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# Breeding Biology of Steller's Eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991–99

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ABSTRACT. The breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, was studied from 1991 to 1999. The number of nests found per year ranged from 0 to 78. Mean clutch size was 5.4 (SD = 1.6, n = 51), incubation period was 24 days, and Mayfield nest success ranged from 0 to 35%. Egg survival was 24% overall (n = 451). Most nests were found on the rims of low-centered polygons near ponds with emergent vegetation. Marked broods remained within 700 m of their nest sites, and duckling survival was low. Steller's eiders nested in five of the nine years studied, corresponding with years of high lemming density and nesting pomarine jaegers (*Stercorarius pomarinus*) and snowy owls (*Bubo scandiacus*). Steller's eiders may choose to nest only in years with abundant lemmings for two reasons: first, abundant lemmings provide an alternative prey source for foxes and other predators of eiders; second, jaegers and owls defending their own nests may inadvertently provide protection to eiders nesting nearby.

Key words: Alaska, Steller's eider, *Polysticta stelleri*, nesting success, habitat selection, nesting associations, periodic nonbreeding

RÉSUMÉ. De 1991 à 1999, on a étudié la biologie de reproduction de l'eider de Steller (*Polysticta stelleri*) près de Barrow, en Alaska. Le nombre de nids trouvés annuellement allait de 0 à 78. La taille moyenne de la couvée était de 5,4 (écart type = 1,6, n = 51), la période d'incubation était de 24 jours et le succès de la couvée calculé selon la méthode de Mayfield allait de 0 à 35 %. La survie des œufs était dans l'ensemble de 24 % (n = 451). La plupart des nids étaient situés sur le bord de polygones concaves près d'étangs avec une végétation émergente. La progéniture marquée restait dans les 700 m du site du nid, et la survie des canetons était faible. L'eider de Steller a niché cinq ans sur les neuf de l'étude, soit ceux correspondant aux années où il y avait une forte densité de lemmings, ainsi que de nids de labbes pomarins (*Stercorarius pomarinus*) et de harfangs des neiges (*Bubo scandiacus*). Il se pourrait que l'eider de Steller choisisse de ne se reproduire que durant les années d'abondance de lemmings pour deux raisons: la première, c'est qu'une abondance de lemmings offre une source alternative de proies pour les renards et d'autres prédateurs de l'eider; la deuxième, c'est que les labbes pomarins et les harfangs qui défendent leurs propres nids pourraient, involontairement, offrir une protection aux eiders qui nichent à proximité.

Mots clés: Alaska, eider de Steller, *Polysticta stelleri,* réussite de la couvée, sélection de l'habitat, association de nidification, non-reproduction périodique

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## INTRODUCTION

The breeding biology of the Steller's eider (*Polysticta stelleri*) is among the least known of all North American waterfowl, partly because of the species' remote breeding range (Bent, 1925; Dement'ev and Gladkov, 1952; Johnsgard, 1975; Cramp and Simmons, 1977; Bellrose, 1980) and its intermittent nesting habits (Solovieva, 1997; Quakenbush and Suydam, 1999).

Currently, the Alaska breeding population occurs as two known subpopulations, one on the Yukon–Kuskokwim Delta (Y–K Delta) in western Alaska and the other near Barrow in northern Alaska. Nesting on the Y–K Delta is believed to occur in very low numbers. Only six nests were found there between 1991 and 1998 (Flint and Herzog, 1999). In northern Alaska, recent nesting records from Barrow to the Colville River indicate that Steller's eiders nest in the western and central portion of northern Alaska, mostly near Barrow (Quakenbush et al., 2002). Historical evidence indicates their former nesting range was from Wainwright (Bailey, 1925, 1948) to Cape Halkett in northwestern Alaska, and a verbal account extends the historical range to Collinson Point near the Alaska/Canada border (Quakenbush et al., 2002).

