The Auk 110(3):436–444, 1993

EFFECT OF NEST-SITE LOCATION ON REPRODUCTIVE SUCCESS OF RED-THROATED LOONS (*GAVIA STELLATA*)

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ABSTRACT.—The Red-throated Loon (*Gavia stellata*) nests on the shores of freshwater ponds of the Arctic tundra and forages in nearby marine waters. We examined the effects of distance of the nest from foraging waters and of microclimate at the nest site on the loon's reproductive success. As distance from the ocean increased, both density and nesting success decreased. Although hatching success did not vary with distance, success in rearing both chicks was significantly lower at distances greater than 9 km from the ocean. Loons with nests further from the ocean fed chicks less often and spent more time on foraging flights than did loons nesting within 9 km of the ocean. Brood reduction in nests far from the ocean presumably resulted from nestling starvation, and possibly also from higher predation due to less effective nest defense. We suggest that the higher density of breeding loons in areas near the ocean reflects preference of these birds for nesting grounds that are closer to their foraging areas. Microclimatic conditions also influenced reproductive success. In areas available for nesting earlier in the year, the loons initiated nesting earlier, but the probability of their reproductive failure due to predation was higher. However, successful pairs in these areas raised larger broods (two chicks) more often than those in areas where birds started breeding later. *Received 2 December 1991, accepted 31 August 1992.*

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 such as those 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 defendable, colonial nesting optimizes foraging efficiency of birds (i.e. Horn 1968). The type and intensity of predation, however, also plays an important role in shaping reproductive strategies. Predation could favor two types of adaptations: (1) it might select for tactics improving nest defense; and (2) it might select for predator-avoidance tactics, such as selection of a safe nesting site, and camouflage of nest and nesting activities.

Some avian species forage in habitats 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. Thus, some birds may have to compromise and this should be reflected in their reproductive success (Martindale 1982, Fagerström et al. 1983). Therefore, when reproductive success of individuals is evaluated for a given population, the investigator should consider each of these factors as they relate to 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 shoreline nest, usually on an island. Predation of eggs and young often is high (Davis 1972, Bundy 1976, 1978, Bergman and Derksen 1977, Gomersall 1986). Predator-avoidance tactics exhibited by loons may include breeding at low densities, nesting on islands, and defense of "escape" ponds (Davis 1972). Adults also actively defend eggs and chicks against small 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 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 two chicks, and all 3 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 (Bergman and Derksen 1977, 7.0 km; Merrie 1978, 8.0 km; Gomersall 1986, <5.0 km; Douglas and Reimchen 1988a, 8.6 km; Eriksson et al. 1990, 7.7 km; 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 study, we 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 the time both adults are on and protecting their territory (usually at least one is on territory). Predation on eggs, thus, could 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 against 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 also may be influenced by microclimatic conditions affecting relative rates of thawing (Chernov 1988) within the nesting area.

Thus, our objective was two-fold. First, we evaluated if distance from foraging waters influences reproductive success by examining success in each reproductive stage and establishing which factors affect differential success in each stage. Second, we investigated the effect of a 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.

METHODS

The study was conducted in the High Arctic, on Bathurst Island, North West Territories (75°44′N, 98°25′W). The study area occupies a 26-km band of wetland extending across the center of the island from the east coast to the west coast, and bordered to the north and south by dry ridges. The geography of the area creates a range of microclimates within the study area, resulting in earlier thaw of the northern half. Spring melt in this region is enhanced by drainage of melt waters into the north, and/or by greater exposure of ponds here to the rising sun in early spring.

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 freshwater fish. Loons in this area, thus, can forage only in marine waters. Other characteristics of this wetland are described in Mayfield (1983).

We monitored all loons nesting within the study area in 1989 and 1990 on a weekly basis from mid-June until 28 August in 1989 and until 10 September in 1990. We observed the breeding loons from a distance of 200+ m with binoculars and flushed the birds from their nests only when we had to determine date of lay or hatch. We 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 for pairs breeding in different distance categories (within 9.0 km of foraging areas) and the need to maintain adequate sample size in the resulting categories determined our 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 evaluated by comparing hatching and prefledging success to laying (1990) or hatching (1989) dates. Finally, we compared pairs within 1.5 km of the base of the southern ridges to those more northerly to examine the effect of north-south position of pairs on date of laying, as well as on breeding success. We used nonparametric statistics (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.

