1989	1 chick	3	7	<0.05
		2 chicks	15	6	
	1990	1 chick	4	7	<0.025
		2 chicks	8	1	

* - G-test of independence calculated using William's correction, unless otherwise indicated.

** - Fisher's exact probability test.

Other events in the loons' reproductive ecology were less influenced by proximity to the ocean. Data from both years indicated no difference between Far and Near pairs in the timing of initial breeding attempt (Table 3.2). Suspected re-nesting attempts were omitted from this analysis (n=3 in 1990).

Other factors influencing reproductive success

Effect of date of laying/hatching on success. Nesting failure in 1990 was not related to date of lay (Table 3.3). However, two-chick broods were more likely to be from early clutches than one-chick broods. In 1990, all one-chick broods were from clutches laid on or after July 3 (n=9), and all two-chick broods were from clutches laid on or before that date (n=7). The 1989 data show the same pattern (Table 3.3). The lack of a relationship between date of lay and distance (Table 3.2), indicates that these two variables act independently of each other on brood size.

Effect of north/south location on success. Date of lay was also influenced by location (Table 3.4) in both years. Reproductive success of pairs in the northern area was significantly less than success of pairs in southern areas in 1990 (Table 3.5: 20% failure in the south, 55% failure in the north). Survival of two-chick broods was also affected by location; pairs in the south more often lost one chick (Table 3.5: south: 63%, n=24; north: 23%, n=26; pooled). However, the brood size versus location relationship was slightly weaker (Table 3.5: 1989: $p < 0.05$; 1990: $0.1 > p > 0.05$) than that of brood size versus distance (Table 3.1: 1989: $p < 0.05$; 1990: $p < 0.025$).

Table 3.2. Date of hatching (1989) and laying (1990) as a function of distance to the ocean. June 1 is date '1' in both years. n = sample size.

Year	Date of hatching/laying						p*
	Near			Far			
	Median	range	n	Median	range	n	
1989	58	53-70	18	61	55-70	12	0.1>p>0.05
1990	33	30-47	17	33	28-40	13	>0.2

* - probability based on two-tailed Mann-Whitney U-test.

Table 3.3. Nesting success and brood size as a function of date of hatching for 1989 and date of laying for 1990 . June 1 is date '1' in both years. Med. = median, n = sample size.

Comparison	Year	Success Class						p*
		Successful			Failed			
		Med.	Range	n	Med.	Range	n	
Nest success	1990	33	30-40	16	33	28-47	14	>0.2
		1 chick			2 chicks			
		Med.	Range	n	Med.	Range	n	
Brood size	1989	62	56-70	7	58	53-69	21	<0.05
	1990	33	33-40	9	33	30-33	7	<0.02

* - probability based on two-tailed Mann-Whitney U-test.

Table 3.4. Date of hatching for 1989 and laying for 1990 as a function of South/North location, for all nesting pairs. June 1 is date '1' in both years. Med.= median date of the range, n = sample size.

Year	South/north location						p*
	South			North			
	Med.	Range	n	Med.	Range	n	
1989	60	56-70	13	58	53-69	17	<0.03
1990	33	31-47	11	33	28-40	19	<0.04

* - probability based on two-tailed Mann-Whitney U-test.

Table 3.5. Nesting success and brood size as a function of South/North location within the study area. South = southern 1.5 km of study area, North = northern 1.5 km of study area.

Comparison	Year	Category	South/north location		p*
			South	North	
Nest Success	1989	Successful	13	18	0.59**
		Failed	0	1	
	1990	Successful	12	9	<0.05
		Failed	3	11	
Brood size	1989	1 chick	7	3	<0.05
		2 chicks	6	14	
	1990	1 chick	8	3	0.1 < p < 0.05
		2 chicks	3	6	

* - G-test of independence calculated using William's correction, unless otherwise indicated.

** - Fisher's exact probability test.

Effect of distance on foraging budgets

Observations of five loon pairs commenced within a day of hatch of the first chick (July 27-30) and observations of the sixth pair (Near) began when the eldest chick was 8 days old (August 7). Of the six pairs, three (1 Near and 2 Far) lost one chick, 1-3 weeks after hatching. One of the Near pairs lost two chicks to predation by wolves 4 days after hatching. Only two pairs (1 Near and 1 Far) successfully raised two chicks until the fourth week of August, when observations on the five remaining pairs were terminated.

Frequency of fish delivery to chicks was greater for pairs nesting near the ocean (controlled for brood size, $p=0.025$), as well as for pairs having two-chick broods (controlled for distance class, $p=0.002$) (Table 3.6). One-chick broods were offered an average of 2.15 ± 1.16 (SD) fish per five hour period, while two-chick broods were offered an average of 4.15 ± 1.32 fish. Near broods received 4.25 ± 1.58 fish / five hrs, while Far broods received 3.13 ± 1.4 fish. Thus, feeding frequency was not equal across the distance classes.

Estimated time required for foraging flights differed between Near and Far pairs (Table 3.7). More time was spent on foraging flights by Far pairs (controlled for brood size, $p=0.0026$) and by pairs having two chicks (controlled for distance class, $p=0.046$). Far pairs accumulated twice the total estimated flight time of Near pairs (70.00 ± 32.2 vs 33.6 ± 11.7 min/5 hrs), and pairs with two chicks were estimated to fly almost twice the time as those with only one chick (62.80 ± 31.6 vs 38.07 ± 24.7 min/5 hrs). These results suggest that Far pairs spent a greater amount of flight time acquiring fewer fish, than Near pairs.

Table 3.6. Number of fish returned by adult loons nesting Near and Far from the ocean. a) Average number of fish offered to one and two chicks broods, Near and Far from the ocean. b) Results of a nested ANOVA examining the effect of distance, brood size and interactions between these two, on average number of fish fed per 5 hours period. F values are determined from Type III Sums of Squares. n = number of five hour observations.

a)	Number of chicks*	Distance class	n	Average number of fish returned per 5 hour period \pm st.dev.
	One	Near	4	2.65 \pm 1.30
	One	Far	7	1.86 \pm 1.07
	Two	Near	11	4.83 \pm 1.27
	Two	Far	16	3.69 \pm 1.20

b) EFFECTS TESTED IN NESTED ANOVA	df	F	p
A) Near to vs. Far from ocean	1	5.66	0.025
B) One chick vs. Two chicks	1	11.68	0.002
C) Interaction of A and B	1	0.86	0.360
D) A and B nested in Loon Pair	5	0.91	0.486

* - all broods began as two chick broods; one chick broods are those from which one chick was lost.

Table 3.7. Estimated minimum flight time from foraging trips, required by loons to forage for their chicks. a) Average estimated flight times required to obtain fish per 5 hours, for one and two chick broods, Near and Far from the ocean. b) Results of nested ANOVA examining the effects of distance, brood size, and interactions between these two on flight time. F values are determined from Type III Sums of Squares. n = number of 5 hour observations.

a)	Number of chicks*	Distance class	n	Estimated flight time** (min./5 hrs. \pm st.dev.)
	One	Near	4	24.16 \pm 10.04
	One	Far	7	46.01 \pm 27.69
	Two	Near	11	37.06 \pm 10.57
	Two	Far	16	80.49 \pm 28.93

b) EFFECTS TESTED IN NESTED ANOVA	df	F	p
A) Near to vs. Far from ocean	1	10.86	0.0026
B) One chick vs. Two chicks	1	4.33	0.046
C) Interaction of A and B	1	0.24	0.626
D) A and B nested in Loon Pair	5	0.95	0.464

* - all broods began as two chick broods; one chick broods are those from which one chick perished.

** - minimum estimate.

Discussion

This study demonstrates that nesting location and the date of lay may affect nesting success and brood size of the red-throated loons. Causes of nesting failure and brood size reduction are discussed in the following sections.

Nesting failure

Most nesting failures occurred during incubation. This implies that predation is the major cause of nesting failure. Potential predators of loon eggs and chicks in the study area include the arctic fox (*Alopex lagopus*), arctic wolf (*Canus lupus*), glaucous gull (*Larus hyperboreus*), jaegers (*Stercorarius pomarinus*, *S. parasiticus*), and snowy owl (*Nictea scandiaca*). These predators forage throughout the entire wetland area and thus have a potentially similar impact on success of loon pairs throughout the study area.

The lack of distance-related failure between Near and Far pairs is in contrast to Davis (1972). Davis (op. cit.) found that loons, which nested in an area with a midpoint at 13 km from the ocean, failed more frequently than those which nested in an area with a midpoint at 9.5 km from the ocean. The lack of distance effect in my study, coupled with the fact that most events causing failures occurred during the incubation stage, suggests that 1) predators had a similar impact on loon success in Near and Far areas, and 2) during incubation, a single adult was as efficient at nest guarding as two adults.

The fact that nests of the northern part of the wetland failed more frequently than those in the south could be explained by the thawing pattern. Because the northern area thawed sooner it is likely that this area generally attracted more breeding birds, which in turn may have attracted more predators (Chernov 1988).

In contrast, date of lay, even though it is correlated with north/south location, did not affect failure. This is not congruent with Bundy (1976) who reported a decrease in success with date of laying. Findlay and Cooke (1982) also found higher failure in colonial snow geese (*Chen caerulescens*) nesting before or after the peak laying period, and reasoned that predator satiation decreased losses during peak nesting. This mechanism however could not operate in this study area because red-throated loons breed here at low densities.

Other factors that could potentially cause nesting failure seem less important. Flooding of nests (Cyrus 1975, Lokki and Eklof 1984, Gomersall 1986) and desiccation of ponds leading to stranding and subsequent abandonment or predation of nests (Bundy 1976, Douglas and Reimchen 1988b, Eriksson et al. 1988) are occasional causes of failure of loon nests. Even though the north of this area received much of the first meltwaters, the water levels at the time of nesting were stable in both years. Flooding or drying of ponds are thus unimportant.

Nest success in other species has been correlated with familiarity of pairs with their territory and neighbours (e.g. Picman 1987, Gauthier 1990). This may account for site tenacity in this loon species (Davis 1972). At least 91% of 32 pond-sites used in 1989 were also used in 1990. Territory re-use from 1989 may have been as high as 100%, as the 3 single-use ponds of 1989 were near single-use pond-sites in 1990, and may have been on the same territories. Four other single-use pond-sites were definitely in new territories. Equal proportions of these were in the north (n=2) and south (n=2), and because one of each failed, new territories did not contribute to the greater failure in the

north.

Factors affecting brood size

Loss of a chick could be caused by nestling starvation or predation. Brood size of successful pairs was affected by distance to the ocean, north/south location, and by date of lay. Brood size decreased with increasing distance of breeding territories from foraging areas. All broods considered in this analysis consisted originally of two-chicks, so the probability of one chick dying before fledging in Far broods is greater than in Near broods.

The time budget study indicated two important differences between pairs nesting near to and far from the ocean which may have influenced chick survival. As predicted, Near pairs foraged for their chicks more often than Far pairs, and required less time to do so. This is consistent with the proposition that one-chick broods resulted from starvation of one of the siblings. However, this could also have resulted from decreased vigilance allowing predation of an otherwise healthy chick. Dickson (1992) suggested that unattended newly hatched chicks are vulnerable to predation by glaucous gulls. I observed that during the first week after hatch, chicks rarely ventured from the brooding adult except when being fed. Chicks were not left unattended until they were several weeks old and were capable of diving to protect themselves (chicks were unattended in weeks 1, 2, 3, and 4+, respectively, for 0.3 of 105 observation hours, 0 of 71 hours, 2.8 of 70 hours, and 6.8 of 36 hours). I also observed that if a disturbed family with both adults present entered the water, each chick was attended by one adult. Thus loon chicks are most vulnerable to avian predators when only one adult is present, and some

terrestrial threat is nearby to force the loons into the water. Although this might explain a few cases of chick mortality, I suggest that this type of predation cannot explain most of the differential chick mortality in the two distance categories. This view is supported by evidence that (1) there was no distance-related difference in nesting failure, which is generally a result of predation, and (2) pairs breeding in the northern region, where nesting failure due to predation was more frequent, had better chances of raising both chicks.

I conclude that the starvation-related death of the younger, weaker sibling is the most likely cause of brood reduction in situations far from the ocean. Sibling rivalry, well documented for red-throated loons (i.e. von Braun et al. 1968, Davis 1972) and described for other related species (i.e. Neuchterlein 1981, Croskery 1989) is intense, and has been the most commonly implicated cause of the rarity of two-chick broods in this species. In addition to lower rates of feeding in Far territories, starvation as the cause of nesting mortality is also supported by the observation that most second chicks disappeared within the first two weeks of hatching, when chicks are especially vulnerable to starvation. Gomersall (1986) likewise found second siblings to disappear within 10 days of hatching.

The higher density of loons near the ocean suggests that Near territories are preferred by the loons. This has also been reported by Davis (1972), although Douglas and Reimchen (1988a) found no effect of distance from the ocean on breeding densities of loons. Larger broods and higher density in the Near region resulted in a chick production per area twice that of the Far region. Similarly, Davis found higher chick production in areas near the ocean than far from the ocean.

The date of laying (1990), or hatching (1989) was similar for Near and Far pairs. However, there was a negative relationship between number of young raised by successful pairs and date of laying/hatching - early laying successful loons more frequently raised both chicks. Gomersall (1986) also found that all surviving two-chick broods were from clutches laid within the first few weeks of the 11 week laying period. The higher incidence of two chick broods in the early thawing northern part of the study area is consistent with these findings. I assume that mechanisms behind enhanced survivorship of northern broods are the same as those enhancing survivorship of early nesters.