The Alaska breeding population of Steller's eiders was listed as threatened under the provisions of the Endangered

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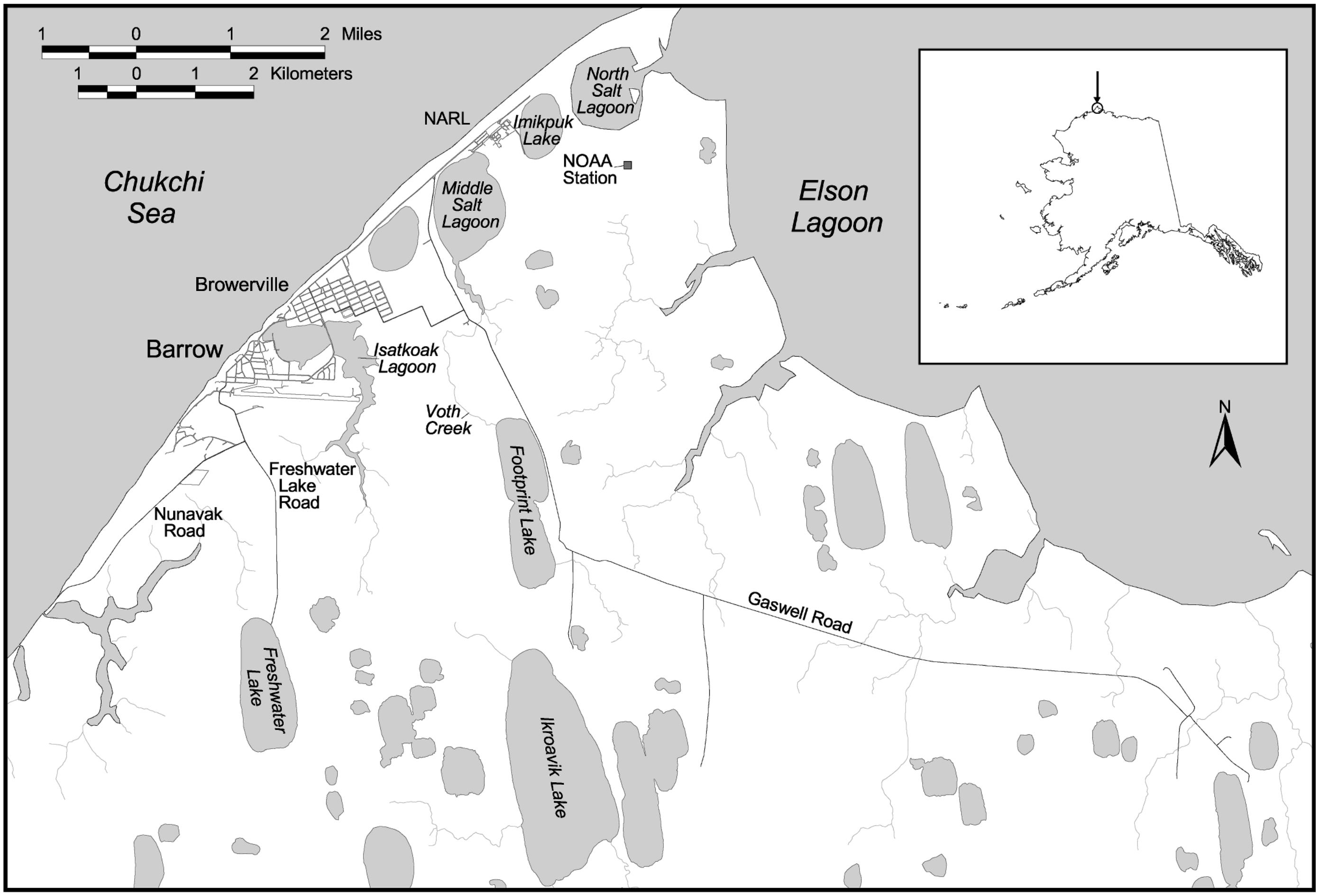

FIG. 1. Steller's eider study area near Barrow, Alaska.