In 1990, we selected six pairs of loons for observation based on the distance of their nest site from the ocean, the ease of access for observation, and the successful hatch of both eggs. Selection was independent of success the previous year. The three far pairs were 10.6, 11.0, and 12.0 km from the nearest coast, while the three near pairs were 3.4, 4.0, and 4.1 km away. Blinds were placed within 150 m of the nests during incubation. Observations were initiated when the first chick hatched, at which 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 0730 and 1730 CST, and were 5 h in duration. Two observation periods of less than 5 h (3 and 4 h) were included by extrapolating activity to a 5-h period. Each pair was observed one to three times per week.

During each observation period, we recorded the number of chicks, duration of attendance by adults, foraging frequency, and success of each feeding event (if observed). Time allocated to foraging for chicks could not be measured directly, but the minimum flight time was estimated from the number of feeding trips, distance to the ocean, and flight speed (70 km/h; Norberg and Norberg 1971, Davis 1971).

To determine whether the numbers of fish delivered to chicks per unit of time were similar regardless of distances to the foraging waters, we compared the number of fish delivered per observation period 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 effects of distance (near vs. far) and brood size (one vs. two) on the dependent variables (feeding frequency and minimum flight time) were tested using a nested two-way ANOVA (Sokal and Rohlf 1981, SAS Institute 1985). Two additional variables were included to control for interaction between the main effects (distance × brood size) and for behavioral variations between pairs (the variable "pair" nested in distance × brood size).

RESULTS

General reproductive success.—In 1989, we located 32 breeding pairs. Except for three shoreline nests, all nests were on islands. Because predators were scarce 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 as of 28 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 Jaegars (*Stercorarius pomarinus*). Brood reduction in all other cases ($n = 8$) occurred within the first week after hatching.

In 1990, we found 36 pairs of loons with at least 38 nests, including second nesting attempts. All but five nests were on islands. Only one single-egg clutch was found; this plus one other clutch (two eggs; same pair as in 1989) were infertile. Nest losses were high; 15 pairs (43%) failed to rear chicks. Most losses occurred during incubation ($n = 12$), while one of the three brood losses was caused by observer interference. Two to four pairs relaid, but only one replacement egg hatched. Of 20 pairs that hatched both eggs and successfully reared young, 9 reared both chicks as of 5 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 11.3 km. Distance to the ocean 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 region, 0.90 and 1.09 pair/km^2 in 1989 and 1990, respectively; far region, 0.63 pair/km^2 during both years). Although a comparison of the nearest-neighbor distances for each year does not reveal a significant difference between near and far regions 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

TABLE 1. Nesting success and brood size as function of distance from ocean.[a] Far locations defined as >9.0 km from ocean; near locations ≤9.0 km from ocean.

Year	Category	Distance class Near	Far	P
	Nest success			
1989	Successful	18	13	0.59
	Failed	1	0	
1990	Successful	13	8	>0.50
	Failed	9	5	
Pooled	Successful	31	21	>0.50
	Failed	10	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	
Pooled	1 chick	7	14	0.005
	2 chicks	23	7	

[a] G-test of independence with William's correction. Used for all evaluations except for nest success in 1989, where Fisher's exact probability test employed.

0.26–1.58 km, n = 42; far, range 0.40–1.79 km, $n = 26$; $U = 726$, $P < 0.05$). Furthermore, density was highest within the westernmost 3 km of wetland habitat, which was within 5.5 km of the ocean (1989, 1.58 pair/km^2 of wetland, n = 12; 1990, 1.71 pair/km^2, n = 13).

During the study, 17 near sites (89.5% of 1989 nests) and 12 far sites (92.3% of 1989 nests) were used both years ($G = 0.06$, $P > 0.5$). However, two pond sites within the same territory may have been used for nesting by a single pair over the two years. The total number of nesting pairs increased from 32 in 1989 to 36 in 1990. Although the number of nesting pairs in the far region remained constant (13 pairs both years), the number of nesting pairs in the near region increased (1989, 19 pairs; 1990, 23 pairs). This difference between near and far, however, is not significant (Fisher's exact $P = 0.18$).

