

Breeding Ecology of Sympatric Greater and Lesser Scaup (*Aythya marila* and *Aythya affinis*) in the Subarctic Northwest Territories

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ABSTRACT. We studied the breeding ecology of greater and lesser scaup on islands of the North Arm of Great Slave Lake, Northwest Territories, and on the nearby mainland during 1990–98. The occurrence of nests of both species on the North Arm islands was determined primarily by the distribution of nesting gulls and terns and secondarily by habitat features. Nest parasitism was frequent on the islands, but not on the mainland. Average clutch size was 8.99 ± 0.12 ($n = 169$) for greater scaup and 9.20 ± 0.17 ($n = 93$) for lesser scaup on the North Arm, and 8.71 ± 0.18 ($n = 55$) for lesser scaup on the mainland. No greater scaup nests were found on the mainland. Apparent nest success on the islands was higher (greater scaup 75%, $n = 271$; lesser scaup 77%, $n = 158$) than on the mainland (lesser scaup 37%, $n = 59$). Apparent egg success was 63% ($n = 1485$) for greater scaup and 67% ($n = 934$) for lesser scaup on the islands, and 40% ($n = 435$) for lesser scaup on the mainland. Hatchability of eggs was 98% ($n = 556$) for greater scaup and 94% ($n = 416$) for lesser scaup on islands, and 98% ($n = 435$) for lesser scaup on the mainland. Our findings, when compared to those of previous studies, do not indicate that either clutch size or egg hatchability has declined in recent years. Therefore, it seems unlikely that broad changes in these reproductive parameters are responsible for local or continental declines in lesser scaup populations. However, nest success on our mainland study area may have been too low to maintain the local population.

Key words: *Aythya affinis*, *Aythya marila*, boreal forest, egg success, greater scaup, lesser scaup, hatchability, nest success, Northwest Territories, Subarctic

RÉSUMÉ. De 1990 à 1998, on a étudié l'écologie de reproduction du fuligule milouinan et du petit fuligule sur des îles situées dans le Bras-Nord du Grand Lac des Esclaves (Territoires du Nord-Ouest) ainsi que sur la terre ferme avoisinante. La présence, dans les îles du Bras-Nord, de nids appartenant aux deux espèces était surtout déterminée par la distribution des mouettes et des sternes, et en second lieu par les caractéristiques de l'habitat. Le piratage des nids était fréquent sur les îles, mais pas sur la terre ferme. La taille moyenne des couvées était de $8,99 \pm 0,12$ ($n = 169$) pour le fuligule milouinan et de $9,20 \pm 0,17$ ($n = 93$) pour le petit fuligule dans le Bras-Nord, et de $8,71 \pm 0,18$ ($n = 55$) pour le petit fuligule sur la terre ferme. On n'a pas trouvé de nids de fuligule milouinan sur la terre ferme. Le succès apparent de la nidification sur les îles était plus grand (fuligule milouinan: 75 p. cent, $n = 271$; petit fuligule: 77 p. cent, $n = 158$) que sur la terre ferme (petit fuligule: 37 p. cent, $n = 59$). Le succès apparent de la ponte était de 63 p. cent ($n = 1485$) pour le fuligule milouinan et de 67 p. cent ($n = 934$) pour le petit fuligule sur les îles, et de 40 p. cent ($n = 435$) pour le petit fuligule sur la terre ferme. L'éclosabilité était de 98 p. cent ($n = 556$) pour le fuligule milouinan et de 94 p. cent ($n = 416$) pour le petit fuligule sur les îles, et de 98 p. cent ($n = 435$) pour le petit fuligule sur la terre ferme. Quand on les compare à ceux d'études antérieures, nos résultats ne révèlent aucun déclin au cours des dernières années quant à la taille de la couvée ou l'éclosabilité. Il semble donc peu probable que des changements majeurs dans ces paramètres de reproduction soient responsables des déclin au niveau local ou continental dans les populations du petit fuligule. Le succès de la nidification dans la zone couverte par notre étude située sur la terre ferme peut toutefois avoir été trop faible pour maintenir le niveau de population locale.

Mots clés: *Aythya affinis*, *Aythya marila*, forêt boréale, succès de la ponte, fuligule milouinan, petit fuligule, éclosabilité, succès de la nidification, Territoires du Nord-Ouest, Subarctique

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INTRODUCTION

Greater scaup (*Aythya marila*) and lesser scaup (*Aythya affinis*) breed sympatrically throughout much of northwestern North America (Palmer, 1976; Bellrose, 1980) including the boreal forest of Canada's Northwest Territories

(Godfrey, 1986). With the exception of Trauger's (1971) study of lesser scaup, information on the ecology of scaup in the important Subarctic breeding areas of the Northwest Territories is limited to a few general investigations of waterfowl and other migratory birds (Murdy, 1965; Weller et al., 1969; Trauger and Bromley, 1976; Toft et al., 1982;

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Nudds and Cole, 1991). None of these studies involved the simultaneous investigation of both species of scaup, and information from most studies is now decades old. In light of recent declines in populations of lesser scaup in boreal Canada and elsewhere and the uncertain status of greater scaup, more current information and a better understanding of the ecology of scaup in the region are required for management purposes (Austin et al., 2000).

During 1990–95, we studied sympatrically breeding greater and lesser scaup on islands of the North Arm of Great Slave Lake near Yellowknife, Northwest Territories. In addition, we investigated the breeding ecology of lesser scaup on the mainland near Yellowknife during 1994–98. Our objectives were to (1) document aspects of the breeding ecology of lesser and greater scaup in the region; (2) compare nesting biology of the two species; and (3) evaluate factors potentially limiting reproductive success of local scaup populations.

STUDY AREA

Our study area is located within the Taiga Shield Ecozone (Wiken, 1986), a region of open boreal forest. The climate is Subarctic-continental, characterized by long cold winters, short cool summers, and low annual precipitation (Atmospheric Environment Service, 1993).

North Arm Study Area

The North Arm study area (hereafter North Arm) includes a 384 km² section of the North Arm of Great Slave Lake, bordered by Yellowknife Bay on the southeast (62°22'N, 114°20'W) and Frank Channel on the northwest (62°48'N, 115°58'W) (Fig. 1). The northern boundary of the study area is the northern shore of the North Arm, and the southern boundary occurs approximately 200 m off the outermost islands, a distance of 210–9700 m from the mainland.

Progressing from southeast to northwest, there is a transition from the deeper, relatively clear waters of Yellowknife Bay, approximately 60 m deep at the West Mirage Islands (Rawson, 1950), to the very shallow and turbid waters of Frank Channel, approximately 1 m deep (Rawson, 1950). The North Arm is on the margin of the Canadian Shield. It contains hundreds of rocky islands, which range in size from less than 0.01 ha to approximately 3.5 km². A large number of bays, many with extensive shallow wetlands, are also present. The islands consist of glacially polished granitic or basaltic rock with reliefs of 3–7 m. Organic soil cover ranges from none to extensive, and both abundance and type of vegetation vary greatly from island to island.

The following vegetation descriptions are adapted in part from Porsild and Cody (1980) and Weller et al. (1969). Lichens and mosses occur on rock surfaces and in crevices. Most islands support grasses (mainly *Calamagrostis* spp.), sedges (*Carex* spp.), and forbs such

as saxifrage (*Saxifraga tricuspidata*), wild onion (*Allium schoenoprasum*), and yarrow (*Achillea* sp.). Low shrubs are common and include sweet gale (*Myrica gale*), wild rose (*Rosa acicularis*), currant (*Ribes* spp.), raspberry (*Rubus* spp.), and Labrador tea (*Ledum groenlandicum* and *L. decumbens*). Tall shrubs, primarily willows (*Salix* spp.) and alders (*Alnus* spp.), occur in depressions and along some shorelines. Many islands lack tree cover, and offshore islands generally have fewer, smaller trees than do islands close to the mainland. Trees include white and black spruce (*Picea glauca* and *P. mariana*), jack pine (*Pinus banksiana*), and paper birch (*Betula papyrifera*). On the offshore islands, conifers frequently assume a low, prostrate growth form.