Decreased success in rearing two chicks with date of laying may be age-related. It has been demonstrated in other species that older birds lay earlier than younger birds, and are also more successful (e.g. Perrins 1970). Age of the loons in this study area could not be determined. However, a counter argument against age-related success, relevant in colder areas of the Arctic, is based on the site tenacity exhibited by loons (Davis 1972). Site tenacity implies that the earliest available ponds are not settled by the oldest birds, but by the same tenant pair from the previous year. The generally delayed pond availability at this latitude, coupled with the microclimatic effect, is then responsible for variations in date of lay, and therefore in success.

Brood reduction in late broods could have been caused by a seasonal decline in prey availability. However, there was no decrease in delivery rate of fish to two-chick broods (linear regression of fish returned/chick for all pairs, versus date: $b=0.005$; $t=0.157$, $p=0.88$, $n=48$; see also Dickson 1992). This differs from the findings of

Reimchen and Douglas (1985), who found that the number of fish fed per day decreased with age of a chick. Both early and late nesters in their study fed more smaller fish to young chicks and fewer large fish to older chicks.

Finally, a decreased quality of prey fish could also account for a decrease in chick survival in late broods (i.e. Hedgren and Linnman 1979). Quality of fish, as measured by caloric content, decreases after spawning. Unfortunately the prey species utilized by the Bathurst Island loon population and their spawning times have not been established. Therefore, I cannot test this hypothesis.

To summarize, distance from foraging waters plays an important role in the reproductive success of red-throated loons. Although success during incubation was unaffected by distance in this study (but see Davis 1972), distance had an effect on the survival of both members of two-chick broods. Distance-related chick mortality is likely a result of starvation-related death of the weaker sibling. Microclimatic conditions within the wetland habitat also influenced success. By affecting the relative time of melt of nesting ponds, microclimate can delay the onset of nesting in some areas. The loons nesting in the area that experienced earlier melt also suffered higher predation. However, the date of nesting also influenced success in raising chicks; as compared to late nesters, early nesters more frequently raised two chicks.

(b). The Effect of Proximity to the Foraging Areas on Habitat Distribution and Territory Selection.

Introduction

Bird species commonly breed in more than one type of habitat. Because different habitats vary in their qualities, species distributions (i.e. density and spatial distribution) generally vary between habitats. However, in situations where the species forages outside the nesting habitat, the central place foraging theory must be considered when examining distribution of birds within a habitat. This theory can be used to predict how animals could maximize the net energy intake by reducing (minimizing) costs of travelling to foraging areas (Orians and Pearson 1979). Nesting near the foraging area may increase reproductive success by either increasing the amount of food provided to young, or by allowing a greater time to be devoted to other forms of parental care, as less time is required for foraging.

An increase in red-throated loon reproductive success related to distance to foraging areas was demonstrated in chapter IIIa: loon pairs nesting near the ocean were more successful at rearing two chicks than those far from the ocean. This was likely due to a larger number of fish fed to each chick and hence lower losses of younger siblings (see also Davis 1972) in territories near the ocean. The higher density of loons near the west coast was consistent with this view.

Because of the gradient in habitat suitability with proximity to the foraging area, variation in territory selection and settlement patterns along this gradient can be expected. In this study, I characterize red-throated loon territories near and far from the foraging

areas, and examine settlement patterns of loons.

I also address the question posed in Chapter II regarding the large ponds selected near the ocean. The nesting ponds used by loons in my area were significantly larger than those observed elsewhere (see Chapter II). Figure 3.1 illustrates the predominance of the large ponds within 9 km of the west coast. It is therefore unclear whether loons are selecting the large ponds near the ocean 1) because they prefer ponds of this size, or 2) because there are more large ponds in the wetland near the ocean. I tested these hypotheses as follows. First, I examined nest density and size of nest ponds within 5 km of the east coast, where, in contrast to the west coast, ponds were generally smaller. If loons do require large ponds on which to nest, density along the east coast should be lower. On the other hand, if there is no preference for large ponds, loon densities should be similar along the east and west coasts. Second, I examined pond use further inland, where small ponds are more numerous, to establish whether large ponds are preferentially used even in this area. Frequent utilization of large ponds in this area would indicate that loons prefer large ponds.

Methods

I located all loons nesting in the main study area during 1989 - 1991. Territories were defined as ponds or areas in a large lake which were defended by the pair nesting in or nearby the pond or which were exclusively used for resting or preening by at least one member of the nesting pair. Movement of a pair to a new pond on its territory in the second and third year was determined by proximity of a new nesting pond to a vacated pond, and behaviour of the pair (i.e. utilization of the vacated pond by that pair for resting

or preening). In this way I avoided classifying a pair using an alternative pond on its territory, as a newly established pair. I determined size of territories by summing up the areas of all territorial ponds. If lakes were included in a territory, the area of the defended portion of the lake was included. I calculated densities of breeding loons in three distance-to-ocean (DTO) classes (2-5.5, 5.5-9, and 9-13 km from the coast) and determined size of nesting ponds from a topographic map of the region. The east coast region of the study area, located between 1.5 and 4 km from the ocean, was surveyed on foot twice in 1990 to locate nesting pairs. I determined size of ponds in this area from aerial photographs (1:12,000, obtained from the National Air Photo Library, Energy, Mines and Resources).

Because a decrease in pond use is expected in habitat further from the ocean (see Chapter III), I used a Mantel-Haenzel χ^2 analysis (χ^2_{mh}) to examine the numbers of nesting vs non-nesting ponds at increasing distances from the ocean for each size class. Distances from the ocean were categorized as above (2.5-5.5, 5.5-9.0, and 9.0-13.5 km). I also examined use of the different pond classes within each distance category, also using Mantel-Haenzel χ^2 analysis, to examine whether there is a decrease in proportions used with decreased size. Because loons generally nest on islands, only non-nesting ponds with islands were considered in the analysis. Data from the three years were pooled when more than 20 percent of the expected frequencies in the contingency tables exceeded 5 (Zar 1984).

Results

Settlement of new pairs

Within the three years of study, several ponds were abandoned, and a few others newly occupied. Nine pairs relocated to an alternative pond in their territory. Four new territories were occupied and used for nesting for the first time during this study (3 in 1990 and 1 in 1991). These new territories were located between 5.5 and 8 km from the coast, in the area of intermediate density (Table 3.8). No new territories were established in the high density area (between 2.5-5.5 km from the ocean). Two other new territories were occupied in 1991, but it is uncertain whether their owners nested. One was in the intermediate density area (5.5-9 km from the ocean), the other in the low density area (9-13 km from the ocean, Table 3.8).

Territory size

The average number of ponds per territory in Near, Intermediate and Far DTO areas is 1.75 ± 0.62 (SD; $n=12$), 1.82 ± 0.60 (SD; $n=11$), and 1.95 ± 0.69 (SD; $n=13$) ponds, respectively. There were no significant differences in territory area, with Near territories having a water area of 8.4 ± 3.36 ha; Intermediate territories, 10.3 ± 7.25 ha; Far territories, 8.9 ± 6.98 ha (Kruskal-Wallis $\chi^2=0.52$, $p=0.771$). A contingency table comparing number of territories with more than one pond with those having at least one pond greater than 5 ha indicates no trend: territories which include large ponds do not contain a smaller or greater total number of ponds (Table 3.9).

Pond size selection: east coast survey

Seven pairs nested along the east coast. Ponds used by these loons ranged between 0.3-21.7 ha (mean= 4.97 ha ± 7.705). Only three ponds were over 5 ha in size:

Table 3.8. Density of loons in the main study area in 1989, 90 and 91 and by the East coast in 1990.

	Western study area			East coast area
	Near	Intermediate	Far	
Area (km ²)	7.6	11.6	22.8	5.4
Density (n)				
1989*	1.6 (12)	0.6 (7)	0.6 (13)	
1990*	1.7 (13)	0.9 (10)	0.6 (13)	1.3 (7)
1991*	1.7 (13)	1.0 (11)	0.6 (13)	
1991**	1.7 (13)	1.0 (12)	0.6 (14)	

* - includes territories with confirmed nests.

** - includes territories in which nesting was not verified.

Table 3.9. Frequency of territories containing one or more ponds versus those with at least one pond greater than five hectares in size. $\chi^2=0.002$, $p=0.964$.

Number of ponds in territory	Size of pond	
	<5 hectares	>5 hectares
One	3	8
More than one	7	18

Table 3.10. Nearest neighbour distances at varying distances to the ocean (DTO) and significant differences by the Mann-Whitney U-test. The ends of each horizontal line (—) indicate areas with nearest neighbour distances which are significantly different.

	Area			
	Near: east coast (DTO= 1.5-4.0 km)	Near: west coast (DTO= 3.0-5.5 km)	Intermediate (DTO=5.5 - 9.0 km)	Far (DTO= 9.0-13.0 km)
x (n)	0.64 (7)	0.49 (13)	0.78 (10)	0.85 (13)
p<0.05		—————		

two were used for nesting and the third pond was included in a territory of a loon nesting nearby (200 m) on a 0.3 ha pond.

Density of nesting loons in this area was 1.3 pairs per square kilometer ($n=7$, Table 3.8). Density of loons nesting along the west coast (2.5-5.5 km from the ocean) was between 1.6 and 1.7 pair/km² ($n=12$, $n=13$ and $n=13$ in 1989, 1990 and 1991, respectively). Nearest neighbour distances were not significantly different between the two areas (Mann-Whitney U-test; $U=60.5$, $n_1=13$, $n_2=7$, $p>0.05$; Table 3.10). However, the sample size of loons nesting near the east coast was small. There was also no significant difference between nearest neighbour distances of loons nesting 5.5-9 or 9-13 km from the ocean, and those from the east coast ($U=42.5$, $n_1=10$, $p>0.05$; $U=59$, $n_1=13$, $p>0.05$, respectively).

Nesting versus non-nesting pond proportions

Ratios of nesting and non-nesting ponds of three size classes, from the three DTO classes are given in Table 3.11. In general, pond use decreased with distance from the ocean (1989: $\chi^2_{mh}=2.89$, $p=0.089$; 1990: $\chi^2_{mh}=4.04$, $p=0.044$; 1991: $\chi^2_{mh}=4.68$, $p=0.031$). However, when all ponds were classified into three size classes, small and medium ponds were selected for nesting in equal proportions in all three DTO classes ($\chi^2_{mh}=1.54$, $p=0.21$, $\chi^2_{mh}=0.99$, $p=0.32$, pooled). Only the ponds over 5 ha were selected less frequently with increasing distance from the ocean ($\chi^2_{mh}=15.27$, $p<0.001$, pooled). Removal of the multiply used lakes ($n=3$, area greater than 70 ha) to create a new category of ponds greater than 5 but less than 70 ha in size, indicated a consistent use of ponds in this class ($\chi^2_{mh}=2.71$, $p=0.1$, pooled) with distance from the ocean. Two of

Table 3.11. Occurrence of nesting red-throated loons on three pond sizes, at three distances from the ocean. Data from 1989, 1990 and 1991 are pooled*.

Pond size	Pond status	Number (%) of ponds selected vs rejected by nesting loons at various distances from the ocean (km)			χ^2_{mh} (p)
		2.5-5.5	5.5-8.5	8.5-13.0	
0.2-1.0 ha	Nesting	4 (7.4%)	0 (0%)	3 (2.8%)	1.65 (0.2)
	Non-nesting	50	45	105	
1.0-5.0 ha	Nesting	3 (14.3%)	16 (28.1%)	25 (23.8%)	0.21 (0.65)
	Non-nesting	18	41	80	
5.0+ ha	Nesting	28** (80.8% [§])	15 (50%)	10** (41.2% [§])	8.83 (0.003)
	Non-nesting	5	15	11	
χ^2_{mh} (p)		51.77 (<0.0001)	25.85 (<0.0001)	33.81 (<0.0001)	

* - Non-pooled data show similar trends, but in all cases contingency tables include $>20\%$ of expected frequencies less than 5.

** - Count includes sites on lakes used by more than one pair: eight sites were located on two lakes in the 2.5-5.5 km DTO class.

§ - Percentage based on number of used vs unused lakes/ponds, not number of pairs at the lakes.

these lakes (lying between 3-6 km from the ocean, accounted for 22 nesting pairs in 3 years. The third lake, lying between 7-11 km from the ocean, accounted for 8 nesting pairs in 3 years. The decrease in use of large ponds can therefore be explained by the multiple occupancy of three large lakes.

In spite of the decrease in the lake sites used for nesting with increased DTO, the ratio of the nesting/non-nesting large ponds between 5 and 70 ha in size was 1/1, which is much larger than that seen for both the medium (1/3) and small (1/30) ponds (see also Table 3.11 and Chapter II). Thus, percentage of ponds used for nesting increased with pond size: ponds <1 ha: 3% (n=207), ponds 1-5 ha: 24% (n=183), ponds 5-70 ha: 42% (n=53), and ponds >70 ha: 100%, (n=3). In a further breakdown to examine selection of ponds within each DTO class, Mantel-Haenzel χ^2 values for selected versus rejected ponds of three size classes indicate that use of ponds increases with size in all distance classes (Near: $\chi^2_{mh}=51.77$, $p<0.0001$, Intermediate: $\chi^2_{mh}=25.85$, $p<0.0001$, Far: $\chi^2_{mh}=33.81$, $p<0.0001$).