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 association between distance and nesting failure (Table 1; $P > 0.5$, pooled). 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 1). We found that 70.0% of all one-chick broods were in far territories, and 79.3% of two-chick broods were from near territories.

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 attempts (Table 2). Suspected renesting attempts (three in 1990) were omitted from this analysis.

Other factors influencing reproductive success.—Nesting failure in 1990 was not related to dates eggs were laid (successful pairs, range 30 June–10 July, n = 16; failed pairs, range 28 June–17 July, n = 14; U = 129, $P > 0.2$). 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 3 July (n = 9), and all two-chick broods were from clutches laid on or before that date (n = 7). The 1989 data show a similar pattern (Table 3). The lack of a relationship between dates of laying and distance (Table 2) indicates that these two variables act independently of each other on brood size.

Laying date also was influenced by location (Table 4); the median laying date for northern nesting pairs was two days before that of the more southerly pairs ($n = 60$). Reproductive success of pairs in the northern area was significantly less than that of pairs in southern areas in 1990 (Table 5; 20% failure in south, 55% in north). Survival of two-chick broods also was

TABLE 2. Date of hatching (1989) and laying (1990) as function of distance to ocean. For both years, 1 June is date "1." Values given for pooled data standardized such that 1 equals first recorded date of hatch for 1989 and date of laying for 1990. Median (range, n).

Year	Distance category Near	Far	P[a]
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
Pooled	5 (1–15, 35)	6 (1–14, 25)	0.1 > P > 0.05

[a] Two-tailed Mann-Whitney U-test, for individual years, with normal approximation of test used for evaluation of pooled data.

TABLE 3. Brood size as function of hatching date for 1989 and laying date for 1990. For both years, 1 June is date "1." Values given for pooled data standardized such that 1 equals first recorded date of hatching for 1989 and date of laying for 1990. Median (range, n).

Year	Brood size: 1 chick	2 chicks	P^a
1989	62 (56–70, 7)	58 (53–69, 21)	<0.05
1990	33 (33–40, 9)	33 (30–33, 7)	<0.02
Pooled	6 (4–15, 16)	5 (1–14, 14)	<0.05

[a] Two-tailed Mann-Whitney U-test.

TABLE 5. Nesting success and brood size as function of south/north location within study area. South indicates southern 1.5 km of study area; north indicates northern 1.5 km.

Year	Category	South/north location: South	North	P^a
		Nest success		
1989	Successful	13	18	
	Failed	0	1	0.59
1990	Successful	12	9	
	Failed	3	11	<0.05
Pooled	Successful	25	27	
	Failed	3	12	>0.50
		Brood size		
1989	1 chick	7	3	
	2 chicks	6	14	<0.05
1990	1 chick	8	3	
	2 chicks	3	6	$0.1 < P < 0.05$
Pooled	1 chick	15	6	
	2 chicks	9	20	0.005

[a] G-test of independence with William's correction. Used for all evaluations except for nest success in 1989, where Fisher's exact probability test employed.

affected by location; pairs in the south more often lost one chick (Table 5; south, 63%, $n = 24$; north, 23%, $n = 26$; 1989 and 1990 data pooled). However, the brood size versus location relationship was not as strong (Table 5; 1989, $P < 0.05$; 1990, $0.1 > P > 0.05$) as that of brood size and distance (Table 1; 1989, $P < 0.05$; 1990, $P < 0.025$).