Shoreline marshes occur in bays and typically are sheltered from heavy waves by barrier islands. However, fluctuations in water levels occur in these marshes because of wind seiches. Most marshes have influent creeks, and bottom substrates vary from clay to rich organic deposits. Common emergent plants include sedges and horsetails (*Equisetum* spp.), which often are interspersed with cattail (*Typhalatifolia*) or bulrushes (*Scirpus* spp.). Submergent plants include pondweeds (*Potamogeton* spp.), bladderworts (*Utricularia* spp.), and milfoils (*Myriophyllum* spp.).

Located near the southeastern corner of the study area are the West Mirage Islands, an isolated archipelago of 97 islands lying about 6 km from the mainland. The phenology on this archipelago is delayed from that on the mainland, and the avifauna shows an affinity with Low Arctic areas more than 300 km north of Yellowknife (Weller et al., 1969; LaRoi and Babb, 1974).

For further information on the physical features and avifauna of the North Arm of Great Slave Lake, see Sirois et al. (1995).

Yellowknife Study Area

The Yellowknife study area (YKSA) consists of a 38 km² roadside transect beginning 16 km west of Yellowknife, Northwest Territories, continuing 48 km west, and extending 0.4 km on each side of the road. Of the 575 ponds on the YKSA, 262 are natural in origin and 313 are man-made. Man-made ponds developed where surface materials were removed during road construction, circa 1960. Ponds range in size from less than 0.1 ha to 18.2 ha. Man-made ponds are generally smaller, shallower, and less permanent than natural ponds.

Additional details on the physical environment, wetlands, and vegetation of the YKSA were reported by Fournier and Hines (1999).

METHODS

North Arm

During the summers of 1990–95, we searched 485 islands for the presence of breeding waterfowl. Many

islands were visited in more than one year. We used a combination of random and systematic sampling to select islands. We randomly selected 1 × 1 km blocks from 1:50 000 maps of the study area and set out to search every island within each block. This often proved impractical because of time and weather constraints. In such situations, we searched as many islands per block as possible. In addition, we searched every island encountered on which we suspected there were breeding gulls or terns (larids). Effectively, this meant we visited most larid breeding islands on the North Arm each year. Overall, we believe that our sample reflected the range of physical and biotic features of the islands within the study area and adequately satisfied the assumptions of the statistical methods employed in data analysis.

We visually estimated the percentages of each island covered by different vegetation types (forbs, grasses/sedges, low shrubs, tall shrubs, trees, and total cover). An index to the area of each island was obtained using a dot grid overlaid on 1:50 000 scale topographic maps. Distance to the mainland was measured from these maps as the shortest distance from the edge of the island to the shore.

Thorough nest searches on each island were conducted in mid to late June by two people on foot. Vegetation on the islands was generally limited in extent and patchily distributed, so all of the available nesting cover could be searched effectively. Whenever possible, we attributed scaup nests to species by observing the wing stripes of females as they flushed from their nests (Russell, 1975; Fix, 1985; Wilson and Ankney, 1988). When the sex of the bird is known, the percentage of scaup that can be identified accurately by this method approaches 100% (Fix, 1985). However, Russell (1975) and Wilson and Ankney (1988) noted that a few greater scaup females with unusually dark wings could not be correctly identified by this method.

At each nest, we recorded clutch size, incubation status (incubating or laying), and type of plant cover present. As nests were visited only once prior to hatch (i.e., at the time of discovery), clutches were considered complete and included in the calculation of mean clutch size only if there was ample evidence that incubation had begun. Evidence of incubation included warmth of eggs (following Weller et al., 1969), amount of down present in the nest (both species of scaup add down to nests mainly during incubation; Bellrose, 1980), and behaviour of the nesting female (once incubation has begun, females become reluctant to leave the nest; Johnsgard, 1975). Each nest was marked with a numbered plastic disc approximately 4 cm in diameter, which was buried beneath the nest material. We revisited each nest in late July or early August to determine its fate (i.e., hatched, abandoned, or destroyed by a predator). Criteria used to identify hatched and abandoned nests follow Klett et al. (1986). Causes of nest losses were determined from criteria outlined in Rearden (1951) and Sargeant et al. (1998).

During 1990–93, clutches for which no female was observed were recorded simply as scaup. In 1994 and

1995, all eggs were measured and those of uncertain origin were classified to species using a discriminant function analysis (Kleinbaum and Kupper, 1978; SAS Institute, 1990). The discriminant function, based on measurements of lengths and widths of 432 lesser and 471 greater scaup eggs, was 98% accurate for classifying individual eggs (Fournier and Hines, unpubl. data).

The discriminant function was used to classify some clutches to species and also to identify possible instances of inter-specific nest parasitism involving both lesser and greater scaup. We defined intra-specific parasitism as occurring when the clutch exceeded 12 eggs, following Weller et al. (1969).

Apparent nest success is the percentage of nests found in which one or more egg hatches. In waterfowl studies, it typically overestimates true nesting success (Miller and Johnson, 1978). To overcome this possible bias and make our estimates more directly comparable to some other values reported in the literature, we converted apparent nest success to Mayfield (1961) nest success, following Green (1989). We refer to these conversions as Mayfield-Green estimates throughout the paper. The reliability of the Green (1989) estimator was evaluated on both real and simulated data by Johnson (1991), who found that it produced results similar to those produced by the Mayfield method.

For 1994–95 only, we estimated apparent egg success (percentage of all eggs that eventually hatched) from the presence or absence of egg caps or membranes, the number of unhatched eggs remaining in the nest, and the number of eggs found outside the nest. If no egg caps or membranes were found, we assumed that all eggs in a clutch had been destroyed, whereas the presence of one or more egg caps or membranes was considered to indicate that all eggs in a clutch had hatched, unless there was evidence to the contrary.

A map showing the number of nests found on different parts of the North Arm was generated with the Spatial Analysis extension of ArcView 3.1 (Environmental Systems Research Institute Inc., 1996). We used a kernel method of density calculation, a resolution (cell size) of 100 m, and a search area of 10 km² in map production.

Yellowknife Study Area

Ground surveys of breeding pairs on the YKSA, conducted in May and June of 1994–98, helped us identify areas in which to concentrate nest searches (Fournier and Hines, 1998). However, we searched not only the ponds where pairs were observed, but a number of nearby ponds and other ponds on the study area as well. The proportion of the YKSA searched each year was approximately 10–15% and was similar to the percentage of the North Arm islands searched. We concentrated nest searching during June and early July to coincide with egg-laying and early incubation. A team of 2–3 people searched for nests by wading or canoeing through the emergent vegetation of