Species Act in 1997 because the species' nesting range and overall abundance in Alaska were believed to have decreased (U.S. Department of the Interior, 1997). This study was initiated in 1991 to better understand the species and aid in its recovery. Our objectives were to document the reproductive biology of Steller's eiders nesting near Barrow, including nesting phenology, habitat use throughout the breeding season, nest and egg characteristics, clutch size, incubation period, nesting success, brood movements, and duckling survival.

## STUDY AREA

This study was conducted near Barrow (71˚18' N, 156˚40' W), at the northernmost point of the Arctic coastal plain of Alaska (Fig. 1). Gaswell Road (also known as Cakeater Road) extends approximately 19 km to the east of Barrow and was used for road-based surveys and access to some areas to search for nests. Freshwater Lake Road, which extends approximately 4 km south of Barrow, was also used to access nesting areas. The Barrow area has low relief, mostly less than 2 m above sea level, with numerous shallow northwest–southeast oriented lakes and drained lake basins, all underlain by continuous permafrost (Bunnell et al., 1975). Major relief features are shores of drained lakes, stream banks, and old beach ridges. Microrelief is provided by ice-wedge polygons. Additional relief has resulted from repeated past use of trails by heavy equipment. Damage to the insulating tundra mat has caused the underlying permafrost to melt along these trails, forming flooded channels edged by berms of disturbed tundra. Plant communities are strongly dominated by sedges, primarily *Carex aquatilis*, and secondarily by *Eriophorum* spp. A grass, *Dupontia fischeri*, is also common in upland meadow and wet meadow habitats (Webber, 1978). *Carex aquatilis* and *Arctophila fulva* (pendant grass) are the dominant species of emergent vegetation found in shallow ponds (Bunnell et al., 1975). Deciduous woody shrubs, represented by small prostrate willows (*Salix* spp.), are sparsely distributed. Evergreen shrubs, also low in stature, are represented by *Cassiope* and *Vaccinium*. Bryophytes, primarily mosses (*Calliergon*, *Drepanocladus*, *Polytrichum*, *Sphagnum*) and lichens (*Thamnolia*, *Dactylina*, *Cetraria*, *Cladonia*), are also abundant (Webber, 1978).

Terrestrial mammalian diversity is low in the Barrow area. Caribou (*Rangifer tarandus*) are commonly seen near Barrow in small groups. The most important herbivores are lemmings. Brown lemmings (*Lemmus trimucronatus*) undergo large population fluctuations, and collared lemmings (*Dicrostonyx groenlandicus*) are also present, usually in lower numbers. When lemming numbers are high, they support breeding predatory mammals (arctic foxes, *Alopex lagopus*; least weasels, *Mustela nivalis*; and short-tailed weasels, *M. erminea*) (Pitelka et al., 1955).

The Barrow area supports one of the highest reported concentrations of breeding waterfowl and shorebirds on the Arctic Coastal Plain of Alaska (Schamel, 1978). Twenty-two species of birds breed there regularly, and 13 species breed occasionally (Pitelka, 1974). Snowy owls (*Bubo scandiacus*) and pomarine jaegers (*Stercorarius pomarinus*) are regular breeders near Barrow during highs in the lemming population cycles. Short-eared owls (*Asio flammeus*) nest rarely near Barrow, regardless of the lemming population. In years when lemming densities are low, these avian predators are scarce or absent as breeders, but may still be present during the summer (Pitelka et al., 1955; Maher, 1974; Quakenbush and Suydam, 1999). One pair of common ravens (*Corvus corax*) has been resident in Barrow since at least 1991 and successfully fledged young in most years of this study. Several hundred to several thousand glaucous gulls (*Larus hyperboreus*) are present regardless of lemming numbers, although few gulls appear to be breeding near Barrow.

Snowmelt begins on the tundra in late May to early June. The tundra is typically snow-free by mid to late June. Sea ice usually breaks up by the first week of July. In the fall, snow may begin to accumulate in September, about the same time that tundra ponds begin to freeze. Sea ice forms between September and December; however, persistent leads occur off Barrow throughout the winter and spring.