Discussion

The habitat of a species is defined by the biologically relevant features both physical and biological nature, within an area (Fretwell 1972). To account for habitat selection by species which forage outside of their nesting habitat, the scope of this definition must be broadened to consider the spatial gradients between food resources and the nesting habitat. The red-throated loon distribution and settlement patterns along this distance gradient demonstrates the importance of this modification. The value of nesting close to the ocean is demonstrated by the greater reproductive success in Near

regions (Chapter IIIa). Thus the habitat in the Near regions has a higher density (Chapter IIIa) and new territories are established predominantly in the zone of intermediate distance to the ocean.

Another important consideration in describing distribution of nesting birds in different habitats, is whether the success of individuals varies between habitats. If success of birds in a preferred habitat (i.e. high density habitat) equals that in a less preferred habitat (low density), then the distribution is termed ideal free (Fretwell and Lucas 1970, Fretwell 1972). In this situation, territoriality merely functions as an index of habitat suitability (i.e. it does not directly set an upper limit to population density). The newly settling individuals thus select a habitat also based on their assessment of population density. If success of birds in a preferred habitat is always higher than that in less preferred habitat, then the distribution is termed ideal despotic (Fretwell and Lucas 1970, Fretwell 1972). In this situation, territoriality functions to directly prevent new individuals from establishing a territory in a habitat already occupied by a certain density of individuals/pairs.

Because success of loons from areas Near and Intermediate in distance from the ocean is greater than that Far from the ocean, the distribution of loons tends toward ideal despotic. This view is supported by observations that during this study, population density was constant in the wetland near the ocean, and settlement of new pairs was limited to the intermediate zone. These data suggest that the loon settlement on Bathurst Island corresponds to the second stage of Brown's (1969) model on population buildup. According to this model, nesting pairs first settle in high quality habitat (first stage), where

reproductive success is greatest. Settlement here continues until a threshold density is achieved where resident individuals no longer allow settlement of new pairs. At this point settlement of new pairs continues in the lower quality habitat (second stage). When the lower quality habitat is similarly saturated, subsequently arriving individuals become floaters (third stage) that wait for the opportunity to reproduce once some breeding space becomes vacated.

Davis (1972) observed that loon territories in his study area included on average 2.86 ponds, regardless of territory size (i.e. territory 'size' was determined by number of ponds, not by area of land or water) and distance from foraging areas. Similarly, in my study, most pairs defended two ponds, with a conservative estimate of 1.8 ponds per territory (this number did not vary with distance from the ocean). In addition, I observed that pairs nesting in one of the three lakes defended and used small ponds adjacent to their breeding site on the lake, and that the area of territorial waters was variable and did not increase with the distance to the ocean. This further supports the view that the number rather than the size of pond or area of water, is an important territory characteristic. Multiple ponds may allow escape from mammalian predators (see also Davis 1972). This view is also supported by observations that loons nesting on offshore islands with no mammalian predators, include one pond only in their territories (Davis 1972).

Because the number of nesting loons on the multiple use lakes decreased with distance from ocean, it is evident that high use of ponds larger than 70 ha for nesting is partly due to their high availability near the ocean. But, in all regions, the ratio of used

to unused large ponds is higher, than that of medium ponds and small ponds. Likewise, the ratio of used to unused medium ponds is greater than that for small ponds in all regions. This is in contrast to several other studies, (Davis 1972, Gomersall et al. 1984, Okill and Wanless 1990), in which small ponds were more frequently utilized. And in other areas, where the red-throated loon's key competitor, the pacific loon (*G. arctic pacifica*) does not breed, all pond size classes were used by red-throated loons in equal proportions (Bundy 1976, 1978, Gomersall et al. 1984, Gomersall 1986, Douglas and Reimchen 1988a; see Chapter II).

It could be argued that the more frequent use of large ponds could result from their greater surface area or shoreline length. In other words, if territories of similar size are evenly distributed, then many territories would fall on the large ponds. Conversely, some territories would contain many small ponds, but small ponds would not be subdivided among several territories. However, this factor should presumably also operate for the other loon populations which may freely use the wetland habitat (i.e. when there are no restrictions from competing pacific loons). In these populations, though, loons use ponds proportional to their availability. Furthermore, territories are not of a set size (i.e. in terms of water/land area), as presumed in this argument, but are a function of pond number. This fact is illustrated by the consistent number of territorial ponds in both this study (1.8 ponds/territory) and Davis's study (1972, 2.9 ponds/territory).

Density of loons along the east coast was slightly, but not significantly lower as compared to that along the west coast. This may be due to the limited availability of ponds larger than 5 ha. The density to the east, however, was slightly, but not

significantly, higher than that in the intermediate zone to the west. This supports the preference by loons to nest near the ocean, regardless of pond size. Although the lack of significant differences may be attributed to the small sample size of the east coast sample ($n=7$), these interpretations cannot be regarded as conclusive.

In summary, the settlement patterns exhibited by this population of red-throated loons seem to follow the ideal despotic model. The high nesting numbers of loons on ponds greater than 5 ha in size may partly be a result of greater availability of lakes larger than 70 ha near the ocean, where breeding density and reproductive success of loons were higher (see Chapter IIIa). However, ponds larger than 1 ha were preferred in all areas of the wetland.

This still leaves several unanswered questions regarding my observations on territory and nest site selection. First, why is there a preference for large ponds for nesting? As shown here, this selection is evident even in areas further from the ocean, where smaller ponds were more common. Second, why are territories spaced out? This study has illustrated high success near the ocean and low success far from the ocean, yet the loons do not nest exclusively near the ocean. Evidently, another factor must play a role in determining the pattern of distribution of red-throated loons on Bathurst Island. Otherwise, loons should nest at much higher densities in areas near the ocean only. Finally, why do territories contain more than one pond? The following two chapters address these three questions regarding territory and nest site selection.

Chapter IV: Effect of Predation on Territory Placement and Nest Site Selection by the Red-throated Loon (*Gavia stellata*) in the Canadian High Arctic

Introduction

Predation is a major factor decreasing reproductive success in most bird species. Ground nesting species relying on passive anti-predator tactics such as camouflage and spacing, may be very vulnerable to losses from predation. Therefore there should be high selective pressure on them to optimize these tactics.

The red-throated loon is a monogamous wetland bird species which nests on islands or along shores of fresh-water ponds and lakes. The clutch of 2 eggs is incubated by both adults (Davis 1972, Petersen 1976) for 24-31 days (Davis 1972, Petersen 1976, Bundy 1976, Dickson 1987, Douglas and Reimchen 1988b, Chapter II). The loon is obliged to nest near the water due to its limited mobility on land. In much of its arctic breeding range, however, this habitat offers little cover for concealment of nests. These two factors may allow predators to specialize on their eggs by selectively searching shorelines (Schranck 1972, Enquist 1983, Crabtree et al. 1989). Chicks are fed by both parents for a 5.5 - 8 week pre fledging period (Reimchen and Douglas 1984, Eriksson et al. 1990, Chapter II). During this period, the activities of the brood are restricted to the pond at which the eggs were laid or to a nearby pond, if the chicks have been relocated. This predictability of location of the loon family over several months may also assist in location by predators (Morse 1980). As a result, loon broods are more vulnerable than those of other more mobile precocial waterfowl species. Therefore, red-throated loons are presumably under heavy selective pressure favouring anti-predator strategies.

Predators of the red-throated loon eggs and young include both birds (i.e. jaegar species, gull species, bald eagle, sandhill crane), and mammals (i.e. foxes, wolves and mustelids) (see Table 4.1 for complete list). Loons are large enough to actively defend eggs and young, often successfully, from the smaller avian predators (such as jaegers, gulls; pers. obs., Parmelee et al. 1967, Bundy 1976, Enquist 1983). However, this loon species cannot successfully defend offspring from mammalian predators, such as foxes or wolves nor against larger bird species, such as raptors and cranes. Red-throated loons must therefore rely largely on predator avoidance strategies to protect their reproductive effort.

In this chapter, I investigate some predator avoidance tactics available to breeding red-throated loons. Patterns of predation were examined both experimentally and within the nesting loon population to determine whether territory placement and nest site selection are used effectively to minimize probability of location by predators. With the use of artificial nests, I examined the effect of prey distribution (uniform, random and clumped) and density (high, medium and low), on predation rates. Presumably territory/nest site placement by loons should reflect the spatial pattern of artificial nests which suffer the least predation.

In addition to the experimental studies of predation, I determined nesting success of loons in the study area in 1989, 1990 and 1991. I examined the ponds of depredated and successful nests to establish what characteristics of nesting ponds coincide with reduced predation. I also determined spatial patterns of distribution of depredated nests. Finally, I examined temporal differences in predation within and between years.

Table 4.1. Predators of red-throated loons eggs and chicks. References: 1: Davis 1972; 2: Bundy 1976; 3: Bergman and Derksen 1977; 4: Bundy 1978; 5: Douglas and Reimchen 1988b; 6: Enquist 1983; 7: Eriksson et al. 1990; 8: Furness 1981; 9: Reimchen and Douglas 1984; 10: Schamel and Tracy 1985. Pers. obs. refers to observations of attempted or successful predation of red-throated loon chicks.

Type of predator	Predator	References
Avian predators	Bald eagle, <i>Haliaeetus leucocephalus</i>	9,5
	Goshawk, <i>Accipiter gentilis</i>	7
	Sandhill crane, <i>Grus canadensis</i>	1
	Parasitic jaegar, <i>Stercorarius parasiticus</i> *	1,2,3,6
	Pomarine jaegar, <i>S. pomarinus</i> *	3, pers.obs.
	Great skua, <i>S. skua</i>	2,4,8
	Glaucous gull, <i>Larus hyperboreus</i> *	3
	Great black-backed gull, <i>L. marinus</i>	4
	Lesser black-backed gull, <i>L. fuscus</i>	2
	Herring gull, <i>L. argentatus</i>	1,2
	Snowy owl, <i>Nyctea scandiaca</i> *	pers.obs.
Mammalian predators	Hooded crow, <i>Corvus corone</i>	2
	Red fox, <i>Vulpes fulva</i>	1,10
	Arctic fox, <i>Alopex lagopus</i> *	1,10
	Wolf, <i>Canus lupus</i> *	pers.obs.
	Raccoon, <i>Procyon locor</i>	5

* - Predators occurring on Bathurst Island

Methods

Effect of spatial distribution of nests on predation

To examine the effect of spatial distribution of nests on predation I established three quadrats containing artificial nests arranged in a random, clumped or uniform pattern of distribution. To avoid disturbing nesting loons, and to more effectively control for differences between quadrat layouts, I placed the quadrats in the wet meadow adjacent to wetland ponds. The three quadrats (100x100m) were at least 80 m apart, and each was marked with orange flagging tape on a 30 cm bamboo stake at the corners and every 20 m around the edge. Forty experimental nests, each with one dyed chicken egg (see Chapter I, Methods), were placed in each quadrat in the designated pattern of distribution (see Picman 1990). Eggs were further concealed by draping vegetation over the edges. Orange markers (spray-painted flat pebbles) were placed under each egg to assist in re-location of depredated nests. Each quadrat was checked three times; 24 hours, 3 days and 5 days after establishment (day one, three and five). The experiment was repeated three times, with a resting period of three and five days in between trials. Distributions were randomly allocated to quadrats during the first trial. Subsequently, treatments (distributions) were rotated as a control for unequal predation of the three quadrat locations.

During examination of quadrats, I noted location and condition of depredated eggs. The data were analysed using a three-way multiple contingency analysis (SAS log-linear model, SAS 1985). In addition to distribution, quadrat location and trial number were included as independent variables in the analysis. Because the experimental setup was

based on a Latin Square Design, interaction could not be tested. Data from each of the three checks in each trial were analysed separately.

Effect of density of nests on predation

The procedure for this experiment was similar to that of the previous experiment. To examine the effect of density on predation, I placed dyed chicken eggs in each of three 80x80m quadrats at high (25 eggs), medium (16 eggs), and low (9 eggs) densities. Eggs were uniformly distributed in all quadrats. All eggs were concealed with small amounts of vegetation placed over the edges. I checked these quadrats twice, on day 1 and on day 3, and allowed five days between subsequent trials. The density treatments were rotated between quadrats to control for quadrat location. A three-way multiple contingency test was again used for the analysis (see above).

Red-throated loon nesting ecology and predation

To characterize predation of loon eggs/chicks, I located and monitored all nests at least twice a month during the summers of 1989-1991. Monitoring was more frequent during the weeks of nest establishment, to minimize over-looking nests depredated shortly after establishment. After nest location and confirmation (see below), subsequent nest checks were conducted from a distance to minimize disturbance. Nests of disturbed loons are much more vulnerable to predation (i.e. Bundy 1976, 1978, Furness 1981, Gomersall 1986, Lokki and Eklof 1984, Okill and Wanless 1990).

To recognize renesting attempts during the summers of 1990 and 1991, I dyed loons at their nests, using picric acid when nests became active (see Chapter I, Methods).

If a nest was depredated, I recorded details of location of the nesting pond and

nest, condition of the nest, and approximate date of depredation. In addition, I noted whether the loss occurred during incubation or post-hatching.