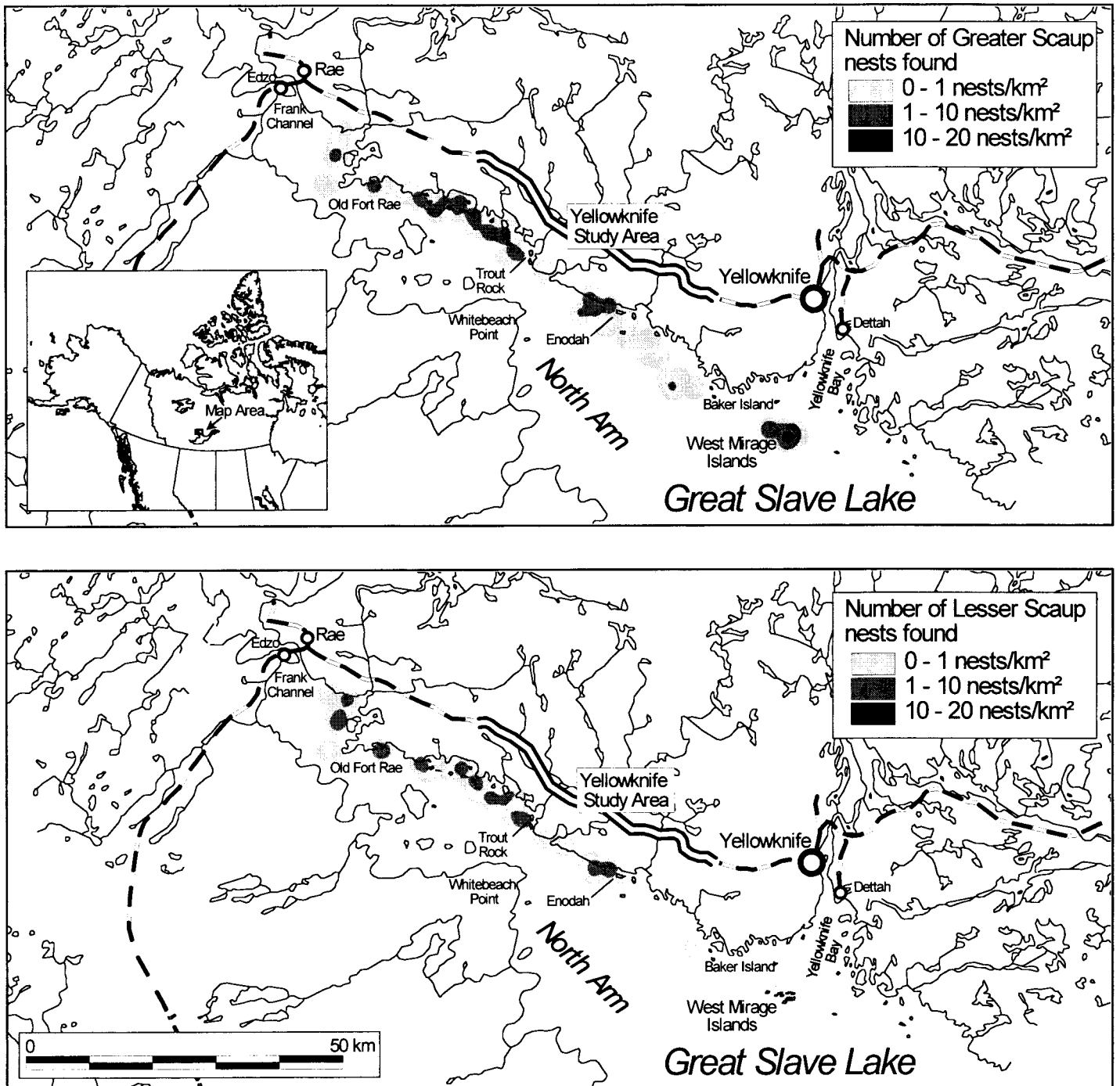


FIG. 1. Distribution of greater and lesser scaup nests on the North Arm of Great Slave Lake, 1990–95.

ponds and by walking the nearby shoreline. Areas around individual ponds were searched only once, as were the islands on the North Arm. Nests were found during laying and incubation on both study areas. On the YKSA, incomplete clutches were revisited every few days (typically twice) until the clutch size remained constant; however, this could not be done on the North Arm islands.

We used similar nest study methods on both areas, except that the YKSA nests were not marked, but were located again by the use of 1:7500 maps (coarse scale) of the study area and hand-drawn maps (fine scale) in a field notebook.

Statistical Methods

We used analysis of variance (PROC ANOVA) followed by Duncan's multiple range test (if the overall F-value was significant) and Wilcoxon or Kruskal-Wallis tests (PROC NPAR1WAY) to compare means or medians of two or more samples (SAS Institute, 1990). To further evaluate the importance of different habitat features for selection of islands by nesting scaup and for nesting success, we followed these tests with both simple direct and multiple direct logistic regression (PROC LOGISTIC) and Wald's χ^2 test (Tabachnick and Fidell, 1996).

Variables were considered in the multiple logistic regression analyses if they demonstrated a significant ($p \leq 0.15$) relationship in the simple regressions (Hosmer and Lemeshow, 1989). To deal with the potential problem of multicollinearity, we eliminated a variable from the multiple logistic regression analysis if its variance inflation factor exceeded 10 (Rawlings et al., 1998). Potential differences in nesting success among study areas, species, and years were evaluated using χ^2 tests based on two-dimensional contingency tables (PROC FREQ) or a logit analysis of a three-dimensional contingency table (PROC CATMOD; Allison, 1999).

RESULTS

We found 605 scaup nests on the islands of the North Arm: 300 nests of greater scaup, 170 of lesser scaup, and 135 for which the species was not determined. On the YKSA, we found 64 lesser scaup nests but no greater scaup nests.

Nesting Habitat on the North Arm

We found greater scaup nests on 89 islands and lesser scaup nests on 55 islands. Both species used 38 of these islands, either simultaneously or in different years. Nesting scaup of unidentified species used an additional 9 islands. Thus, the total number of islands used by scaup was 115.

The distribution of lesser and greater scaup nests on the North Arm is indicated in Figure 1. The two species were not equally distributed throughout the study area, and the proportion of greater scaup in the sample of nests found decreased as we moved from east to west. At the West Mirage Islands, near the southeastern corner of the study area and closest to the main body of Great Slave Lake, 99 of 100 nests (99%) belonged to greater scaup, and only one belonged to a lesser scaup. In the area between Baker Island and Enodah (Fig. 1), 15 of 18 nests found (83%) were of greater scaup, and 3 (17%) were of lesser scaup. On the portion of the North Arm between Enodah and Old Fort Rae, 175 of 316 nests found (55%) belonged to greater scaup and 141 (45%) belonged to lesser scaup. In the relatively shallow northwestern corner of the study area, from Old Fort Rae to Frank Channel, 11 of 36 nests (31%) belonged to greater scaup and 25 nests (69%) belonged to lesser scaup.

Habitat characteristics of greater and lesser scaup nesting islands and of the entire sample of islands visited are presented in Table 1. The results of the analysis of variance and Duncan's multiple range test suggested that selection of islands by scaup was influenced by distance of an island from shore and by several vegetation characteristics (Table 1).

Logistic regression analysis and the resulting values of Wald's χ^2 test demonstrated the over-riding and positive influence of the presence of breeding gulls and terns (family Laridae, hereafter larids) on island use by nesting scaup of both species (Table 2). Only 12 (5%) of the 262

islands without nesting larids supported nesting scaup, whereas 103 (46%) of 223 islands with nesting larids had nesting scaup. Overall, 98% of the scaup nests that we found were on islands with nesting larids. This relationship held for greater scaup (98%), lesser scaup (97%), and unidentified scaup (99%) nests.

In addition to the presence/absence of larids, the logistic regression analysis indicated other factors that may have influenced island choice. For greater scaup, these were the distance of an island from shore (islands farther from shore had more nests) and the presence of tall shrub cover (islands with abundant tall shrubs had fewer nests), although these results were of borderline statistical significance. Lesser scaup were apparently influenced by island size (larger islands had more nests), distance from shore (nearshore islands had more nests), and tree cover (islands with fewer trees had more nests) (Table 2).

Islands used by nesting greater scaup were located, on average, farther from shore than those used by lesser scaup (Table 1). After we eliminated data from the West Mirage Islands, where nesting greater scaup were predominant, the difference between average distances to shore for the two species decreased (from 1443 m to 559 m), but the means ($1991 \pm [SE] 142$ m for greater scaup and 1432 ± 116 m for lesser scaup) remained significantly different (Kruskal-Wallis Test, 1 df, $p < 0.01$).

In all other aspects (area and vegetation characteristics), the islands used for nesting by the two species were similar (Tables 1 and 3).

Grass/sedge was most frequently used as nesting cover by both species of scaup. Low shrubs (such as currant, wild rose, raspberry, and Labrador tea) were also commonly used (Table 4).

Nesting Habitat on the Yellowknife Study Area

Lesser scaup nests were found in the YKSA on the peripheries of 48 different ponds, including 25 natural and 23 man-made ponds. Mean size of ponds used by lesser scaup was 1.89 ± 0.59 ha (median 0.80 ha) for natural ponds, 0.22 ± 0.03 ha (median 0.20 ha) for man-made ponds, and 1.09 ± 0.33 ha (median 0.35 ha) overall.

Like the scaup nesting on islands of the North Arm, scaup on the YKSA most frequently nested in grass/sedge cover (Table 4). In contrast to island-nesting scaup, lesser scaup on the YKSA made little use of low shrubs for nesting cover (one nest in sweet gale), and they occasionally used emergents such as cattail, horsetail, marsh cinquefoil (*Potentilla palustris*) and water-arum (*Calla palustris*), species not widely available to island-nesting scaup. None of the lesser scaup nests found on the YKSA were associated with the small number of breeding larids there.

Clutch Size and Nest Parasitism

Incubated scaup clutches ranged in size from 3 to 33 eggs (neither extreme could be attributed to a species) on

TABLE 1. Characteristics of islands used by nesting greater scaup (GRSC) and lesser scaup (LESC) and all islands surveyed on the North Arm of Great Slave Lake, Northwest Territories, 1990–95.