## METHODS

This study was conducted between June and September from 1991 through 1999. In 1991, our objective was to determine whether Steller's eiders nested in numbers adequate for a study; therefore, research effort was lower in 1991 than in subsequent years. Data from 1991 were therefore excluded from some results to avoid potential bias caused by low effort. Snowmelt dates were determined from radiometric in situ measurements of the solar albedo at the rural tundra site monitored by the Climate Monitoring and Diagnostics Laboratory (CMDL) of the National Oceanic and Atmospheric Administration near Barrow (Dutton and Endres, 1991; D. Endres, pers. comm. 1991; Fig. 2).

Every year, we conducted daily road-based surveys along Gaswell Road from all-terrain vehicles between 6 June and 15 July to determine arrival dates, abundance, habitat use, and locations for future nest searches. The 19 km road provided a transect through all habitat types available in the study area and all habitat types used by nesting Steller's eiders. Observers stopped frequently and scanned both sides of the road at each stop. The entire road corridor was surveyed out to 300 m. For calibration of survey distance, flags were placed periodically at 300 m perpendicular to the road. When Steller's eiders were observed, we recorded location, number of individuals by sex, habitat type, and behavior.

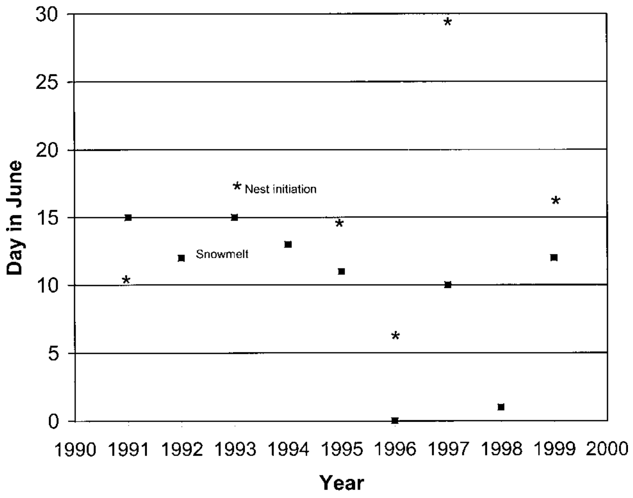

FIG. 2. Spring snowmelt date and earliest nest initiation date for Steller's eiders near Barrow, Alaska, 1991–99. Nesting years are 1991, 1993, 1995–97, and 1999. In 1997, only four nests were found.

Nest searches began as early as 6 June (1998) and as late as 21 June (1994), depending on arrival dates and pair behavior. Standard nest-search methods were not effective. We tried systematically searching plots within the study area, but had little success because of low nest density and variable annual distribution. We found that searching the immediate vicinity of territorial males and pairs or watching a female until she went to a nest proved most effective. Territorial males and pairs would circle back to the same or adjacent pond when flushed, whereas nonterritorial birds would not return. Each year, our nest-search areas were determined primarily by the distribution of pairs in that year. Areas that had been used for nesting in a previous year were searched each year. Snowy owl researchers working in the study area found some nests opportunistically. Additional nests were often found during visits to previously known nests. The total area searched for nests was mapped, and the search area calculated.

Nests were marked with a small wooden marker 1.0 m from the nest, and the nest location was recorded using a hand-held global positioning system (GPS) receiver. We recorded date, nest status (i.e., under construction, laying, incubating, or failed), and number of eggs. Eggs were labeled with a permanent marker, candled to estimate the stage of development (Weller, 1956), weighed to the nearest 0.5 g using a spring scale, and measured (length and width) to the nearest 0.1 mm with calipers.

In 1993, 1996, and 1999, we also recorded the distance to the nearest nests of pomarine jaegers. These distances were estimated either visually or by pacing in 1993; however, in 1996 and 1999, a GPS unit was used to record locations of pomarine jaeger nests. Snowy owl nest locations were determined using GPS in all years by a separate study that included our study area (D. Holt, pers. comm. 1999). The distances between Steller's eider nests and the nests of pomarine jaegers and snowy owls were obtained using MapSource software (Garmin). In 1995, we were not able to record many locations of jaeger nests because of the large number of Steller's eider nests and our limited personnel.