Effect of distance on foraging budgets.—Observations of five loon pairs commenced within a day of hatching of the first chick (27-30 July) and observations of the sixth pair (near) began when the eldest chick was eight days old (7 August). Of the six pairs, three (one near and two far) lost one chick, one to three weeks after hatching. One of the near pairs lost two chicks to predation by wolves four days after hatching. Only two pairs (one near and one far) still had both chicks at the end 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, $F = 5.66$, $P = 0.025$), as well as for pairs having two-chick broods (controlled for distance class, $F = 11.68$, $P = 0.002$; Table 6). Neither the interaction variable, nor the nested variable "pair" were significant ($F_{\text{interaction}} = 0.68$, $P = 0.360$, $F_{\text{pair}} = 0.91$, $P = 0.486$). One-chick broods were offered an average of 2.15 ± SD of 1.16 fish per 5-h period, while two-chick broods were offered an average of 4.15 ± 1.32 fish. Near broods received 4.25 ± 1.58 fish/5 h, while far broods received 3.13 ±

TABLE 4. Date of hatching for 1989 and laying for 1990, as function of south/north location, for all pairs and for successful pairs. South indicates southern 1.5 km of study area; north indicates northern 1.5 km. For both years, 1 June is date "1." Values given for pooled data standardized such that 1 equals first recorded date of hatch for 1989 and day of laying for 1990. Median (range, n).

Year	South/North location: South	North	P^a
	All pairs		
1989	60 (56–70, 13)	58 (53–69, 17)	<0.03
1990	33 (31–47, 11)	33 (28–40, 19)	<0.04
Pooled	7 (3–15, 24)	5 (1–14, 36)	<0.02
	Successful pairs		
1989	60 (56–70, 13)	58 (53–69, 17)	<0.03
1990	33 (31–39, 8)	33 (30–33, 8)	$0.1 > P > 0.05$
Pooled	7 (2–15, 21)	4 (1–14, 25)	<0.01

[a] Two-tailed Mann-Whitney U-test, for individual years, with normal approximation of test used for evaluation of pooled data.

TABLE 6. Average number of fish offered to one- and two-chick broods near or far from ocean (n = number of 5-h observations).

Distance class	n	Average no. fish returned per 5-h period ± SD
One-chick broods[a]		
Near	4	2.65 ± 1.30
Far	7	1.86 ± 1.07
Two-chick broods[a]		
Near	11	4.83 ± 1.27
Far	16	3.69 ± 1.20

[a] All began as two-chick broods; one-chick broods those where one chick lost.

TABLE 7. Average estimated minimum flight times per 5 h required to obtain fish for one- and two-chick broods located near or far from ocean (n = number of 5-h observations).

Distance class	n	Estimated flight time[a] (min/5-h period ± SD)
One-chick broods[b]		
Near	4	24.16 ± 10.04
Far	7	46.01 ± 27.69
Two-chick broods[b]		
Near	11	37.06 ± 10.57
Far	16	80.49 ± 28.93

[a] Minimum estimate.
[b] All began as two-chick broods; one-chick broods those where one chick lost.

1.4 fish/5 h. Thus, feeding frequency was not equal across the distance classes.

Estimated time required for foraging flights differed between near and far pairs (Table 7). More time was spent on foraging flights by far pairs (controlled for brood size, $F = 10.86$, $P = 0.0026$) and by pairs having two chicks (controlled for distance class, $F = 4.33$, $P = 0.046$). Neither the interaction variable, nor the nested variable "pair" were significant ($F_{\text{interaction}} = 0.24$, $P = 0.626$, $F_{\text{pair}} = 0.95$, $P = 0.464$). Far pairs spent twice the total estimated flight time of near pairs (70.00 ± 32.2 vs. 33.6 ± 11.7 min/5 h), 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 h). These results suggest that far pairs spent a greater amount of flight time acquiring fewer fish than did near pairs.

A linear regression of the number of fish returned per chick during an observation period, as a function of date, revealed no relationship between date and number of fish fed per day ($b = 0.005$, $t = 0.157$, $P = 0.88$, $n = 48$).

DISCUSSION

We have demonstrated that nesting location and the date of egg laying may affect nesting success and brood size of the Red-throated Loons. Causes of nesting failure and brood-size reduction are examined 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*), jaegars (*Stercorarius pomarinus* and *S. parasiticus*), and Snowy Owl (*Nyctea 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 the findings of Davis (1972). Davis found that loons nesting in an area approximately 13 km from the ocean failed more frequently than those nesting approximately 9.5 km from the ocean. The lack of distance effect in our 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 southern portion could be associated with 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, laying date, even though it is correlated with south/north location, did not affect failure. This is not congruent with the results of 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 our study area because Red-throated Loons bred at relatively low densities.