	Greater Scaup (n = 89)		Lesser Scaup (n = 55)		Available Islands (n = 485)		ANOVA <i>p</i>	Duncan's multiple range test ¹		
	Mean	SE	Mean	SE	Mean	SE		GRSC	LESC	Available
Grass/sedge (%)	4.5	0.4	3.8	0.4	4.4	0.2	0.45	–	–	–
Forbs (%)	2.2	0.3	1.9	0.2	1.9	0.1	0.61	–	–	–
Low shrub (%)	3.4	0.5	2.6	0.4	5.0	0.3	< 0.01	B	B	A
Tall shrub (%)	1.8	0.3	2.2	0.4	4.5	0.3	< 0.01	B	B	A
Tree (%)	2.5	0.5	2.0	0.4	6.3	0.4	< 0.01	B	B	A
Total cover (%)	14.4	1.6	12.4	1.3	22.1	0.9	< 0.01	B	B	A
Distance to shore (m)	2959	216	1516	141	2058	83	< 0.01	A	C	B
Island area (ha)	0.6	0.1	0.4	0.1	0.5	0.0	0.17	–	–	–

¹ Similar Duncan groupings indicate no significant difference between means ($p > 0.05$).

TABLE 2. Logistic regression analysis indicating the influence of macrohabitat features on use of islands by nesting greater and lesser scaup on the North Arm of Great Slave Lake, Northwest Territories, 1990–95.

Variable	Simple logistic regression				Multiple logistic regression			
	Slope	SE	Wald's χ^2	<i>p</i>	Slope	SE	Wald's χ^2	<i>p</i>
Greater Scaup								
Grass/sedge (%)	0.0175	0.0291	0.3624	0.5472 ²	–	–	–	–
Forbs (%)	0.0426	0.0349	1.4942	0.2216 ²	–	–	–	–
Low shrub (%)	-0.0714	0.0253	7.9490	0.0048	0.0516	0.0382	1.8247	0.1768
Tall shrub (%)	-0.2110	0.0447	22.2554	< 0.0001	-0.1174	0.0659	3.1681	0.0751
Tree (%)	-0.1115	0.0253	19.3429	< 0.0001	-0.0182	0.0407	0.2012	0.6537
Total cover (%) ¹	–	–	–	–	–	–	–	–
Distance to shore (km)	0.0003	0.0001	25.4497	< 0.0001	0.0001	0.0001	3.6473	0.0562
Island area (ha)	0.2007	0.1544	1.6892	0.1937 ²	–	–	–	–
Presence of Larids	2.9506	0.3857	58.5220	< 0.0001	2.6905	0.4119	42.6605	< 0.0001
Lesser Scaup								
Grass/sedge (%)	-0.0624	0.0492	1.6130	0.2041 ²	–	–	–	–
Forbs (%)	0.0094	0.0458	0.0421	0.8374 ²	–	–	–	–
Low shrub (%)	-0.1153	0.0376	9.3800	0.0022	0.0283	0.0584	0.2353	0.6276
Tall shrub (%)	-0.1450	0.0467	9.6227	0.0019	-0.0548	0.0660	0.6881	0.4068
Tree (%)	-0.1392	0.0374	13.8547	0.0002	-0.1350	0.0656	4.2266	0.0398
Total cover (%) ¹	–	–	–	–	–	–	–	–
Distance to shore (km)	-0.0002	0.0001	4.9506	0.0261	-0.0006	0.0001	23.4501	< 0.0001
Island area (ha)	-0.4497	0.3102	2.1012	0.1472	0.8416	0.3833	4.8221	0.0281
Presence of larids	2.7418	0.4795	32.6898	0.0001	2.7865	0.5160	29.1596	< 0.0001

¹ Variable eliminated from regression analysis (Variance Inflation Factor > 10).

² Variable eliminated from multiple regression analysis ($p > 0.15$).

the North Arm and from 6 to 11 eggs for lesser scaup on the YKSA (Table 5). Overall, mean clutch sizes of lesser scaup (10.52 ± 0.30 eggs) and greater scaup (10.13 ± 0.21 eggs) nesting on islands were higher (one-way ANOVA; $F = 6.70$; $df = 2,409$; Duncan's Multiple Range Test, $p < 0.01$) than the mean for lesser scaup (8.71 ± 0.18 eggs) nesting on the YKSA. However, the larger average clutch sizes on the North Arm were apparently due to egg parasitism. After controlling for the effects of parasitism (i.e., eliminating clutches with more than 12 eggs from the calculations), we found no significant differences (one-way ANOVA: $F = 1.76$, $df = 2,314$, $p = 0.17$) in clutch size between island-nesting and mainland scaup (Table 5).

The results of our discriminant function analysis of all eggs measured in 1994 and 1995 and the assumption that clutches with more than 12 eggs were the product of more

than one female led us to conclude that many scaup clutches on the North Arm were parasitized, either inter- or intraspecifically. In 1994 and 1995, 23 (35%) of 65 lesser scaup nests were parasitized by other waterfowl: 17 (26%) by greater scaup, one (2%) by a northern pintail (*Anas acuta*), and 10 (15%) by other lesser scaup. Included in the above total are five (8%) nests parasitized by both a greater scaup and another lesser scaup (i.e., at least three females were laying in the same nest). Similarly, 44 (38%) of 116 greater scaup nests were parasitized by other ducks: 31 (27%) by lesser scaup, 5 (4%) by other species (see below), and 14 (12%) by other greater scaup. Five (4%) of these nests were parasitized by both a lesser scaup and another greater scaup, and one nest was parasitized by both a lesser scaup and a red-breasted merganser (*Mergus serrator*). One such incident led to the concurrent incubation of a

TABLE 3. Logistic regression analysis indicating the differences in macrohabitat features of nesting islands of greater and lesser scaup on the North Arm of Great Slave Lake, Northwest Territories, 1990–95.

Variable	Simple logistic regression				Multiple logistic regression			
	Slope	SE	Wald's χ^2	<i>p</i>	Slope	SE	Wald's χ^2	<i>p</i>
Grass/sedge (%)	0.1443	0.1065	1.8350	0.1755 ²	–	–	–	–
Forbs (%)	0.0700	0.1210	0.3347	0.5629 ²	–	–	–	–
Low shrub (%)	0.0197	0.0555	0.1256	0.7230 ²	–	–	–	–
Tall shrub (%)	-0.1717	0.0876	3.8425	0.0500	-0.1869	0.1126	2.7532	0.0971
Tree (%)	-0.0060	0.0514	0.0135	0.9077 ²	–	–	–	–
Total cover (%) ¹	–	–	–	–	–	–	–	–
Distance to shore (km)	-0.0011	0.0003	10.9906	0.0009	-0.0012	0.0004	9.7491	0.0018
Island area (ha)	0.7377	0.5458	1.8269	0.1765 ²	–	–	–	–
Presence of larids	0.4747	0.7705	0.3796	0.5378 ²	–	–	–	–

¹ Variable eliminated from regression analysis (Variance Inflation Factor > 10).

² Variable eliminated from multiple regression analysis ($p > 0.15$).

TABLE 4. Dominant vegetative cover at greater and lesser scaup nests on islands of the North Arm of Great Slave Lake and on the mainland (YKSA) near Yellowknife, Northwest Territories, 1990–95.

Cover Type	Greater Scaup North Arm (n = 300)		Lesser Scaup North Arm (n = 170)		Lesser Scaup YKSA (n = 64)	
	% of Nests	(n)	% of Nests	(n)	% of Nests	(n)
Rock/moss	< 1	2	< 1	1	0	–
Grass/sedge	79	238	71	120	66	42
Forbs	3	10	5	9	0	–
Low shrub	14	43	19	33	2	1
Tall shrub	1	3	3	5	22	14
Tree	1	4	1	2	2	1
Emergent	–	–	–	–	9	6

TABLE 5. Clutch size of greater and lesser scaup nesting on islands of the North Arm of Great Slave Lake and on the mainland (YKSA) near Yellowknife, Northwest Territories, 1990–95.

	N	Min	Max	Mean	SE
Greater Scaup North Arm					
All clutches	232	4	29	10.13	0.21
Clutches < 12	169	4	12	8.99	0.12
Lesser Scaup North Arm					
All Clutches	125	5	26	10.52	0.30
Clutches < 12	93	5	12	9.20	0.17
Lesser Scaup YKSA					
All Clutches	55	6	11	8.71	0.18

mixed clutch by both a lesser and a greater scaup (Fournier and Hines, 1996).