Laying, incubation, and nest attendance data were collected in 1995, 1996, and 1999 using thermistor probes placed inside hollow chicken eggs that were added to the nests. The thermistor probe (model TMC6-1T, Onset Computer Corporation, Pocasset, MA) was attached to the inside of a hollow chicken egg using silicon. The eggshell was attached to a plastic base and secured to the ground with a 15 cm long nail. The cable from the thermistor was attached to a miniature data logger (HOBO-TEMP, model HTEA-37+46, Onset Computer Corporation) that recorded temperature at five-minute intervals for a period of six days. Data were then downloaded to a laptop computer in the field, and the data logger was reset for another six days if the nest was still active. We calculated egg-laying intervals as the elapsed time between midpoints of sequential nest visits by the female prior to the onset of incubation (as indicated by the temperature record). We defined "nest initiation" as the date the first egg was laid and "incubation period" as the number of days between laying of the last egg and hatch (the date the last chick exited the egg). "Nest attendance" is a female's pattern of incubation and breaks (recesses) in incubation. An "incubation recess" was defined from the temperature data as a drop in temperature (indicating the departure of a female) that spanned at least two sample intervals (i.e., ≥10 min) before a rise in temperature indicating her return. The average percentage of time a female spends on the nest per day throughout the entire incubation period is called "incubation constancy" (Skutch, 1962).

Effective clutch size was defined as the number of eggs in a nest once laying was known to be complete, which may not equal total eggs laid because predators sometimes removed eggs during laying or incubation. Nests were considered successful if at least one egg hatched. Apparent nesting success was defined as the percentage of all nests found that was successful (Klett and Johnson, 1982). Because this calculation may produce biased estimates of nesting success, we also present Mayfield estimates (Mayfield, 1961, 1975). Confidence intervals (95%) for Mayfield estimates were calculated following Johnson (1979). We used 30 days as the average exposure period (the duration between laying of the first egg and hatch) in our Mayfield calculations. Nest revisits were minimized to reduce disturbance, and incubating females were not purposely flushed from nests. Nests without thermistors were checked more often (every 3 days) so that nest failure dates could be determined within a few days. Failed nests were examined for cause of failure. Fledging was considered successful if at least one young per brood survived to fledge.

To study brood movements and habitat use, we tracked Steller's eider females throughout the brood-rearing period in 1995 and 1996, using very high frequency (VHF) radio transmitters attached to females captured on the nest shortly before hatch. We attempted to locate broods every other day in 1995 and every third day in 1996. When broods were located, we recorded the date, time, GPS location, brood size, habitat type (Bergman et al., 1977), and behavior. Females were captured using dip or mist nets, then weighed to the nearest gram using a spring scale and banded with #7 U.S. Fish and Wildlife Service metal bands. Transmitters (weighing 10 g) were attached to the mid-back using 332 Epoxy Adhesive (bird adhesive) formulated by Titan Corporation. Feathers were parted and clipped, and epoxy was placed on the transmitter and on the downy feathers of the mid-back between the scapulae. To increase the surface area for transmitter attachment, we glued a piece of Teflon screen (2.5 cm × 2.5 cm) to the attachment surface of each transmitter.

Diet was determined by necropsy of eiders found dead while conducting nest searches or road surveys. Ingesta from the proventriculus and gizzard were preserved in 75% alcohol and examined under a dissecting scope.

Habitat characteristics of nest sites were collected each year in August, when the fate of nests was known and birds were no longer present. At each nest, we recorded the habitat type of the nest location (low-centered, low, or high-centered polygons, sedge meadow, stream banks, islands; Walker et al., 1980) and the proximity and description of the nearest permanent and ephemeral water bodies. Ephemeral water bodies were defined as depressions that held water during spring but drained or evaporated later in the summer. Water bodies were classified according to Bergman et al. (1977). In some cases, the nearest permanent water body was in the "trough" between the rims of polygons; therefore, we added troughs to our classification scheme in 1995.