Other factors that potentially could cause nesting failure seem less important. Flooding of nests (Cyrus 1975, Lokki and Eklof 1984, Gomersall 1986) and desiccation of ponds leading to stranding, abandonment or predation of nests (Bundy 1976, Douglas and Reimchen 1988b, Eriksson et al. 1988) may sometimes cause nesting failure. Even though the northern portion of this area received most of the first melt waters, the water levels at the time of nesting were stable in both years. Thus, for our study, flooding or drying of ponds was unimportant.

Nesting success in other species has been correlated with familiarity of pairs with their territory and neighbors (e.g. Picman 1987, Gauthier 1990). Enhanced success 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 three ponds that were used only in 1989 were near pond sites that were used only in 1990, and may have been on the same territories. Four other pond sites that were used in one year only were definitely in new territories; two were in the north and two were in the south. Because loons in one of each failed, the greater failure of loon nests in the north cannot be explained by a different number of new territories in the two areas.

Factors affecting brood size.—Loss of a chick could be caused by nestling starvation or predation. Brood size of successful pairs was correlated with distance to the ocean, south/north location, and laying date. Brood size decreased with increasing distance of breeding territories from foraging areas. Because all broods considered in this analysis originally consisted of two chicks, we conclude that brood reduction occurs more frequently in far broods than in near broods.

Our time-budget study indicated two important differences between pairs nesting near to and far from the ocean that 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, decreased vigilance allowing predation of an otherwise healthy chick also could produce a similar result.

Dickson (1992) suggested that unattended newly hatched chicks are vulnerable to predation by Glaucous Gulls. We observed that, during the first week after hatch, loon 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 105.0 h of observation, 0 of 71 h, 2.8 of 70.0 h, and 6.8 of 36.0 h). We 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 nearby forces the loons into the water. Although this might explain a few cases of chick mortality, we suggest that this type of predation is not responsible for 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.

We 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 loon 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 the Red-throated Loon. 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 that second siblings disappeared within 10 days of hatching.

The higher density of loons near the ocean suggests that near territories are preferred by the loons. This also has 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 dates of laying (1990), as well as of hatching (1989), were 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. We 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 also are more successful (Perrins 1970). Ages of 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 responsible for variations in laying date 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 (see also Dickson 1992). This is not consistent with findings of Reimchen and Douglas (1985), who found that the number of fish fed per day decreased with the 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 also could 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. Because the prey species consumed by the Bathurst Island loon population and their spawning times have not been established, we cannot test this hypothesis.

To summarize, distance from foraging waters played an important role in the reproductive success of Red-throated Loons. Although success during incubation was unaffected by distance in our study (but see Davis 1972), distance had an effect on survival of both siblings in two-chick broods. Distance-related chick mortality is likely a result of (1) starvation-related death of the weaker sibling and (2) predation of inadequately guarded chicks. 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.

Our data suggest that both predation and limited food play a role in territory and nest-site selection of Red-throated Loons. Loons seem to reduce nest predation by breeding on islands, by nesting at low densities, and by constantly guarding their brood. Long distances of foraging areas from the breeding territories, however, may set a limit to reproductive success in our population. Higher reproductive success in areas near the ocean may promote a higher density of breeding pairs in this region.

Acknowledgments

We thank D. R. Gray of the Canadian Museum of Nature for allowing us to conduct this research at the C.M.N. High Arctic Research Station. We also thank J. Geale and R. Holt for their invaluable assistance in the field. We are indebted to D. A. Gill for his continual support throughout the study. D. L. Dickson, A. J. Gaston and H. McMurter provided valuable comments on the manuscript. We are also thankful to J. M. Hagan and R. J. Steidl for constructive criticism. Logistic support was provided by the Polar Continental Shelf Project. Financial support was provided by an NSERC grant to J.P. and grants to C.E. from the Northern Studies Training Program and from the North American Loon Fund.

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