During 1990–95, species that laid eggs in scaup nests on the North Arm included northern pintail ($n = 2$ nests), gadwall (*Anas strepera*) ($n = 3$), northern shoveler (*A. clypeata*) ($n = 2$), and red-breasted merganser ($n = 2$). On the North Arm, scaup eggs were found in the nests of a number of other species, including northern pintail ($n = 4$ nests), gadwall ($n = 2$), northern shoveler ($n = 1$), mallard (*Anas platyrhynchos*) ($n = 1$), canvasback (*Aythya valisineria*) ($n = 1$), and red-breasted merganser ($n = 2$). In addition to cases of parasitism involving other species of waterfowl, we found a scaup egg in the nest of a ring-billed gull (*Larus delawarensis*) and a ring-billed gull egg in a scaup nest (Fournier, 2000).

On the YKSA, no clutches exceeded 11 eggs, so there was no evidence of intraspecific parasitism based on the criterion of Weller et al. (1969). However, the results of our discriminant function analysis suggested that five of 51 lesser scaup clutches contained greater scaup eggs. The eight parasitic eggs represented less than 2% of all eggs measured ($n = 432$). No greater scaup nests were found on the YKSA, and greater scaup sightings there have been infrequent. Therefore, it seems possible that the discriminant function analysis incorrectly classified some of these eggs to species.

Nest Success

We determined apparent nest success and derived Mayfield-Green estimates for 271 greater scaup nests and 158 lesser scaup nests on the North Arm and 59 lesser scaup nests on the YKSA. A three-way contingency table indicated that apparent nest success differed significantly between study areas ($\chi^2 = 13.9$, 1 df, $p < 0.01$), but not between species ($\chi^2 = 0.20$, 1 df, $p = 0.65$) or years ($\chi^2 = 12.6$, 7 df, $p = 0.08$) (Table 6). Overall, the success of nests on the North Arm was virtually the same for greater scaup (75%) and lesser scaup (77%), and was much higher than for lesser scaup on the YKSA (37%). As expected, the Mayfield-Green estimates for these three samples were much lower than the apparent nest success estimates, and averaged 58%, 61%, and 18%, respectively.

We examined the influence on scaup nesting success of habitat characteristics of different islands (macrohabitat) and the presence of larids, using both univariate comparisons (Table 7) and logistic regression (Table 8). Because of the small number of islands ($n = 12$) with scaup nests but without larids, we pooled data from both scaup species for the logistic regression and any other comparisons involving this particular variable.

Only one variable had a clear effect on nest success: successful nests of scaup were most frequently located on islands that supported nesting gulls and terns. Overall, nest success on islands with nesting larids was higher (75%, $n = 525$) ($\chi^2 = 6.96$, $df = 1$, $p < 0.01$) than on islands without larids (42%, $n = 12$). In addition, there was some evidence (of borderline statistical significance) that nests located closer to shore were more successful than those located farther offshore (Table 8).

Where possible, we examined nesting success in relation to the type of vegetation in which nests were concealed (microhabitat). Sample sizes for each species were too small for meaningful comparisons involving forb, tall shrub, and tree cover (Table 4). As there were no differences (χ^2 tests, $p \geq 0.59$) in nest success between greater and lesser scaup in grass/sedge and low shrub cover, we pooled data for both species and included data from unidentified scaup for comparisons of cover types. There were no significant differences ($\chi^2 = 3.22$, 4 df , $p = 0.52$)

among cover types. Apparent nest success was 73% in grass/sedge ($n = 406$), 81% in forbs ($n = 27$), 78% in low shrubs ($n = 85$), 88% in tall shrub cover ($n = 8$), and 57% for nests under prostrate branches of trees ($n = 7$).

On the YKSA, there was no difference ($\chi^2 = 0.09$, 1 df , $p = 0.76$) in apparent nest success between lesser scaup nests located on natural ponds (35%, $n = 31$) and those located on man-made ponds (39%, $n = 28$). Sample sizes were too small to test for differences in nest success among most vegetation types (Table 4). There was no difference ($\chi^2 = 1.50$, 1 df , $p = 0.22$) in the success of nests located in grass/sedge and tall shrub, the two most frequently used cover types.

Egg Success

Apparent egg success of greater scaup (63%) and lesser scaup (67%) on the North Arm was similar and considerably higher than that of lesser scaup on the YKSA (40%) (Table 9). The difference in egg success between areas was attributable to the much higher rate of egg predation on the YKSA (57%) than on the North Arm (14%). The observed difference would have been even greater had the rates of nest abandonment and the number of unhatched eggs left in successful nests been similar between study areas. Rates of abandonment were higher on the North Arm (6% for greater scaup and 12% for lesser scaup) than on the YKSA

TABLE 6. Apparent and Mayfield-Green estimates of nest success of greater and lesser scaup on islands of the North Arm of Great Slave Lake and on the mainland (YKSA) near Yellowknife, Northwest Territories, 1991–98.

Year	Greater Scaup North Arm			Lesser Scaup North Arm			Lesser Scaup YKSA		
	Apparent Success (%)	Mayfield-Green (%)	n	Apparent Success (%)	Mayfield-Green (%)	n	Apparent Success (%)	Mayfield-Green (%)	n
1991	94	90	18	100	100	7	No data	–	–
1992	79	64	29	67	47	12	No data	–	–
1993	82	68	61	81	67	42	No data	–	–
1994	72	52	78	71	51	49	33	15	6
1995	67	47	85	77	61	48	9	2	11
1996	No data	–	–	No data	–	–	38	18	8
1997	No data	–	–	No data	–	–	43	22	7
1998	No data	–	–	No data	–	–	48	27	27
Mean	75	58	271	77	61	158	37	18	59

TABLE 7. Macrohabitat characteristics of successful and unsuccessful greater and lesser scaup nests on the North Arm of Great Slave Lake, Northwest Territories, 1991–95.

	Greater Scaup					Lesser Scaup				
	Successful (n = 212)		Unsuccessful (n = 72)		p^1	Successful (n = 118)		Unsuccessful (n = 38)		p^1
	Mean	SE	Mean	SE		Mean	SE	Mean	SE	
Grass/sedge (%)	4.3	0.1	4.5	0.4	0.63	3.9	0.2	3.5	0.3	0.25
Forbs (%)	2.1	0.2	2.4	0.5	0.72	1.8	0.1	2.0	0.2	0.46
Low shrub (%)	3.3	0.3	4.3	0.6	0.22	2.6	0.2	1.9	0.4	0.07
Tall shrub (%)	1.6	0.1	1.6	0.2	0.52	1.7	0.2	2.5	0.5	0.35
Tree (%)	1.9	0.3	2.9	0.6	0.09	1.1	0.2	1.9	0.5	0.22
Total cover (%)	13.2	0.9	15.6	1.9	0.26	11.1	0.6	11.7	0.2	0.70
Distance to shore (m)	3192	144	3759	260	0.05	1444	76	1624	136	0.16
Island area (ha)	0.5	0.0	0.7	0.1	0.19	0.3	0.0	0.34	0.1	0.97

¹ Kruskal-Wallis test results.

TABLE 8. Logistic regression analysis indicating the influence of macrohabitat features on nest success of greater and lesser scaup (combined) on the North Arm of Great Slave Lake, Northwest Territories, 1990–95.

Variable	Simple logistic regression				Multiple logistic regression			
	Slope	SE	Wald's χ^2	<i>p</i>	Slope	SE	Wald's χ^2	<i>p</i>
Grass/sedge (%)	- 0.0009	0.0418	0.0005	0.9829 ²	–	–	–	–
Forbs (%)	- 0.0320	0.0346	0.8520	0.3560 ²	–	–	–	–
Low shrub (%)	- 0.0229	0.0254	0.8161	0.3663 ²	–	–	–	–
Tall shrub (%)	- 0.0755	0.0525	2.0690	0.1503 ²	–	–	–	–
Tree (%)	- 0.0537	0.0261	4.2287	0.0397	- 0.0344	0.0275	1.5648	0.2110
Total cover (%) ¹	–	–	–	–	–	–	–	–
Distance to shore (km)	- 0.0001	0.0001	3.2591	0.0710	- 0.0001	0.0001	3.0127	0.0826
Island area (ha)	- 0.1904	0.1847	1.0629	0.3026 ²	–	–	–	–
Presence of larids	1.5786	0.6557	5.7968	0.0161	1.5569	0.6757	5.3093	0.0212

¹ Variable eliminated from regression analysis (Variance Inflation Factor > 10).