Data on relative numbers of the collared lemming (*Lemmus groenlandicus*), the major prey species of the local carnivores, was examined with respect to predation pressure on loons. Loons may be an alternative prey item in lemming low years.

Statistical analyses of nesting loon data

I evaluated distribution of nesting loons using the nearest neighbour technique described by Clark and Evans (1954). To determine which nest pond characteristics account for variation in loon success, I applied logistic regression (SAS 1983) in which I regressed pond size, water depth, distance of nesting island from the shore, and distance to nearest neighbour, against nesting success (depredated versus successful nests). Depth and area of a pond may be important physical barriers to mammalian predators, while distance of the nesting island from shore (DTS) may act as both a physical and a predator detection barrier. The nearest neighbour distance may influence predation if foraging predators use an area concentrated search tactic (Krebs 1971). Each variable was examined individually (simple logistic regression), and then together in a stepwise multiple logistic regression. For the latter regression, I used a significance level of $p=0.15$, to enter variables into the model, as suggested by Hosmer and Lemeshow (1989). I examined data from each year separately, as well as pooled.

To describe whether nest predation was random or area-restricted, I applied an Association Contingency Test (Southwood 1978, χ^2_{ns}), modified by using a 'nest success' category as 'species A' and 'success of nearest neighbour' category as 'species B'. To

determine the relative importance of distance to the nearest depredated neighbour and the pond variables previously examined, I included this variable in a multiple logistic regression with DTS, pond depth, pond size, and nearest neighbour distance.

Results

Appearance of depredated experimental nests

In both experiments, predation by the 3rd and 5th day was very high. In all cases, at least 67% of eggs were destroyed by Day 5. Appearance of the eggs was consistent except in the first trial of both the density and distribution experiments. Here, many eggs ($n=103$) were lost to a raven (possibly a pair), which was observed carrying away the eggs to cache. Subsequent to these trials, most depredated eggs (82.7%, $n=202$) had a hole between 1.0 and 4.0 cm across. Few depredated eggs (8.5%, $n=202$) were crushed or removed completely after the first trial.

Effect of spatial distribution on predation

Predation in the uniform, clumped and random quadrats was variable and essentially unpredictable with respect to prey distribution (Table 4.2). The effects of the other treatment variables (position and trial number) were more pronounced. The position effect was significant after the first day of quadrat exposure, with the western quadrat more heavily depredated than the central quadrat ($\chi^2=18.33$, $p<0.0001$), and the eastern quadrat ($\chi^2=16.21$, $p<0.0001$). This was likely due to a pomarine jaeger territory overlapping the western quadrat. After the third day of quadrat exposure, all variables had a significant effect on predation: eggs in trial 1 were more heavily depredated than eggs in trial 2 ($\chi^2=13.79$, $p=0.0002$) and trial 3 ($\chi^2=22.56$, $p<0.0001$); egg predation in all

Table 4.2. Total number of eggs depredated within each treatment of the experiment investigating the effect of prey distribution on predation rates. A total of 120 eggs were offered, except in blocks marked with "*", where 114 eggs were distributed.

Day when checked	Nest distribution		Quadrat position		Trial number	
Day 1						
	random	10	east	5	one	10
	even	22*	middle	11	two	19*
	clumped	24	west	40*	three	27
Day 3						
	random	57	east	51	one	93
	even	77*	middle	73	two	60*
	clumped	76	west	86*	three	57
Day 5						
	random	101	east	100	one	120
	even	110*	middle	111	two	94*
	clumped	109	west	99*	three	96

quadrat locations differed significantly with the highest rate of predation in the western quadrat and the lowest in the eastern quadrat (west vs central, $\chi^2=4.87$, $p=0.03$; west vs east, $\chi^2=25.73$, $p<0.0001$; central vs east, $\chi^2=9.12$, $p=0.003$); finally the only difference in distribution effect was found between the uniform and random nest distributions ($\chi^2=7.18$, $p=0.007$). The uniformly distributed eggs were the most heavily depredated, while the randomly distributed eggs, the least. No difference was found between the clumped and uniform distributions ($\chi^2=1.04$, $p=0.31$), nor the clumped and random distributions ($\chi^2=3.53$, $p=0.06$). Predation of eggs during the final check on day 5 was not significantly different between levels of any of the three variables, presumably because of generally very heavy predation (70-100% of the experimental nests were destroyed).

Effect of density on predation

None of the three independent variables had an effect on predation in the density of quadrats (Table 4.3). Total predation was similar to that in the previous experiment (86%, $n_{\text{density}}=150$ vs 88%, $n_{\text{distribution}}=354$).

Distribution and success of nesting red-throated loons

Distribution of the nesting sites of the loons in all three years was uniform (Table 4.4). The average nearest neighbour distance was 0.73 ± 0.40 km. The area used in determining the distribution excluded the areas of open water of two large lakes. Having no islands, these areas are not used for nesting by loons. Of 104 observed nesting attempts, 92 (88.5%) were on islands. Of the 12 remaining nests, 7 (6.7%) were actually on the shoreline and 5 (4.8%) on mossy hummocks within 2 or 3 meters of the shoreline

Table 4.3. Proportion of eggs depredated within each treatment of the experiment investigating the effect of nest density on predation rates.

Day when Checked	Nest Density		Quadrat Position		Trial Number	
Day 1	High	26/75	East	23/50	1	27/50
	Medium	27/48	Middle	22/50	2	18/50
	Low	12/27	West	20/50	3	20/50
Day 3	High	68/75	East	43/50	1	46/50
	Medium	41/48	Middle	44/50	2	39/50
	Low	20/27	West	42/50	3	44/50

Table 4.4. R-values and probability of random distribution of red-throated loons on Bathurst Island. 'R' represents the departure of loon spacing patterns from random distribution: $R=1$ demonstrates random distribution; $0 \leq R < 1$ demonstrates clumped distribution; $1 < R \leq 2.14$ demonstrates uniform distribution. Probabilities based on Fisher type III distribution due to small sample size.

	1989	1990	1991
R	1.24	1.41	1.31
Sample size	32	36	36
Probability of random distribution	<0.05	<0.05	<0.05
Distribution	Uniform	Uniform	Uniform

(see also Chapter II). Predation was similar for the island vs shoreline nests: 54.9% of island nests (n=71) and 66.7% (n=6) of shoreline nests were depredated in the 1990 and 1991 ($G=0.29$, $p>0.50$).

Stepwise logistic regression of nearest neighbour, pond area, pond depth, and distance of island to shore, revealed that DTS had a significant effect on success in both years (1990: $\chi^2_w=2.87$, $p=0.09$; 1991: $\chi^2_w=3.28$, $p=0.07$). The pooled data show similar results ($\chi^2_w=5.49$, $p=0.02$); pooled means and Wald chi-squares for simple logistic regression of each variable are shown in Table 4.5.

Association Analysis was completed for data from 1990 and 1991; 1989 data was omitted from analysis as no nests were lost to predation in that year. Association of depredated and of non-depredated nests, as tested for each of 1990 and 1991 was not significant (1990: $\chi^2_s=2.68$, $0.05>p>0.1$; 1991: $\chi^2_s=1.32$, $p>0.25$). Pooling the data resulted in equal proportions of depredated and undepredated nests as well as increasing the sample size, increasing the power of the statistical analysis in two ways. Pooled data (Table 4.6) indicated a significant association between depredated nests, and between successful nests ($\chi^2_s=6.35$, $p<0.025$). Although several depredated nests were isolated from other depredated nests, no successful nest was similarly isolated. Figure 4.1 illustrates the distribution of depredated and successful nests in 1990 and 1991.

To compare relative relationships between success and this variable (nearest depredated nest (NPN)) and the former variables (DTS, nearest nest, pond area, and pond depth), I included NPN in the stepwise logistic model. NPN was more highly associated with predation than DTS (Table 4.7).

Table 4.5. Pooled means and ranges for variables included in the multiple logistic regression for pond success. Wald chi-squares obtained by simple logistic regression are shown.

Variable	Non-depredated nests		Depredated nests		Wald χ^2 (P)
	Mean \pm st.dev.	Range	Mean \pm st.dev	Range	
Distance of island to shore (m)	33.7 \pm 28.16	0-100	20.2 \pm 13.77	0-60	5.49 (0.02)
Depth of pond (cm)	53.8 \pm 10.23	35-75	49.5 \pm 9.92	30-75	3.32 (0.07)
Size of pond (ha)	80.5 \pm 145.79	1.0-445.3	56.0 \pm 108.44	0.9-445.3	1.38 (0.24)
Distance to nearest nest (km)	0.73 \pm 0.400	0.26-1.79	0.71 \pm 0.400	0.22-1.79	0.04 (0.84)

Table 4.6. Association contingency table for success of nests and of nearest nests. Data from 1990 and 1991 are pooled. $\chi^2_s=6.35$, $p<0.025$.

Success of nearest nesting loons	Success of nesting loons		
	Depredated	Successful	Total
Depredated	28	12	40
Successful	12	20	32
Total	40	32	72

Figure 4.1 Distribution of successful and depredated loon nests in 1990 and 1991. Empty squares represent locations of depredated nests, filled squares represent locations of undepredated nests.

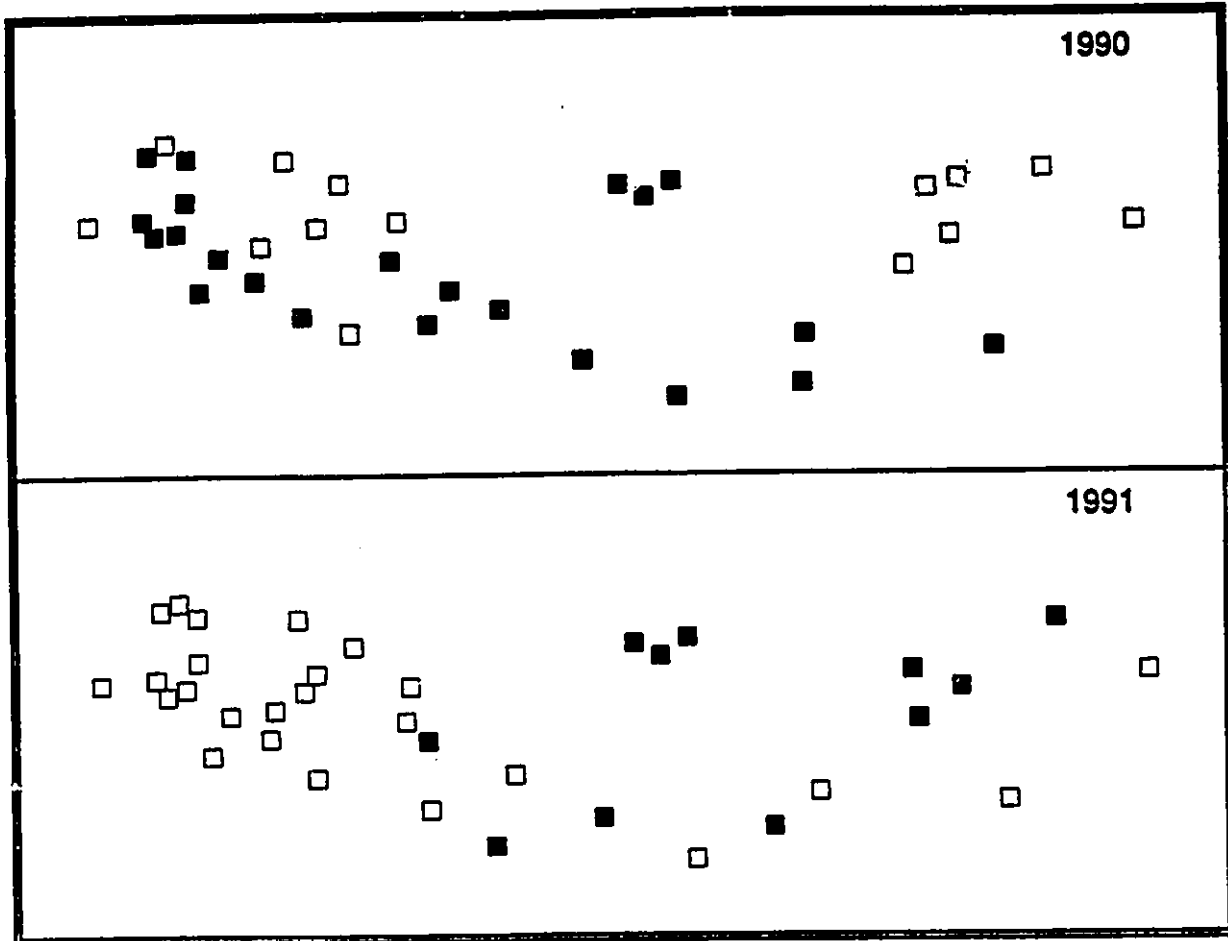


Table 4.7. Means, range and Wald chi-square for NPN (distance to nearest depredated neighbour) versus pond success.

Successful nests		Depredated nests		Logistic regression Wald χ^2 (P)
Mean \pm st.dev.	Range	Mean \pm st.dev	Range	
1.88 \pm 0.985	0.37-3.89	1.03 \pm 0.719	0.26-2.81	11.71 (0.001)

Temporal variation in loon predation

Within season variation. Most nests (84.4%, $n=32$) were depredated during incubation (mostly during the first week, see Chapter II), although predation of young chicks up to one week in age was suspected/observed in at least 9 cases. Two of these cases involved chicks, probably left unguarded, from second clutches laid near the depredated first nest, and one involved a chick exposed due to human disturbance. The prevalence of clutch loss (29.4%, $n=104$) over chick loss (12.7%, $n=71$) demonstrates the value of selecting nest sites which are relatively safe from predators. It also suggests the importance of cryptic behaviour and active nest defense through nest guarding during incubation.