Statistical analyses were performed using S-Plus 2000 (Mathsoft, Seattle, WA). Because summary statistics for all egg and duckling measurements were calculated by clutch, the means reported are grand means. Only eggs weighed before the third day of incubation (n = 17) were used to determine mean egg weight. We used regression analysis to analyze changes in nest attendance as incubation progressed and single-factor ANOVA to compare female body weights among years. Logistic regressions were performed to examine the relationship between Steller's eider nesting success and distance to nests of pomarine jaegers and snowy owls in 1996 and 1999.

## RESULTS

### *Arrival, Abundance, and Nest Initiation*

Steller's eiders were observed arriving in the study area on 2, 4, and 7 June in 1996, 1997, and 1999, respectively.

TABLE 1. Number of Steller's eider nests per general nesting area near Barrow, Alaska, in 1992–99. Percentages of total nests are in parentheses.

| Year | Number of Steller's eider nests (%) | | | | Total Nests |
|---|---|---|---|---|---|
| | Area 1 (1.5 km$^2$) | Area 2 (0.8 km$^2$) | Area 3 (0.6 km$^2$) | Area 4 (0.1 km$^2$) | |
| 1992 | 0 | 0 | Not searched | 0 | 0 |
| 1993 | 16 (80) | 0 | 0 | Not searched | 20 |
| 1994 | 0 | 0 | 0 | Not searched | 0 |
| 1995 | 25 (32) | 22 (28) | 16 (20) | 7 (9) | 78 |
| 1996 | 13 (62) | 2 (10) | 4 (19) | 2 (10) | 21 |
| 1997 | 0 | 1 | 1 | 0 | 4 |
| 1998 | 0 | 0 | 0 | 0 | 0 |
| 1999 | 11 (31) | 2 (6) | 4 (11) | 0 | 36 |
| Total | 65 (41) | 26 (16) | 24 (15) | 9 (6) | 159 |

In all other years, they were already present by the second week of June, when we arrived. Birds appeared to be paired within flocks upon arrival. In 1992, only one pair was observed during the season (on 15 June). The tundra was snow-free as early as 30 May (1996) and as late as 15 June (1991 and 1993; Fig. 2).

The greatest number of eiders observed during a road survey varied considerably among years, from two (1992 and 1998) to 68 (1993). In non-nesting years, birds arrived on tundra ponds and appeared to be paired within flocks, but they did not disperse or set up breeding territories as they did in years when nesting occurred. The number of nests found ranged from zero (1992, 1994, and 1998) to 78 (1995; Table 1). Nest-search effort was comparable from 1993 to 1998. In 1999, a larger area was covered with a greater search effort. We searched previous nesting areas and areas around observed eiders in 1992, 1994, and 1998 but did not find any active nests, freshly constructed nest bowls, or eggshell remnants indicative of failed nests or nest attempts.

Egg laying began on 6 June in 1996 and between 10 and 17 June in 1991, 1993, 1995, and 1999 (Fig. 2). Nest initiation was not synchronous among female Steller's eiders within years. The average laying period (number of days from the first egg laid to the last egg laid by all females) was 21 days (range: 15–28 days) for all years combined.

Feeding occurred in tundra ponds. Two breeding female Steller's eiders found dead had midge larvae (Chironomidae) all more than 20 mm long in their proventriculi, plus a few cranefly (Tipulidae) larvae and some vegetation. One duckling (21 days old) contained fairy shrimp (Order Anostraca), midge larvae (< 15 mm in length), two tadpole shrimp (*Lepidurus arcticus*), and a few partial stems of plant material.