² Variable eliminated from multiple regression analysis ($p > 0.15$).

(< 2%), as were the numbers of unhatched eggs left in successful nests (8% for greater scaup and 9% for lesser scaup on the North Arm and 1% for lesser scaup on the mainland), probably as a result of parasitism.

Hatchability of eggs (the percentage of incubated eggs in successful clutches that eventually hatched) was 89% ($n = 1485$ eggs) for greater scaup and 88% ($n = 934$) for lesser scaup on the North Arm, and 98% ($n = 435$) for lesser scaup on the YKSA. When parasitized clutches were excluded from the analysis, hatchability of greater and lesser scaup eggs on the North Arm increased to 98% ($n = 556$ eggs) and 94% ($n = 416$ eggs), respectively.

DISCUSSION

Habitat Use

Our study areas provided a variety of habitat types for nesting scaup. Lesser scaup were the more widely distributed of the two species and used a greater variety of cover types for nesting. The only area that did not support many lesser scaup was the West Mirage Islands (Fig. 1). Despite the abundance of nesting greater scaup on the North Arm of Great Slave Lake, particularly on the West Mirage Islands, we found no nests of this species on the mainland. Thus, the overall distribution pattern of breeding scaup in the region was lesser scaup on the mainland, greater scaup on the West Mirage Islands, and a zone of overlap on the remainder of the North Arm islands.

Islands used by greater scaup tended to be farther from shore and have smaller amounts of tall shrub cover than all available islands. Islands used by lesser scaup were, on average, closer to shore, and had less tree cover than available islands. Islands with few tall shrubs or trees offer fewer perching sites for ravens, probably the most frequent predator of duck eggs in both study areas (see below), and were possibly selected for this reason. The tendency of greater scaup to nest farther offshore than lesser scaup (and thus near deeper and clearer water)

appeared to hold throughout the North Arm. It is unclear why greater scaup, in general, nest farther offshore and why the West Mirage Islands, in particular, are used almost exclusively by greater scaup. Given the similar preferences in nesting habitat of the two species in terms of vegetation and associations with larids, we suspect that the difference in distribution reflects some ecological difference between species other than selection of nesting habitat. Perhaps the difference in distribution reflects differences in feeding behaviour and food habits of the two species during the pre-nesting, nesting, or brood-rearing periods, but further study is required to test these hypotheses.

The most important factor affecting island selection by both species was the presence or absence of larids. Scaup were frequently found nesting in larid colonies. Ducks and other aquatic birds (e.g., grebes) apparently benefit from such associations because larids are effective at defending the nesting area against some types of predators (Koskimies, 1957; Hilden, 1964; Kistchinski and Flint, 1974; Newton and Campbell, 1975; Nuechterlein, 1981; Burger, 1984; Young and Titman, 1986; Burger and Gochfeld, 1995). However, such advantages might be offset by high duckling mortality when ducks nest among highly predatory larids, such as California gulls (*Larus californicus*) and herring gulls (*Larus argentatus*) (Vermeer, 1968; Dwernychuk and Boag, 1972).

Nesting Success

Overall, apparent nest success on islands with breeding larids (75%) was higher than either nest success of scaup on islands without larids (42%) or nest success of lesser scaup on the YKSA (37%), as has been reported for other waterfowl (Kistchinski and Flint, 1974; Newton and Campbell, 1975; Gerell, 1985; Gotmark and Ahlund, 1988; Gotmark, 1989). The similar nest success of scaup nesting on islands without larids and on the mainland is of interest because many other studies have reported higher waterfowl nest success on islands, even in the absence of larids

TABLE 9. Apparent egg success of greater and lesser scaup nesting on islands of the North Arm of Great Slave Lake in 1994–95 and on the mainland (YKSA) near Yellowknife, Northwest Territories, in 1995–98.

	Greater Scaup North Arm	Lesser Scaup North Arm	Lesser Scaup YKSA
Hatched	940 (63%)	625 (67%)	173 (40%)
Cracked	28 (2%)	7 (<1%)	0 –
Displaced from nest	22 (2%)	0 –	1 (<1%)
Predator destroyed	269 (18%)	97 (10%)	249 (57%)
Abandoned	85 (6%)	110 (12%)	7 (2%)
Failed to hatch ¹	113 (8%)	83 (9%)	4 (1%)
Dead duckling ²	21 (1%)	10 (1%)	1 (<1%)
Miscellaneous ³	7 (<1%)	2 (<1%)	0 –
Total eggs	1485	934	435

¹ Left in nest after hatch—does not include abandoned clutches.

² Dead ducklings or pipped eggs found in nest after hatch.

³ Abnormal (dwarf) eggs and eggs buried under nest material.

(Hammond and Mann, 1956; Duebbert, 1966, 1982; Vermeer, 1968; Young, 1968; Long, 1970; Lokemoen, 1991; Lokemoen and Woodward, 1992). We believe this similarity likely occurred because ravens were the dominant predator in both study areas. Predation of duck and grebe eggs by ravens was reported previously for the YKSA (Murdy, 1963, 1965; Fournier and Hines, 1999) and has been reported for other waterfowl breeding areas (Sargeant et al., 1998). During the course of fieldwork on the North Arm, we visited two islands with active raven nests and found numerous destroyed eggs of scaup and other ducks. Eggs destroyed in a similar fashion were observed on many other islands as well, and were frequently found near typical raven perching sites (tall shrubs or trees), indicating the widespread nature of egg predation by ravens on the North Arm.

Austin et al. (1998) summarized average nest success of lesser scaup by different geographic regions and habitat types, as follows: prairie parklands 30%, prairie islands 31%, prairie grasslands 37%, and northern boreal forest 57%. Our Mayfield-Green estimate for nest success of lesser scaup on the North Arm (61%) was similar to Austin's estimate for the boreal forest in general, but our estimate for the YKSA (18%), which is probably more typical of lesser scaup in the region, was lower than Austin's estimates for all other areas.

The few reported estimates of greater scaup nest success (Shepherd, 1955: 25%, Mayfield-Green estimate 10%, $n = 16$; Kirkpatrick and Buckley, 1954, cited in Bellrose, 1980: 45%, Mayfield-Green estimate 24%, $n = 20$) are much lower than what we observed on the islands of the North Arm (75%, Mayfield-Green estimate 58%, $n = 284$).

Clutch Size and Hatchability

Clutch sizes of scaup in our study areas were similar to values reported previously. Weller et al. (1969) reported an overall mean clutch of 9.3 eggs and, after controlling

for parasitism, a mean clutch of 8.5 eggs for greater scaup nesting at the West Mirage and several nearby islands. In the same area, Trauger and Bromley (1976) observed an average clutch of 9.0 eggs overall and 8.5 eggs after parasitic eggs were eliminated (Bellrose, 1980). Thus, our averages of 10.1 eggs per clutch overall and 9.0 eggs per unparasitized clutch indicate clutch sizes of greater scaup have not declined in recent decades on the North Arm.

Although there are no published data on clutch sizes of lesser scaup from the Great Slave Lake region, two accounts provide data from other northern breeding areas. Nelson (1953) gave an average clutch of 8.6 eggs for Alaska, and Townsend (1966) reported an average clutch of 9.0 eggs at the Saskatchewan River Delta. Our average estimate of 8.7–9.2 eggs suggests no long-term change in average clutch size of lesser scaup.

Hatchability of eggs in our study areas (88–98%) was similar to that previously reported for both lesser scaup (Miller and Collins, 1954: 88%; Rienecker and Anderson, 1960: 93%; Keith, 1961: 83%; Vermeer, 1968: 93%) and greater scaup (Hilden, 1964: 96%). As well, data collected in Alberta in 1998 indicated a high rate of hatchability (95%) for lesser scaup eggs there (D. Duncan, pers. comm. 1999). Despite the comparatively high rate of hatchability observed both in the YKSA and on the North Arm, we did observe a difference in hatchability of eggs between our study areas. Lesser scaup in the YKSA averaged approximately 10% higher hatchability than did either species on the North Arm. Several previous studies also reported higher rates of hatchability of eggs from mainland versus island nests (Hammond and Mann, 1956; Duebbert et al., 1983; Hines and Mitchell, 1983). High densities of waterfowl nesting on islands have frequently led to increased levels of egg parasitism (Hilden, 1964; Vermeer, 1968; Giroux, 1981; Hines and Mitchell, 1984; Robertson et al., 1992), and lower hatchability of eggs (Newton and Campbell, 1975; Duebbert et al., 1983), which is probably due to age differences between host eggs and parasitically laid eggs. Once parasitized clutches were eliminated from our analyses, the hatchability of eggs in both study areas was similar.