Between Years. Predation was lowest (only one chick depredated) in the first year and highest in the third year of the study (see Figure 2.3, Chapter II). Human interference during colour dyeing of the nests in 1990 and 1991, is the most parsimonious explanation for this; however, many of the depredated nests ($n=8$) had not been disturbed before predation occurred (Table 4.8). Most others for which data are available ($n=12$), were depredated more than a week after disturbance.

An examination of lemming abundance reveals that lemmings were least abundant in 1988, (one seen in three months), moderately abundant in 1989 (seen at least twice a week), and most abundant in 1990, (seen at least every second day; also, 26 were trapped in one week in an area less than 0.5 km² by Burton Lim of the Royal Ontario Museum). In 1991, the lemming population again crashed shortly before the arrival of spring (indicated by numerous winter nests exposed at snow melt, coupled with low

Table 4.8. Success versus predation of nests in relation to human interference (nest dying).

Year	Successful Nests		Depredated Nests				Total
	Not dyed	Dyed	Not dyed	Dyed			
				Loss >1 wk after dyed	Loss <1 wk after dyed	Unknown when Lost	
1990	0	23	2	5	2	4	36
1991	2	9	6	7	4	8	36

numbers; <20 seen between June, July, August).

Discussion

Experimental study

The results of the experimental study suggest that density and distribution of artificial prey have no effect on predation. Of the 18 comparisons between test variables made in the two studies, only one significant difference was found; that between the uniform (high predation) and random (low predation) distribution quadrats during the final check. This difference was unexpected, as uniform distributions generally suffer the least predation, and clumped distributions, the heaviest (Andersson and Wiklund 1978, Picman 1990), while here, predation on the clumped nests was intermediate. Because no other differences were found between quadrats of different distributions or densities, this effect could be spurious.

This lack of experimental effect may have been related to high predation by individual predators or pairs of predators. Nests in the first trials of both experiments (run concurrently) were depredated largely by a transient raven, which systematically removed and cached most of the experimental eggs, causing the significant difference in egg loss in trial one of the distribution experiment. In addition, the western distribution quadrat was heavily depredated during the first three days of exposure, probably by a pair of Pomarine Jaegers nesting 200 meters to the west of this quadrat. This bias produced by the presence of single or pairs of birds cannot be controlled without an extensive knowledge of territory locations and probability of appearances by transient predators, especially corvids. Corvids have been implicated in heavy losses of experimental nests

(Dwernychuk and Boag 1972, Andren et al. 1985, Angelstam 1986) and real nests (Gaston et al. 1985). In natural situations, transients have also been implicated in higher than normal predation rates. This was observed by Dickson (1992), when non-nesting sandhill cranes (*Grus canadensis*) caused high clutch losses in one year of a three year study of loon ecology.

Use of artificial nests to examine predation patterns is a common research tool in the field of avian ecology. Many other shortcomings are inherent in this approach to the study of natural pressures on nesting birds. The presence of a human observer and potential conditioning or learning by predators to follow humans visually or by smell, is the most obvious potential bias which may affect the results of an experimental study (Lenington 1979, Strang 1980). The arctic offers especially little cover to conceal the experimenter from predators, which may be in sight several kilometers away. I noted several times jaegers following me during establishment of the quadrats, consuming eggs as I laid them out (such eggs were replaced when the predator was gone).

Another shortcoming of predation experiments often noted, is that the profile of predator types destroying artificial nests generally differs from that of predators destroying real nests. Predators of artificial nests are more frequently avian, whereas the real nests being simulated in these studies are more frequently attacked by mammals (Storaas 1988, Willebrand and Marcstrom 1988). This is reportedly due to methods used by predators to locate prey (visual location by birds, and olfactory location by mammals; Storaas 1988) and ability of adults to defend their offspring against avian predators (experimental nests are not thus protected).

This difference in predator types has major implications when comparing artificial and real nest predation especially if the species examined is large enough to successfully defend its progeny from avian predators (Morse 1974, Goransson et al. 1975, Sedinger 1990). Although avian predators may have nearby territories, loons are able to defend their nest from individual gulls and jaegers (Manning et al. 1956, Bundy 1976, Enquist 1983, pers. obs), both when on or nearby their nest or chick. A predation study which suggests prevalence of avian predators cannot emphasize the real predator threat to nesting loons, which are more seriously threatened by mammals. Avian predators were most likely responsible for the majority of eggs losses in my experimental study; mammals tend to crush eggs they depredate, while birds peck holes into them, as observed in 86.2% of the depredated eggs which were not removed by the ravens.

Several studies on loon ecology implicate avian predators as the cause of most losses of red-throated loon clutches. These studies examined populations located near gull colonies or large populations of other avian predators (Bundy 1978, Furness 1981, Enquist 1983). No predatory bird colonies occur immediately in the Polar Bear Pass area; avian predators have not been observed to be important nest predators of loons here.

The experimental design used in both the density and the distribution experiment had other unavoidable flaws. First, to facilitate setup of the defined densities and distribution, the quadrats were placed in wet meadow habitat adjacent to the loon nesting habitat. Despite the proximity to the loon habitat, this placement was also in an area where loons cannot nest, and where other prey species (i.e. other nesting bird species

and lemmings) are found. These other species are less often found on islands where loons are nesting. Predators foraging for these other species in the wet habitat will have switched to the artificial nests as a result of their availability. The resulting predation patterns may not resemble patterns used to forage on island nests.

Another flaw in the design was the relative densities used for both the distribution and the density experiments. The lowest experimental density of nests was 0.112 nests/m² (9 nests/ha), a density which would be considered colonial in loons (Palmer 1962, Lokki and Eklof 1984). Therefore, the uniformly distributed quadrat could be considered a clumped distribution from the perspective both of the nesting loon, whose highest density in this area is 1.7 pair/km² (0.0000017 pr/m²) and of the predator, whose home range may cover many hectares (avian), or many square kilometers (mammalian).

This high density of nests combined with the regularity of egg availability, most likely drew a high frequency of predator visits. This is substantiated by the appearance of the transient raven during the first trial of the distribution experiment. Sightings of ravens are generally infrequent and usually involve individuals flying through the Pass. This raven, however, remained long enough to remove most if not all experimental clutches.

Despite the above flaws with the experimental design, two important conclusions relevant to loon ecology may be drawn from the results. First, predation potential is very high. Few other predation studies using artificial nests have had a predation intensities, in a comparable period of time (5 days) at between 75 and 100%, as in most of the trials of these experiments. This is especially interesting considering that no loon clutches

were depredated in this year of the study. Second, unprotected eggs are extremely vulnerable to avian predators. These results emphasize the value to red-throated loons of adopting an effective anti-predator tactic, such as camouflage and nest guarding.

Predator avoidance tactics

Although the experimental studies did not demonstrate a lower rate of predation on nests at lower densities, several other studies of predation of both natural and experimental nests indicate a positive relationship between spacing out and nest success. Tinbergen et al. (1967) first demonstrated this under experimental conditions, using quadrats with eggs at densities of 0.4 to 9 eggs/m². Studies that examined predation using artificial nests at densities and conditions more similar to those of focal species showed that predation was lower where artificial nest densities were low (Goransson et al. 1975, Page et al. 1983), but only above a lower density threshold (O'Reilly and Hannon 1989, Andren 1991). Densities below this threshold density, show no difference in predation than those at this density. This threshold may be determined by the maximum distance at which a predator can detect prey during an area concentrated search (Tinbergen et al. 1967, Andren 1991).

Loons are very vocal and conspicuous, even when on their territory, and may be obvious to a predator from a greater distance than other, less conspicuous species. This may decrease the effective lower density threshold. At Polar Bear Pass, the nesting loons were spaced out, with average nearest neighbours distance between 0.70 and 0.74 km. Although density increased nearer the ocean (see Chapter III), the overall distribution was statistically uniform. This distribution minimizes the probability of location by

predators by maximizing the nearest neighbour distance. In a few areas where mammalian predators are numerous, red-throated loons have been reported to nest colonially on more inaccessible islands, with neighbouring individuals just a few meters apart (Palmer 1962).

The positive relationship between distance of nest to the shore and success during the two years with predation demonstrates that in years of predation (2 of 3 years in this study) distance of nest to shore was an important variable. However, only nests on islands at 100 meters from the pond shore were predictably spared from nest predation during this study. Nests in all other distance classes were depredated, although those less than 20 meters from shore suffered heavier predation.

Although pond size was correlated with DTS ($r_s=0.342$, $p<0.002$, $n=72$), it was not related to success. This is in agreement with Davis (1972). Examination of his data on predation rates of sympatric red-throated and pacific (sic arctic) loons (*G. arctica pacifica*), reveals no difference in loss rates of eggs between the two species (38.4%, $n=73$ and 37.5%, $n=80$, respectively). These species nested on ponds averaging 0.32 and 2.5 ha in size, respectively. The behaviour of the two species is quite similar, and both nest predominantly on islands (81.7% ($n=93$) and 83.5% ($n=97$) of all nests were on islands, respectively), thus supporting the view that predation rates are similar on 'large' and 'small' ponds of that study. Davis (op. cit.) gave no details, however, of distance of nesting islands from shore.

In contrast, studies of the Shetland Island population indicate that losses of loon nests are highest on the larger tarns. Four explanations have been advanced to account

for this (Gomersall 1986, Okill and Wanless 1990). First, large ponds generate larger waves which may destroy nests. Second, interactions with other breeding pairs using the same large ponds/lakes may interfere with nesting activities (Gomersall et al. 1984). Third, since these ponds are frequently used as reservoirs, they are prone to water fluctuations (Eriksson et al. 1988). Finally, larger ponds are used for fishing and other human activity (Booth 1982). As previously discussed, human disturbance may reduce loon's success through decreased vigilance and corresponding increased predation of nests (Gomersall 1986, Okill and Wanless 1990).

In my study area, there are no human inhabitants or development in the wetlands. Therefore, only the first two explanations apply to my study area. The three lakes each have multiple pairs, but these nest far enough apart that they do not interfere with each other. Action by waves does not seem important. However, during spring melt, when ice from the lake bottom breaks off and floats to the surface, waves thrust these blocks onto shore: 3 nest losses have been attributed to this ice damage on the large lakes.

Predation of loon nests - spatial patterns

The analysis of association indicates that area-restricted search is the method used by predators to forage: once a foraging area is established, it will be used extensively and completely. There were no cases of a successful loon nest surrounded exclusively by depredated nests. There were, however, very few cases of depredated nests isolated from other depredated nests. Only 17.5% of 40 depredated nests occurred outside of three main areas utilized by predators.

This type of area-restricted search over a period of time (i.e. not during one

foraging effort) has been described by O'Reilly and Hannon (1989), from an artificial nest study conducted using evenly distributed experimental quail eggs. In this study, eggs placed within 20 meters of a site where an egg was depredated the previous week were more frequently depredated, than eggs placed nearby an undepredated site. They also found that at densities of 50 and 100 eggs per square km, the likelihood of an egg being depredated was greater if an adjacent egg was also depredated. Likewise, Krebs (1971) found the probability of Great Tit (*Parus major*) predation increases if neighbouring nests are depredated.

The only defense nesting loons have in this situation is to isolate their nests from others and defend large territories. Territories including more than one pond, as reported by Davis (1972, but see Merrie 1978) and in Chapter IIIb, may reflect a significant pressure exerted by predators for spacing out. Furthermore, the actual placement of territories in low density areas was relatively uniform, with much buffer zone including non-territorial ponds between adjacent territories. Territories in sub-optimal habitats do not increase in size (Davis 1972, Chapter IIIb). Maximal dispersion of nests is apparently achieved by placement of the territories with buffer ponds in between.

Predation of loon nests - temporal patterns

Arctic foxes have been observed swimming between 150 and 500 meters to an island where eiders were nesting colonially (Quinlan and Lehnhausen 1982). In this study area, mammalian predators, such as wolves or foxes, can and will wade or swim to nests islands (pers. obs.). Therefore predator avoidance by loons nesting on islands may be ineffective some years, especially if alternative food availability is low (Bergman and

Derksen 1977, Schamel and Tracy 1985, Dickson 1992). This is especially relevant if the loon is a neighbour of another depredated loon, as shown in this study.

Summers and Underhill (1987) describe fluctuations in reproductive success by several birds species in the Taimyr Peninsula (see also Summers 1986 and Owen 1987), in relation to lemming and fox cycles. Predator/prey cycles are a common phenomenon in the Arctic (Lack 1954); the most frequently studied cycle is that between lemmings (*Dicrostonyx* and *Lemmus*), and their predators. Lemming populations fluctuate for unknown reasons, on a three year cycle (Krebs 1965). Following a population crash of lemmings, predator populations also crash, but only after a lag period of one year (Dhondt 1987). In their study, Summers and Underhill (1987) elaborate on the necessity of predators to switch prey following crashes in lemming populations, and discuss the impact this has on the alternative prey species. Predator pressure on the alternative species increases immediately following the lemming crash and then subsides to a low before the full recovery of lemming populations.