### Clutch and Egg Size

Effective clutch size ranged from 1 to 8 eggs, with a mode of 5 (29%; Table 2). The mean effective clutch size ranged from 4.8 to 5.9 eggs, with an average of 5.4 for all years combined (Table 2). There was no evidence to suggest that clutches contained eggs laid by more than one Steller's eider female or that females of other species laid eggs in Steller's eider nests. Clutch size declined significantly with later nest initiation; however, nest initiation date did not explain much of the variation ($r^2 = 0.15$, $n = 40$, $p < 0.01$, $y = 20.69 - 0.09x$). Mean egg length was 59.1 mm (range 57.2–59.9, SD = 1.0, n = 80), and mean egg width was 41.4 mm (range 40.6–41.8, SD = 0.4, n = 80). Mean fresh egg weight was 57.4 g (range 51.7–63.6, SD = 3.4, n = 17).

### Egg Laying and Incubation

Five egg-laying intervals were recorded in 1995, three intervals in one nest and two in another. The time between laying of consecutive eggs ranged from 20.9 to 24.7 hours, with a mean of 23.13 hours (SD = 1.67).

The incubation period for Steller's eiders, calculated for three nests found early in laying and monitored with thermistors, was 24 days. The three female Steller's eiders began incubating with the laying of the penultimate egg; however, the incubation period, as defined by convention, begins on the day the last egg is laid. In a sample of eight successful nests found during laying but not monitored with thermistors, the mean number of exposure days from the onset of laying to hatch was 29.75 (SD = 1.2), and the mean clutch size for this sample was 6.1 (SD = 1.0).

Nest attendance was monitored for 15 female Steller's eiders for a total of 181 days. Incubation constancy was 81% (SD = 0.09). Females averaged 6.15 recesses per day (SD = 1.90) lasting an average of 42 minutes (SD = 16.43) each. Females spent less time on nests as incubation progressed ($r^2 = 0.15$, $p < 0.001$, $y = 0.869 - 0.004x$) by taking more recesses of the same duration. Early in incubation, females averaged 4.74 recesses per day (SD = 1.89, n = 10 females), later the average increased to 6.78 per day (SD = 1.55, n = 10 females). To inspect daily incubation patterns, we divided the day into four equal time periods. More recesses (37%) occurred around midday (1200–1800, Alaska Daylight Time) than during any other time period. The fewest (14%) occurred between midnight and 0600. Recesses were approximately equal between 0600 and noon (23%) and between 1800 and midnight (26%). Females left the nest to feed several times a day during incubation, suggesting that local sources of food were important for energy used in reproduction.

TABLE 2. Effective clutch size frequencies for Steller's eiders near Barrow, Alaska, in 1992–99.

| Year | Clutch size | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | n | Mean | SD |
| 1992 | - | - | - | - | - | - | - | - | 0 | - | - |
| 1993 | 0 | 0 | 2 | 1 | 1 | 1 | 0 | 2 | 7 | 5.3 | 2.1 |
| 1994 | - | - | - | - | - | - | - | - | 0 | - | - |
| 1995 | 0 | 1 | 2 | 1 | 5 | 3 | 1 | 0 | 13 | 4.8 | 1.4 |
| 1996 | 1 | 0 | 0 | 1 | 3 | 0 | 4 | 1 | 10 | 5.6 | 2.1 |
| 1997 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 5.5 | 0.7 |
| 1998 | - | - | - | - | - | - | - | - | 0 | - | - |
| 1999 | 0 | 0 | 0 | 2 | 5 | 6 | 5 | 1 | 19 | 5.9 | 1.1 |
| Total | 1 | 1 | 4 | 5 | 15 | 11 | 10 | 4 | 51 | 5.4 | 1.6 |

We weighed a total of 17 adult females in July of 1995, 1996, and 1999. The mean weight was 743.6 g (SD = 57.3, n = 7) in 1995, 690 g (SD = 48.2, n = 3) in 1996, and 688.3 g (SD = 44.6, n = 7) in 1999. Female weights did not differ among years (single factor ANOVA, $p = 0.13$). For all years combined, the mean weight for females was 711.4 g (SD = 55.1, n = 17).