Status of Breeding Populations & Management Implications

The lesser scaup population has declined throughout its range (Austin et al., 2000), and the status of the greater scaup population is uncertain. We have no survey data on long-term population changes of greater scaup on the North Arm of Great Slave Lake, although we can use the results of nesting studies at the West Mirage Islands as an index of population change. On this archipelago, Weller et al. (1969) found 40 greater scaup nests on 72 islands searched in 1968, an average of 0.6 nests per island. During 1993–95, we searched an average of 22 islands per year and found an average of 28 greater scaup nests per year (or 1.3 per island), and we are confident that 40 or

more nests would have been found each year had more islands been searched. These data suggest that no decline has occurred in this breeding population since the 1960s. However, numbers of lesser scaup on the nearby mainland have decreased by approximately 30% since 1962–65 (Hines and Fournier, unpubl. data), a rate of decline similar to or slightly higher than that observed for the continental population of this species over the same time interval (see Austin et al., 2000).

A number of hypotheses have been put forward to explain the continental decline of lesser scaup (and the possible decline of greater scaup) (Austin et al., 2000). Our data bear on some of these hypotheses, particularly those pertaining to low reproductive success as a cause of population reduction. Negative effects of contaminants on reproductive parameters such as clutch size, egg hatchability, and nest success have been invoked as possible explanations for decreasing scaup numbers (Austin et al., 2000). However, average clutch sizes on our study areas (from data collected mainly during the period when lesser scaup were declining) were not lower than values previously reported for either species. Similarly, the hatchability of eggs in our study areas was as high as that found in earlier studies, and the success of scaup nests on islands of the North Arm was as good or better than that reported in most studies prior to the population decline. Therefore, if contaminants are impairing reproductive output of scaup, we believe their effect would have to be manifested through reduced breeding propensity of adults or lower survival of ducklings, and not through their influence on nest or egg success.

Given that greater and lesser scaup have somewhat different wintering areas and migration routes (Palmer, 1976; Bellrose, 1980), the similarly high nest success of the two species on the North Arm and the low success of lesser scaup on the nearby mainland are of interest. This pattern suggests that local conditions on breeding areas are more apt to limit nest success (and perhaps overall population productivity) than are conditions distant from the breeding grounds.

The main cause of nest failure in both of our study areas, and in most previous studies of waterfowl nesting, was clutch predation. Our study areas provided a steep gradient of habitat quality in terms of accessibility to predators: mainland (accessible to both avian and mammalian predators); islands without nesting larids (mammalian predators reduced, but avian predators still common); and islands with nesting larids (both mammalian and avian predators reduced). Nest success was high only under the latter condition, suggesting that avian nest predators such as ravens had a substantial impact on nest success.

The 18% average nest success in our mainland study area was low compared to that found elsewhere in the boreal or other regions, but was similar to that needed to maintain populations of dabbling ducks (15–20%) (Cowardin et al., 1985; Klett et al., 1988). However, many female scaup (particularly young birds 1–2 years of age)

do not breed in some years (Afton, 1984), and scaup are a late-season nesting species with presumably very limited opportunity to reneest in the Subarctic. The overall productivity of lesser scaup on the YKSA was lower (on average, 23% of the paired females produced broods during 1985–98; Hines and Fournier, unpubl. data) than the level required to maintain other populations of ducks (> 30%) (Cowardin et al., 1985). Thus, the nest success observed on the YKSA may not have been sufficient to maintain the local lesser scaup population without exceptionally high survival of adult females and their ducklings. The possible role of low nest success and other demographic parameters (such as survival of adult females and their broods) in limiting the growth of lesser scaup populations warrants further investigation.

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REFERENCES

- AFTON, A.D. 1984. Influence of age and time on reproductive performance of female lesser scaup. *Auk* 101:255–265.
- ALLISON, P.D. 1999. Logistic regression using the SAS system: Theory and application. Cary, North Carolina: SAS Institute Inc. 304 p.
- ATMOSPHERIC ENVIRONMENT SERVICE. 1993. Canadian climate normals 1961–1990. Yukon and Northwest Territories. Ottawa: Environment Canada. 58 p.
- AUSTIN, J.E., CUSTER, C.M., and AFTON, A.D. 1998. Lesser scaup (*Aythya affinis*). In: Poole, A., and Gill, F., eds. *Birds of North America*, No. 338. Philadelphia: The Birds of North America, Inc. 32 p.
- AUSTIN, J.E., AFTON, A.D., ANDERSON, M.G., CLARK, R.G., CUSTER, C.M., LAWRENCE, J.S., POLLARD, J.B., and RINGELMAN, J.K. 2000. Declining scaup populations: Issues, hypotheses, and research needs. *Wildlife Society Bulletin* 28:254–263.
- BELLROSE, F.C. 1980. *Ducks, geese and swans of North America*. 3rd ed. Harrisburg, Pennsylvania: Stackpole Books, and Washington, D.C.: Wildlife Management Institute. 540 p.
- BURGER, J. 1984. Grebes nesting in gull colonies: Protective associations and early warning. *American Naturalist* 123: 327–337.
- BURGER, J., and GOCHFELD, M. 1995. Nest site selection by eared grebes in a Franklin's gull colony: Structural stability parasites. *Condor* 97:577–580.