The results of this study suggest that the red-throated loon may be considered an alternative prey for lemming predators. Although there is only data from three years on loons and 4 years on lemmings, the data support the pattern demonstrated by Summers and Underhill (1987). In 1989, one year after a crash in lemming populations, no loons nests were depredated, presumably because predators populations had also either crashed or were not breeding. Those predators which did survive the lemming crash were able to feed from the moderate lemming numbers of 1989. The following year, 1990, lemmings occurred in high numbers, and many lemming predators, such as owls and

foxes, bred (pers. obs.). During this year, predation on loon nests was moderate (33%). The lemming population again crashed in 1991, and subsequently, there was high predation on loon nests (66.7%). This was expected if predator populations crash one year after lemming populations crash.

In summary, the experimental study revealed that exposed (i.e. unguarded) eggs suffered heavy avian predation. Therefore defence of clutches by constant attendance by adult loons is vital. In spite of continuous parental attendance, predation is heaviest during incubation, and is most likely a result of mammalian predators. Spatial patterns of predation indicate predators use area-restricted searches, and prefer nests on islands closer to the pond shore. Other passive tactics of defence are thus required for successful nesting. Mechanisms forcing high dispersal seem to operate, and result in low nesting densities, and a uniform distribution of nests. Inclusion of multiple ponds in territories may reflect a tactic forcing dispersion, or may provide escape ponds in the event of predator presence. Because predation varies between years, these tactics will likely be most important in years of moderate predation.

Chapter V. The Effect of the Short Breeding Season on Nest Site Selection by the Red-throated Loon (*Gavia stellata*) In the High Arctic

Introduction

Extremities in abiotic elements may limit reproductive success of birds. Stability of water level (Fair 1979, Post 1981, Eriksson et al. 1988) and severity of climate (Pattie 1977, Mayfield 1978, Hannon et al. 1988) are two examples of abiotic factors which may restrict success in rearing young. Both may therefore have a major effect on selection of territory and/or nest site, acquisition of food, and time of breeding.

The high arctic is noted for its severe and sometimes unpredictable weather, even during the short summer season. The length of the summer season can vary with the time of both spring arrival and with the onset of fall. Summer temperature regime, a function of numerous factors such as wind speed and direction, and levels of solar radiation, may determine the rate of snow melt. Often temperatures plummet below zero at night; snow falls are an expected event during the summer.

This unpredictability limits the phenology of breeding birds, both in the spring, when they must nest as early as possible, and in the fall, when offspring must be adequately prepared for migration south. As a result, onset of nesting is often closely correlated with time of snow melt (Barry 1962, Sealy 1975, Hannon et al. 1988, North and Ryan 1988), to maximize available time to raise offspring.

In years of late spring arrival, many species fail to breed (i.e. Cooch 1961, Mayfield 1978, Mayfield 1983). Late arrival of spring not only prevents use of snow covered habitat but also decreases availability of food by delaying corresponding phenologies of

prey species (insects, migrant bird species, and plants) (Slagsvold 1975). Reproductive attempts in years with late spring frequently fail due to starvation or exposure of the young, and are therefore costly for adults.

The red-throated loon (*Gavia stellata*), is unique among high arctic birds in its requirement for open fresh water for nesting. All loons require open water from which to take off and to land, although to take flight, the red-throated loon requires a shorter running distance than other loon species. Furthermore, the offspring of nesting loons are generally confined to the nesting pond for the entire pre fledging period, with only limited ability to move should the pond freeze over.

As described in Chapter II, open water must be available for at least 85 days for a pair of loons to successfully lay eggs and fledge chicks in the high arctic. This allows a minimum two week pre-nesting period, when only the pond surface need be open, 26 days for incubation, and 45 days to raise chicks to fledging age. The length of occupation of the natal pond may be circumvented if chicks are moved to a neighbouring pond, following predation, or freezing of the nesting pond.

In Chapter II, I reviewed the current theory of red-throated loon evolution. This theory states that during the Pleistocene ice age, these loons evolved to use small ponds for nesting because they were available in the spring sooner than larger ponds (Davis 1972, Irving 1972). The use of very large nesting ponds in this study contradicts this hypothesis.

The purpose of this Chapter is to establish why red-throated loons use large ponds in my study area. I present circumstantial evidence which suggests requirement of large

ponds over small ponds. I propose that loons select large ponds because they are open longer than small ponds. Based on this, I predict that small, shallow ponds of my study area thaw at a similar rate as large, deep ponds. I also predict that small ponds freeze over more rapidly in the fall than large ponds, because they have less stored heat at the end of the summer than large ponds and therefore do not have as great a buffer period delaying freeze-over in late summer.

Therefore the goal of this study is to establish spring thaw and fall freeze-over patterns, and relate these to pond availability. More specifically, I will examine spring thaw in relation to pond size and water depth. Because drainage affects thawing patterns (see Chapter IIIa), the effect of north/south position must also be considered. Then I will examine fall freeze-over patterns in relation to pond area, water depth, and number of islands. Using the results of the two analyses, I will establish the role of thawing and freeze-over in pond availability and subsequently, pond selection by loons.

Methods

I monitored nesting red-throated loons on a biweekly basis during the summer of 1989-1991. Adults were dyed at the nest in 1990 and 1991, to assist following movements of loons and their broods between ponds (see Chapter I for more details). Observations continued until late August in 1989, and mid-September in 1990 and 1991.

Weather details, including temperature and wind velocity, were recorded twice a day throughout the summer by Canadian Museum of Nature staff, at 7:00 and at 14:00, as required by the Polar Continental Shelf.

I conducted two helicopter surveys of the study area to determine melting

sequence of ponds of different size classes and regions. The survey dates were June 28, 1990 and June 14, 1991. Because the survey of 1990 was later in the season, ponds were considerably more melted than in the 1991 survey. The observations for both surveys were recorded as ranks, with frozen ponds ranked as '1', and melted ponds ranked as 5.

In the fall of 1991 (Sept 4), when loon chicks were still not fledged, and ponds were at various stages of freeze-over, I observed and recorded the percentage of open area remaining on ponds, as visible from the camp's observation tower. A 40x zoom binocular telescope (CarlZeiss/Jena, 80/5000) was used to observe ponds at a distance of up to 10 km. Only observations of small ponds within 5 km were recorded, due to loss of power through the scope with distance.

I used partial correlation analysis to determine factors contributing to variations in spring melt rates and fall freeze-over rates. Spring melt data from two years (1990 and 1991) were correlated with pond size, depth and region in the study area. I also correlated fall freeze-over data from 1991 with pond depth and size, and number of islands.

Pond size was considered an important variable in thaw and freeze-over as it represents the amount of area exposed to the fluctuating air temperatures. Both pond size and depth affects the amount of wave action on the pond, which may influence freeze-over. Depth is important as it corresponds to the ponds volume as a heat sink. Number of islands was used in the model for partial correlation with freeze-over rates, as freezing begins along shores, and islands may add considerably to the shoreline length.

Finally, region (distance to the southern ridges) was included in the model for spring melt, as drainage patterns and resultant spring hydrology of certain regions may effect a differential melting pattern (see also chapter III; the Pass slopes downward from south the north). Variables were transformed as required.

Results

Loon Phenology In Relation to Pond Ice

Spring Melt

In 1990 and 1991, loons regularly visited territorial ponds soon after the surface opened (within one week). Nesting, however, began only when water levels had subsided. This was most obvious in 1991 when levels of several ponds remained high long after all ice on the ponds had melted. Because this submerged their traditional nesting islands, pairs at these ponds delayed nesting until the islands were available.

In some years nests have been found on ponds still having considerable amounts of ice in them, especially ice frozen to the pond floor. This was quantified in 1991 (Table 5.1), for those ponds in which loons were colour dyed at the time the first egg was laid. Fifty-five percent of these ponds (n=20) still had ice on the pond floor. Two of the completely melted 'ponds' were actually ice-free nesting territories on large lakes which were still largely frozen. Grouping these two with those ponds with ice, indicates only 35% of the loons nested after ponds were completely ice-free. The two pairs which delayed nesting until water levels subsided were in this group.

Ice on the pond floor persists much longer than surface ice, and eventually breaks off from the bottom and floats to the surface. This may be a hazard to nesting loons

Table 5.1. State of ice on pond floors at the time of nest initiation in 1991. Note: these pairs did not lay on the same dates.

Pond Size	Pond Entirely Melted	Less than 50% Ice-Cover on Pond Floor		Greater than 50% Ice Cover on Pond Floor	
	Number of Ponds	Number of Ponds	% Ice on Floor	Number of Ponds	% Ice on Floor
0-1 ha	1	—		—	
1-5 ha	5♦	2	10-50%	1	70%
5+ ha	3**	5*	20-30%	3	70-90%

♦ - two of these were late nesting pairs. Delay was due to high water level.

* - Each ** represents a territory (as opposed to pond) in a large, otherwise frozen lake. In the three cases indicated, the state of melt in the immediate territory is reported.

should winds drive this ice into the nest. Destruction of nests by ice occurred at least three times in the three study seasons.

Movement of Broods

The broods of ten loon pairs (9.6% of all nesting pairs, n=104; 15.9% of successful pairs, n=63) relocated to new ponds in three years of observations (Table 5.2). Six of these moves occurred in mid-season, when chicks were still relatively young (a few days to 4 weeks). Of these, only one move (#19) resulted from loss of one of the broods' chicks when the chick was 4 weeks old. Its sibling was relocated to a pond one kilometer from the nest pond. One day before the move, a pair of pomarine jaegers were observed harassing the chick of a neighbouring pair, suggesting predation caused the loss of pair #19's chick.

Cause for midseason relocation was not apparent in the other five broods, as no chicks were lost immediately preceding the move. All of these moves were from ponds smaller than 1.1 ha, to a nearby larger pond. In two of these cases, the same pair (#18) moved their chicks two years in a row, and in two other cases (#10, #31), the small ponds (<0.5 ha in both cases) were only used one year (in 1989). In the fifth case (#21), loons moved their chick to a pond used unsuccessfully by that pair the previous year. Distance of relocation for the later five pairs was between 20 and 35 meters, whereas the remaining chick of pair #19 moved to a pond almost a kilometer away.

The other four relocations of loon chicks occurred after ponds began to freeze. Chicks of this group were older (between 5.5 and 6 weeks of age). The nesting ponds used by this group were larger than 1.5 ha in size, and moves were to ponds with less

Table 5.2. Details of relocations of chicks from nesting ponds to other ponds. All broods were of one chick except those marked with an asterisk (*). S.W.=move through shallow water connecting the two ponds. Not deep enough to swim. O.L.=move overland by 'frog-hopping'. O.L./W.=move a combination of overland and presumably through ponds along the way.

Pair Number	Distance of Move (m)	Age of Eldest Chick	Method of Move	Characteristics of New Pond			Presence of Ice
				Larger	Deeper	# of Islands	
31-89	20	<1 week*	S.W.	Yes ^a	Yes	Fewer	No
10-89	20	2 weeks*	O.L.	Yes ^a	Yes	Fewer	No
18-89	35	18 days	O.L.	Yes ^a	Yes	Same	No
18-90	35	16 days	O.L.	Yes ^a	Yes	Same	No
21-91	30	<12 days	S.W.	Yes	No	Same	No
19-89	900	27 days	O.L./W.	Yes	Yes	Same	No
1-90	35	37 days*	O.L.	No	Yes	Fewer	Yes
1-91	35	fledged	O.L.	No	Yes	Fewer	Yes
14-91	100	41 days	O.L./W.?	Yes	Yes	Fewer	Yes
16-91	940	41 days	Flight	Yes	?	Fewer	Yes

^a - move from pond <1.0 ha to one >>5 ha.

ice on them. In two cases (#14, #16) the new pond was larger and deeper, and in two (pair #1, two years), the pond was deeper and connected by a small strait, frozen on the surface, to the 450 ha lake. The previous year, one of the 2 chicks reared by this pair perished as the nesting pond froze.

In 1991, two loon families which were located on a 450 ha lake were forced out of their territory by encroaching ice. One of these families remained along the ice edge closest to the territory, as another pair with a fledged chick had a territory in nearby more open water. The other family was forced to move out of its sheltered bay to the opposite side of the lake two kilometers away due to wind and wave action which drove loose ice into the territory waters. Both these moves occurred at a time when most other loons were tending their chicks on the ocean and therefore were no longer defending their territories.

Fall Freeze-over

Fall freeze-over is initially a gradual process. Freezing begins when air temperatures drop below zero at night, allowing pond edges to freeze. Generally, temperatures rise above zero the following day (Appendix 1). This, plus heat of the water, allows the ice to melt during the day. Thus, the night temperature may drop below zero for several weeks before ponds actually close over. Because freezing begins at the shorelines of ponds, islands may enhance the freezing of the pond surface. Ice formation then advances from the edges at a more-or-less linear rate. A pond two meters across will therefore freeze-over faster than a pond 4 meters across, as the linear rate of ice-over from the edges is the same.

In both 1990 and 1991, ponds began to freeze before chicks were fledged. In 1990, freeze-over began at least a week earlier than in 1991, and within 17 days several chicks were confined to small openings in their ponds which adults could not land in. The fate of these chicks is not known, as weather and night prevented continuous observation. The age of these chicks bordered the fledging age as observed in 1991 (see Chapter II, and Figure 3b) and if they in fact did not fledge, most of them were within a day or two of being able to. This situation clearly illustrates the advantage of shortened phenology discussed in Chapter II.

Freeze-over before fledging of some chicks is suspected for 1989, as a dead, almost fledged chick was found in early 1990 along the shore of the second largest lake, near a nest used in 1989. This chick was presumably from this nest, one established relatively late in 1989 (\approx July 12). The lake, 190 ha in size, was most likely the second last to freeze completely.

Variables affecting spring melt and fall freeze-over

Scatterplots and corresponding correlation coefficients of the independent variables (pond depth, size, and distance from southern ridges) of ponds surveyed during spring thaw are shown in Figure 5.1 a-c. Results of the partial correlation analysis on data from both 1990 (late in the melt) and 1991 (early in the melt) indicate that neither size, nor depth contributed to variation in melting rates (Table 5.3). However, in 1990, distance of ponds from the southern ridges affected degree of thawing ($r_p=0.216$, $p<0.05$, $n=65$): ponds near the southern ridges were less thawed at the time of the survey than those further north. This trend was not observed in 1991 perhaps due to the earlier time of

Figure 5.1 Scatterplots and simple correlation coefficients of degree of thaw in 1990 and (a) pond depth, (b) pond size, and (c) distance of pond to southern ridges.

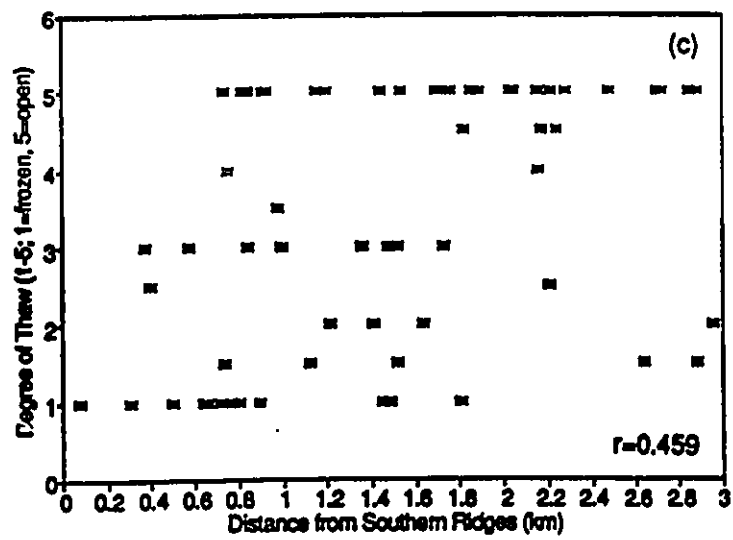
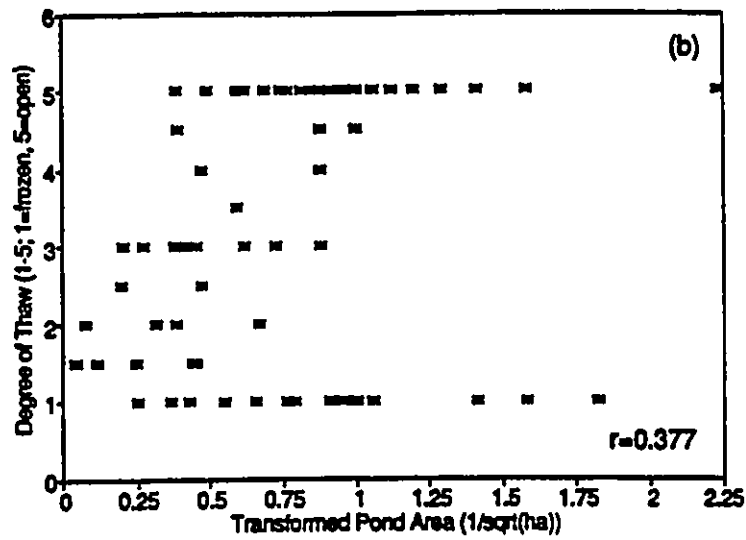
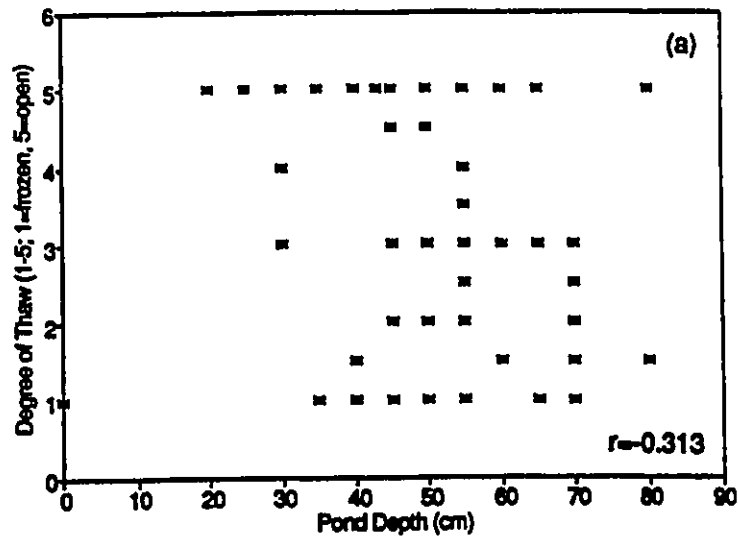


Table 5.4. Type II partial correlations of pond depth, pond area, and distance of ponds from the south with degree of melting in spring 1990 (n=67) and 1991 (n=78).

* -transformed to normalize; $1 / (\text{area})^{0.4}$

Variable	Partial correlation			
	1990		1991	
	r_p	P	r_p	P
Depth	0.011	>0.05	0.007	>0.05
Area*	0.148	>0.05	0.095	>0.05
Distance from South	0.216	<0.05	0.002	>0.05

survey (as melting is related the accumulation of meltwaters, melting is accelerate in areas receiving meltwaters). Overall, the thawing rate was consistant for ponds surveyed in both years (spearman rank; $r_s=0.291$, $p<0.05$, $n=53$).

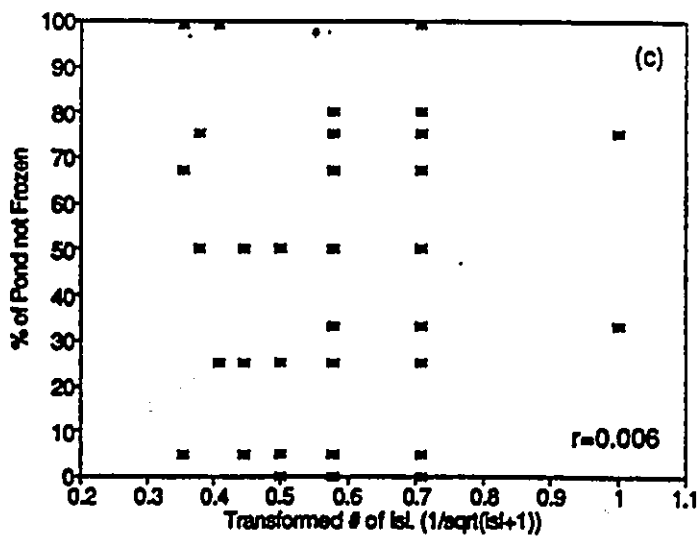
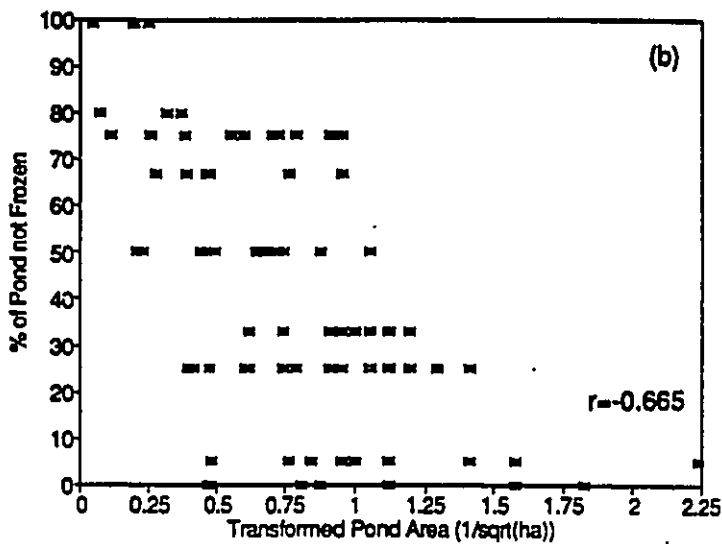
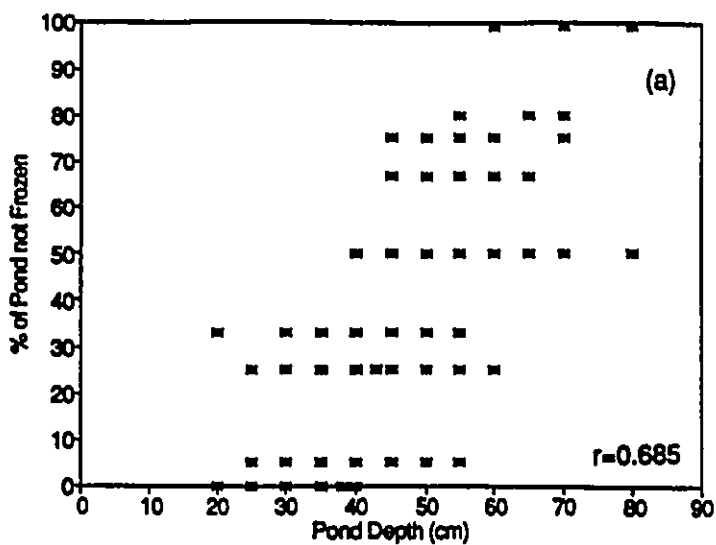
Correlation of pond depth, size, and number of islands with pond freeze-over rates are illustrated in Figure 5.2a-c. The partial correlation analysis on this data ($n=95$) indicate that freeze-over was strongly influenced by both depth ($r_p=0.236$, $p<0.025$) and size ($r_p=0.316$, $p<0.001$) of the pond. Number of islands did not influence freeze-over ($r_p=0.151$, $p>0.1$).

Discussion

It is evident that this population of red-throated loons is at a limit with respect to successfully fledging chicks before freeze-over. In both years in which observations continued into the fall, chicks were still unfledged when the ponds began to freeze over. In one case, the pond had so little open water that the adults only visited the chick successfully once in 48 hours, and the chick was forced to take its fledging flight to more open water on its own (see Gray and Eberl in prep). Similar situations have been documented by other authors (i.e. Manning et al. 1956) including actual freezing of chicks into ice (MacDonald 1954, Uspenskii 1984). The time constraint is severe.

Evidence suggests that this situation may be circumvented by either the moving of young chicks to larger ponds, or the moving of older chicks to ponds which are less frozen than those which they occupy (see Dickson 1992). The former event occurred two years in a row for one pair. Three other pairs which nested successfully on ponds smaller than 1.0 ha only did so one year. In all cases nesting ponds less than 1 ha in

Figure 5.2. Scatterplots and simple correlation coefficients of degree of freeze-over in 1991 and (a) pond depth, (b) pond size, and (c) number of islands in pond. N=95.



size were abandoned by the occupant loon family within 3 weeks of the chicks hatching.

Chicks are vulnerable to predation when on land, because of limited mobility. Therefore, moving to other ponds places chicks at considerable risk. Ten broods (16%) were observed to move into other ponds; only one of these was a result of predation. No other red-throated loon study has reported such a high frequency of brood relocation; Bergman and Derksen (1977) report only 1 of 26 relocating and Dickson (1992) reports 4 of several hundred nesting pairs moving. Because failure due to predation on chicks in general was lower than in other studies (8.7% of 69 hatched broods, compared with Bundy (1978): 36.4% of 107 broods, Davis (1972): 39.7% of 58 broods), and because most one chick broods were reduced (possibly by predation, but see Chapter III) at least a week before the move, these relocations were not likely due to predator harassment. This supports the hypothesis of chick relocation to ponds with delayed freeze-over.

Evidence also suggests that the large ponds which loons of this area prefer are open marginally longer than the smaller ponds. Selection of these ponds for nesting may be the only option that these loons have if successful fledging of chicks is to be achieved.

The size classes tested showed no effect of size or depth on melting rate. This does not necessarily contradict Irving (1972), Ravelling (1978), and Saville and Oliver (1964; as cited in Davis 1972), who report that small ponds are ice-free sooner than large ponds. These authors suggest that small ponds are also shallow, and because of this, small ponds are ice-free soonest. The 'shallow' ponds of my study were generally much deeper than the shallow ponds used by nesting loons in other studies (i.e. only 8% of the 110 ponds surveyed for this study were less than 27 cm, the average depth of red-

throated loon nesting ponds reported by Bergman and Derksen (1977)), and can therefore not be considered as shallow. Furthermore, the surveys of my study area were completed before many ponds were ice-free, and most of the ice-free ponds included in surveys were in areas known to thaw rapidly in the spring. Therefore, the lack of size effect on melt rate may be an artifact of sampling time and location. This is supported by the more advanced melt of ponds toward the north of the study area in 1990, when the survey was completed later in the spring.