- COWARDIN, L.M., GILMER, D.S., and SHAIFFER, C.W. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildlife Monographs* No. 92. 37 p.
- DUEBBERT, H.F. 1966. Island nesting of the gadwall in North Dakota. *Wilson Bulletin* 78:12–25.
- . 1982. Nesting of waterfowl on islands in Lake Audubon, North Dakota. *Wildlife Society Bulletin* 10:232–237.
- DUEBBERT, H.F., LOKEMOEN, J.T., and SHARP, D.E. 1983. Concentrated nesting of mallards and gadwalls on Miller Lake Island, North Dakota. *Journal of Wildlife Management* 47: 729–740.
- DWERNYCHUK, L.W., and BOAG, D.A. 1972. Ducks nesting in association with gulls: An ecological trap? *Canadian Journal of Zoology* 50:559–563.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE INC. 1996. ArcView spatial analyst. Redlands, California: Environmental Systems Research Institute Inc. 147 p.
- FIX, D. 1985. Notes on scaup identification. *Oregon Birds* 11: 146–151.
- FOURNIER, M.A. 2000. Incidents of mixed clutches among scaup and ring-billed gulls. *Waterbirds* 23:114–116.
- FOURNIER, M.A., and HINES, J.E. 1996. Nest sharing by a lesser scaup and a greater scaup. *Wilson Bulletin* 108:380–381.
- . 1998. Productivity and population increase of subarctic breeding canvasbacks. *Journal of Wildlife Management* 62: 179–184.
- . 1999. Breeding ecology of the horned grebe *Podiceps auritus* in subarctic wetlands. Occasional Paper Number 99. Ottawa: Canadian Wildlife Service. 32 p.
- GERELL, R. 1985. Habitat selection and nest predation in a common eider population in southern Sweden. *Ornis Scandinavica* 16:129–139.
- GIROUX, J.F. 1981. Use of artificial islands by nesting waterfowl in southeastern Alberta. *Journal of Wildlife Management* 45: 669–679.
- GODFREY, W.E. 1986. The birds of Canada. Rev. ed. Ottawa: National Museum of Natural Sciences, National Museums of Canada. 595 p.
- GOTMARK, F. 1989. Costs and benefits to eiders nesting in gull colonies: A field experiment. *Ornis Scandinavica* 20:283–288.
- GOTMARK, F., and AHLUND, M. 1988. Nest predation and nest site selection among eiders *Somateria mollissima*: The influence of gulls. *Ibis* 130:111–123.
- GREEN, R.E. 1989. Transformation of crude proportions of nests that are successful for comparison with Mayfield estimates of nest success. *Ibis* 131:305–306.
- HAMMOND, M.C., and MANN, G.E. 1956. Waterfowl nesting islands. *Journal of Wildlife Management* 20:345–352.
- HILDEN, O. 1964. Ecology of duck populations in the island group of Valassaaret, Gulf of Bothnia. *Annales Zoologici Fennici* 1:153–279.
- HINES, J.E., and MITCHELL, G.J. 1983. Breeding ecology of the gadwall at Waterhen Marsh, Saskatchewan. *Canadian Journal of Zoology* 61:1532–1539.
- . 1984. Parasitic laying in nests of gadwalls. *Canadian Journal of Zoology* 62:627–630.
- HOSMER, D.W., and LEMESHOW, S. 1989. Applied logistic regression. New York: John Wiley and Sons. 373 p.
- JOHNSGARD, P.A. 1975. Waterfowl of North America. Bloomington, Indiana: Indiana University Press. 575 p.
- JOHNSON, D.H. 1991. Further comments on estimating nest success. *Ibis* 133:205–207.
- KEITH, L.B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildlife Monographs* No. 6. 88 p.
- KIRKPATRICK, R.G., and BUCKLEY, J.L. 1954. Migratory waterfowl survey, 1954. Progress Report W-3-R-9. Juneau: Alaska Game Commission. Cited in Bellrose, 1980.
- KISTCHINSKI, A.A., and FLINT, V.E. 1974. On the biology of the spectacled eider. *Wildfowl* 25:5–15.
- KLEINBAUM, D.G., and KUPPER, L.L. 1978. Applied regression analysis and other multivariate methods. North Scituate, Massachusetts: Duxbury Press. 556 p.
- KLETT, A.T., DUEBBERT, H.F., FAANES, C.A., and HIGGINS, K.F. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. Resource Publication 158. Washington, D.C.: U.S. Fish and Wildlife Service.
- KLETT, A.T., SHAFFER, T.L., and JOHNSON, D.H. 1988. Duck nest success in the prairie pothole region. *Journal of Wildlife Management* 52:431–440.
- KOSKIMIES, J. 1957. Terns and gulls as features of habitat recognition for birds nesting in their colonies. *Ornis Fennica* 34:1–6.
- LAROI, G.H., and BABB, T.H. 1974. Canadian national directory of IBP areas, 1968–1974. Edmonton, Alberta: Canadian Committee for the International Biological Programme, University of Alberta.
- LOKEMOEN, J.T. 1991. Brood parasitism among waterfowl nesting on islands and peninsulas in North Dakota. *Condor* 93: 340–345.
- LOKEMOEN, J.T., and WOODWARD, R.O. 1992. Nesting waterfowl and water birds on natural islands in the Dakotas and Montana. *Wildlife Society Bulletin* 20:163–171.
- LONG, R.J. 1970. A study of nest-site selection by island-nesting anatids in central Alberta. M.Sc. Thesis, University of Alberta, Edmonton, Alberta. 123 p.
- MAYFIELD, H. 1961. Nest success calculated from exposure. *Wilson Bulletin* 73:255–261.
- MILLER, A.W., and COLLINS, B.D. 1954. A nesting study of ducks and coots on Tule Lake and Lower Klamath National Wildlife Refuges. *California Fish and Game* 40:17–37.
- MILLER, H.W., and JOHNSON, D.H. 1978. Interpreting the results of nesting studies. *Journal of Wildlife Management* 42:471–476.
- MURDY, H.W. 1963. Progress report on the Yellowknife waterfowl study area, Northwest Territories. Jamestown, North Dakota: U.S. Fish and Wildlife Service. 41 p.
- . 1965. Progress report on the Yellowknife waterfowl study area, Northwest Territories. Jamestown, North Dakota: U.S. Fish and Wildlife Service. 11 p.
- NELSON, U.C. 1953. Waterfowl breeding ground survey, 1953 in Alaska. In: *Waterfowl populations and breeding conditions*,

- summer 1953. Special Scientific Report Wildlife No. 25. Washington, D.C.: U.S. Fish and Wildlife Service. 1–6.
- NEWTON, I., and CAMPBELL, C.R.G. 1975. Breeding of ducks at Loch Leven, Kinross. *Wildfowl* 26:83–102.
- NUDDS, T.D., and COLE, R.W. 1991. Changes in populations and breeding success of boreal forest ducks. *Journal of Wildlife Management* 55:569–573.
- NUECHTERLEIN, G.L. 1981. Information parasitism in mixed colonies of western grebes and Forster's terns. *Animal Behaviour* 29:985–989.
- PALMER, R.S., ed. 1976. Handbook of North American birds. Vol. 3. Waterfowl. New Haven, Connecticut and London: Yale University Press. 560 p.
- PORSILD, A.E., and CODY, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. Ottawa: National Museum of Natural Sciences. 667 p.
- RAWLINGS, J.O., PANTULA, S.G., and DICKEY, D.A. 1998. Applied regression analysis. 2nd ed. New York: Springer-Verlag. 657 p.
- RAWSON, D.S. 1950. The physical limnology of Great Slave Lake. *Journal of the Fisheries Resources Board of Canada* 8: 3–66.
- REARDEN, J.D. 1951. Identification of waterfowl nest predators. *Journal of Wildlife Management* 15:386–395.
- RIENECKER, W.C., and ANDERSON, W. 1960. A waterfowl nesting study on Tule Lake and Lower Klamath National Wildlife Refuges, 1957. *California Fish and Game* 46:481–506.
- ROBERTSON, G.J., WATSON, M.D., and COOKE, F. 1992. Frequency, timing and costs of intraspecific nest parasitism in the common eider. *Condor* 94:871–879.
- RUSSELL, W. 1975. Field identification notes. *Birding* 7: 232–236.
- SARGEANT, A.B., SOVADA, M.A., and GREENWOOD, R.J. 1998. Interpreting evidence of depredation of duck nests in the prairie pothole region. Jamestown, North Dakota: U.S. Geological Survey, Northern Prairie Wildlife Research Center, and Memphis, Tennessee: Ducks Unlimited, Inc. 72 p.
- SAS INSTITUTE. 1990. SAS/STAT User's Guide. Version 6, 4th ed. Cary, North Carolina: SAS Institute. 1686 p.
- SHEPHERD, P.E.K. 1955. Migratory waterfowl studies nesting and banding. Selawik area. Progress Report W-3-R-11. Juneau: Alaska Game Commission. 34–52.
- SIROIS, J., FOURNIER, M.A., and KAY, M.F. 1995. The colonial waterbirds of Great Slave Lake, Northwest Territories: An annotated atlas. Occasional Paper No. 89. Ottawa: Canadian Wildlife Service. 59 p.
- TABACHNICK, B.G., and FIDELL, L.S. 1996. Using multivariate statistics. 3rd ed. New York: Harper Collins. 880 p.
- TOFT, C.A., TRAUGER, D.L., and MURDY, H.W. 1982. Tests for species interactions: Breeding phenology and habitat use in subarctic ducks. *American Naturalist* 120:586–613.
- TOWNSEND, G.H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. *Canadian Field-Naturalist* 80: 74–88.
- TRAUGER, D.L. 1971. Population ecology of lesser scaup (*Aythya affinis*) in subarctic taiga. Ph.D. Thesis, Iowa State University, Ames, Iowa. 118 p.
- TRAUGER, D.L., and BROMLEY, R.G. 1976. Additional bird observations on the West Mirage Islands, Great Slave Lake, Northwest Territories. *Canadian Field-Naturalist* 90:114–122.
- VERMEER, K. 1968. Ecological aspects of ducks nesting in high densities among larids. *Wilson Bulletin* 80:78–83.
- WELLER, M.W., TRAUGER, D.L., and KRAPU, G.L. 1969. Breeding birds of the West Mirage Islands, Great Slave Lake. *Canadian Field-Naturalist* 83:344–360.
- WIKEN, E. 1986. Terrestrial ecozones of Canada. Ecological Land Classification Series No. 19. Ottawa: Lands Directorate, Environment Canada. 25 p.
- WILSON, S.F., and ANKNEY, C.D. 1988. Variation in structural size and wing stripe of lesser and greater scaup. *Canadian Journal of Zoology* 66:2045–2048.
- YOUNG, C.M. 1968. Island nesting of ducks in northern Ontario. *Canadian Field-Naturalist* 82:209–212.
- YOUNG, A.D., and TITMAN, R.D. 1986. Costs and benefits to red-breasted mergansers nesting in tern and gull colonies. *Canadian Journal of Zoology* 64:2339–2343.