In regions of the loon range which have no permafrost, small ponds may in fact melt faster because they are also drawing heat from below. In contrast, high arctic ponds only absorb heat in the spring, through the pond surface. The ponds of the study area are all relatively 'shallow' (<1.5 meters), and freeze to the bottom in the winter. Ponds shallower than 20 cm were not surveyed, as they are never used for nesting here. However, Bergman and Derksen (1977) report that red-throated loons of Storkerson, Alaska utilize ponds averaging 27 cm in depth. Ponds of this depth may routinely thaw out faster, but may correspondingly freeze-over more quickly in the fall, especially over night in early fall.

The relevance of an ice-free state in spring is, however, small as most loons began to nest before ponds were ice-free. Perhaps a more important variable in determining availability is depth of melted water in the pond. Because all ponds begin to melt from the surface, a small pond will melt at the same rate as a large pond, not in proportion to volume, but as a linear function of depth (i.e. melting of 50 cm of ice on a 50 cm deep pond will render it 100% ice-free, whereas similar melting on a meter deep pond will

render it only 50% ice-free). Therefore the functional availability of shallow and deep ponds in spring should be similar.

The more important variable in determining duration of availability is therefore resistance of ponds to freeze-over in the fall. A deep and large pond freezes over more slowly, presumably due to greater heat capacity of the larger volume of water, in addition to greater wave action. A small pond presumably lacks this heat buffer and freezing can occur more rapidly. Because of this extended open period in the late summer/early fall, large ponds remain open longer in the summer and allow loon broods to mature and fledge before freeze-over is complete.

In summary, the high arctic population of red-throated loons of this study exhibited tactics which enhanced the likelihood of their broods fledging before freeze-over of their nesting ponds at the end of the summer. This was accomplished by nesting on larger than average ponds, or by actively moving broods to ponds which are open longer, either soon after hatch when chicks are more mobile or after the natal pond has begun to ice over.

Chapter VI. General Conclusion

Decisions on breeding location are based on factors which influence reproductive success of a given species. These factors operate with different degrees on the different levels in the selection of the breeding location. These levels include habitat selection, territory selection and nest-site selection (Lack 1968, Morse 1980).

In the preceding chapters, I examined various factors which should affect selection of breeding sites by red-throated loons in the high arctic. The main objectives of my study were to describe differences in the breeding ecology of red-throated loons in the high arctic and in regions to the south, and by considering this information, to determine how food, predation, and climate influence the selection of the breeding location. First I determined whether my high arctic population of these loons differed from more southern populations in breeding phenology and pond selection. The lack of competition from the pacific loon, the key competitor for breeding space in more southerly areas, was considered in the analysis of pond selection. Second, I examined the effect of distance to foraging areas on success. Higher success of loons nesting near the ocean should be reflected in the loons habitat settlement patterns. Thirdly, I considered the effect of predation on the breeding location of loons. I determined temporal patterns in predation, both within each year and between years, to determine the importance of predation in reproductive failure of loons. Spatial patterns of predation should influence breeding location, as loons should adapt to minimize this source of reproductive loss. Finally, I examined the effect of the high arctic climate on pond availability throughout the season. Although small ponds open sooner in most areas (Davis 1972, Irving 1972, Forbes et al.

1992), the selection of large ponds may be related to their availability late in the season.

I found, first, that the loons of my high arctic study site had a shortened phenology and used larger ponds compared to those from more southern populations. Because small ponds were rarely used for nesting, despite their abundance, absence of the pacific loon was not sufficient to explain the prevalence of large pond use (Yeaton and Cody 1974, Bundy 1976, Reimchen and Douglas 1984, Gomersall 1986, Douglas and Reimchen 1988a). I also determined that reproductive success was higher near the ocean foraging areas, and that density of breeding pairs was higher in these regions.

I observed several temporal and spatial trends in predation pressure. Predation varied from year to year from very low (0%) to high (67%), and occurred mostly during incubation. Loons that nested on islands nearer the pond shoreline were more likely to have their nests depredated than if they nested further from the shore. However, predators tended to forage in a site specific manner, and nests of neighbours of depredated nests were also usually depredated. The use of islands for nesting, the preference for islands further from shore, and the spacing out of territories are therefore presumably anti-predator tactics.

The high arctic climate limits pond availability, with the large ponds freezing over more slowly in the fall than the small ponds. This provides another explanation for the use of large ponds. From these findings, I conclude that each of the variables examined affects selection of breeding location in the red-throated loons of Bathurst Island.

Habitat selection

With respect to distance from the ocean, the wetland represented in my study area

can be divided into two habitat areas; wetland near the ocean, where density and reproductive success were higher, and wetland far from the ocean, where density and reproductive success were lower. Selection of habitat in this area should thus be determined by proximity to foraging grounds. However, if the selective pressure to nest near foraging grounds was the only pressure affecting distribution, then all loons should nest near the ocean, possibly colonially (see Palmer 1962, Lack 1968, Merrie 1978), and nest far from the ocean only when nesting sites are unavailable near the ocean. Although the loons were nesting in higher densities near the ocean, the pattern of distribution of their nests was uniform and certainly not colonial. This suggests that another factor plays a role in spacing out of breeding pairs.

Territory selection

Because loons cannot defend their nests against larger predators (i.e. mammals such as the arctic fox and wolf), loons must use a nesting strategy which minimizes location and accessibility by predators. This could be achieved by concealment of adults and their nests. Although concealment of adults was not quantified in this study, my observations and other studies (Bent 1919, vanOordt and Huxley 1922, Keith 1937) indicate that loons are cryptic in both behaviour and appearance when incubating. Spacing of territories presumably also promotes nest concealment because it decreases the likelihood of location by predators. This is supported by the area specific searches employed by predators during my study. Nests which were far from depredated nests were less likely to be themselves depredated. Selection for spacing out, presumably due to predation, thus results in breeding in suboptimal habitat (far from the ocean) despite

the lower success in these regions.

Predation may also play another role in territory selection. Davis (1972) suggested that the inclusion of several ponds in the territory also observed in this study may be a predator avoidance strategy. The non-breeding territorial ponds may be used for resting by a non-incubating parent or as a refuge by disturbed adults, or by a surviving chick, should its sibling be depredated (see also Davis 1972).

However, the results of my study suggest multiple ponds may provide an alternative territorial pond in case the natal pond freezes over before chicks fledge in the fall. A relatively high percentage of chicks moved to another pond either when young and most mobile, or when they were older and their natal ponds began to freeze over. In other studies, movement of chicks between ponds has been attributed to predator harassment (Davis 1972). However, few chicks in this arctic wetland were depredated (see chapter IV) and movement of a chick immediately following predation of its sibling only occurred once. Therefore another function of multiple territorial ponds could be to provide an alternative source of open water if the natal pond is likely to freeze over before chicks fledge. This function would be pertinent only in the high arctic.

Nest site

Previous studies reported that loons generally nest on islands. I found that 90% of nests were on islands and that nests on islands near the shore were more frequently depredated than those further from shore. Because an island to shore distance is dependent on size of a pond, it is possible that the apparent preference of large ponds reflects selection for ponds with islands far from the shoreline. Conversely, the loons may

select a large pond for another reason, and then choose an island which is furthest from shore. This may be the case if large ponds are used because they are available longest in the season. The use of all pond size classes for nesting in areas more temperate in climate and where mammalian predators also occur, supports this later hypothesis (Douglas and Reimchen 1988a).

In conclusion, the results suggest that all three factors, proximity to foraging areas, predator pressure, and climate affect selection of the breeding location by red-throated loons in the high arctic. Because loons must fly to foraging areas outside their nesting habitat, loons should prefer nesting habitat near the ocean. Spacing out due to predation however forces some individuals to breed in suboptimal habitat further from the ocean. To further decrease the probability of predation, loons nest on islands, and may nest on large ponds because these offer 'safer' islands further from the shoreline. However, breeding on large ponds also reduces chances of fledging failure due to pond freeze-over at the end of the season. The selection of large ponds may thus be adaptive with respect to both predation and climate.

Inclusion of more than one pond in territories may provide adults and young refuge during and after a predation attempt. On the other hand, climate in the high arctic may be another factor promoting the inclusion of multiple ponds in territories. Multiple ponds provide an alternative pond to loon families should the natal pond freeze-over.

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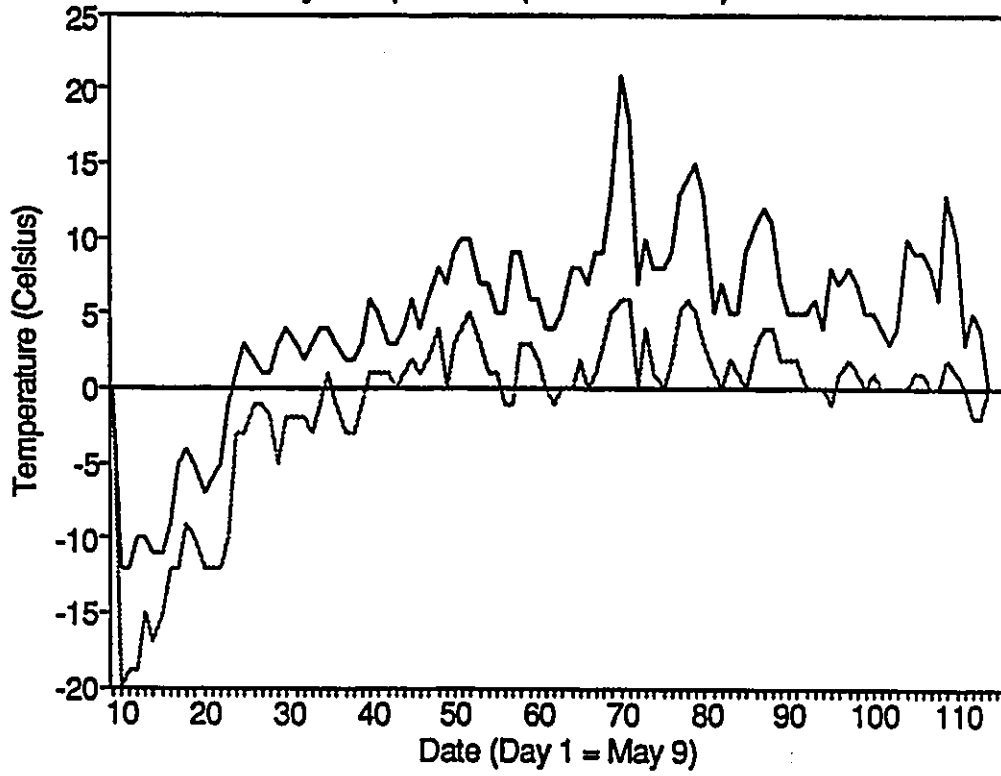
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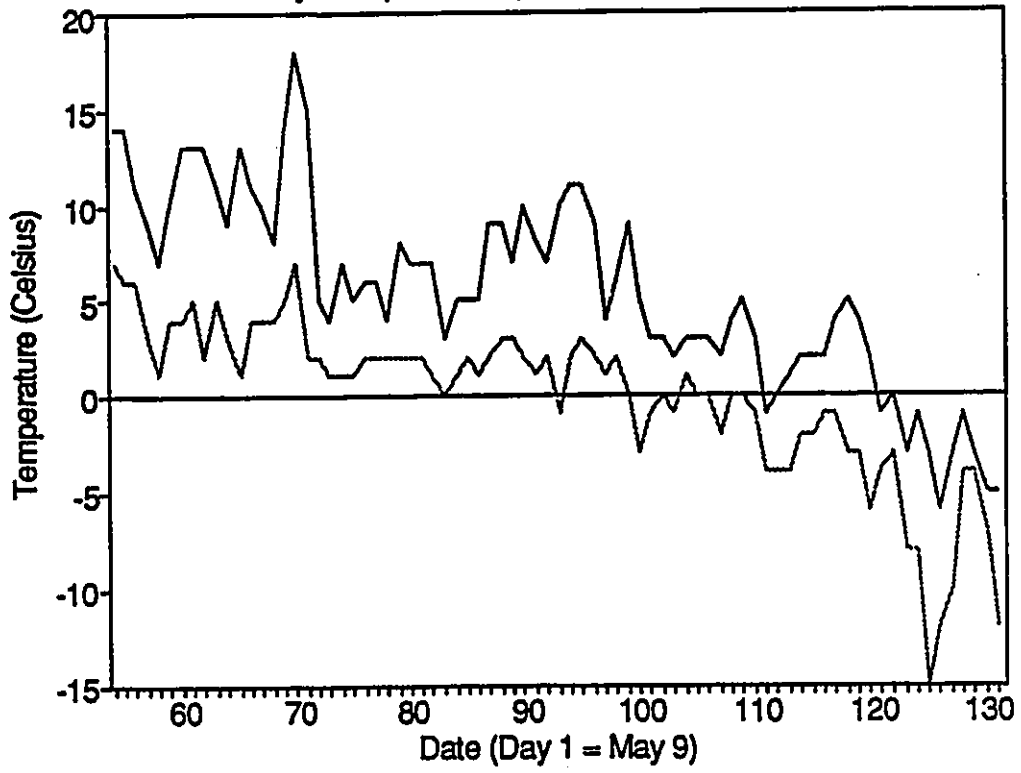
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Appendix One. Minimum and maximum daily temperatures at Bathurst Island, N.W.T., during the field seasons of 1989, 1990 and 1991.

Daily Temperature (Min. and Max) 1989



Daily Temperature (Min. and Max.) 1990



Daily Temperature (Min. and Max.) 1991