### *Hatch and Nesting Success*

In spite of similar search efforts, the number of nests we located varied from year to year. No nests were found in three of nine years of the study (1992, 1994, and 1998). In 1997, only four nests were found. In these four years, few or no Steller's eiders attempted to nest. Mayfield estimates of nest success (Mayfield, 1975) ranged from 0% in 1997 to 35% in 1996 (Table 3). Apparent nest success (Klett and Johnson, 1982) ranged from 0% in 1997 to 27% in 1996 (Table 3). Egg success ranged from 0% to 42% (24% overall), with 108 ducklings hatching from a total of 451 eggs.

Mean hatch dates ranged from 14 to 28 July in 1991, 1993, 1995, 1996, and 1999. The mean for all years was 19 July. Mean hatch weights of ducklings by clutch (from eight clutches, four each from 1995 and 1996) ranged from 32.5 g to 39.6 g. The mean of the clutch means for 1995 was 37.5 g (SD = 1.77, n = 4) and for 1996, it was 38.2 g (SD = 2.46, n = 4).

Depredation accounted for 62–100% of annual egg mortality during this study. In five nesting years combined, depredation accounted for 82% of all eggs lost (280 of 343 eggs). Of the 280 eggs lost to predators, 137 disappeared with no trace of eggshells. Few depredation events were witnessed, however. Common ravens were seen removing whole eggs from five nests attended by female Steller's eiders. Fox predation was not observed during this study; however, arctic foxes were present in our study area in all years and produced pups in some years. Pomarine jaegers were observed visiting and occasionally eating eggs at nests. We found eggshells with pecked holes near nest sites and believed this to be evidence of pomarine jaeger predation; however, glaucous gulls were also present and may have similar predatory behavior (Barry and Barry, 1990; Sargent et al., 1998). Some nest failures could have been due to early abandonment; However, if we found the eggs scavenged, we attributed their fate to depredation.

TABLE 3. Apparent and Mayfield estimates of nesting success for Steller's eiders nesting near Barrow, Alaska, in 1992–1999.

| Year | Apparent | | Mayfield | | 95% Confidence Limits |
|---|---|---|---|---|---|
| | % | n | % | n | |
| 1992 | 0 | 0 | – | 0 | – |
| 1993 | 20 | 20 | 18 | 13 | 5–55 |
| 1994 | 0 | 0 | – | 0 | – |
| 1995 | 10 | 78 | 14 | 25 | 5–36 |
| 1996 | 27 | 22 | 35 | 11 | 14–88 |
| 1997 | 0 | 4 | 0 | 3 | 0–56 |
| 1998 | 0 | 0 | – | 0 | – |
| 1999 | 19 | 36 | 9 | 27 | 3–25 |

Thirteen nests were known to be partially depredated prior to hatch or failure. Of these, seven (54%) produced at least one duckling. Predators removed eggs from eight of these nests during incubation (62%) and from three during laying (23%). For the other two nests, the timing of depredation was unknown.

Nest location data collected in 1996 and 1999 provided evidence that the spatial distribution of eider nests and the probability of eider nesting success were related to distance from the nearest jaeger and nearest snowy owl. During our study, pomarine jaegers and snowy owls nested only in the same years as Steller's eiders. Because jaegers and owls prey on both eggs and young of Steller's eiders, we looked at eider nest distribution and apparent nesting success (Klett and Johnson, 1982) in relation to distance from jaeger and owl nests. At distances greater than 200 m from jaegers and 1200 m from snowy owls, no Steller's eider nests were found, despite the existence of suitable habitat at these locations (Figs. 3 and 4). In addition, no nests were found closer than about 25 m from jaegers (range 28–633, SD = 112, n = 57) or about 200 m (range 209–2400, SD = 488, n = 58) from snowy owls. The observed probability of success at nests located far from jaegers (>150 m) and far from snowy owls (> 800 m) was zero (0 of 9 nests), while the probability of success when close to jaegers (≤ 150 m) or snowy owls (≤ 800 m) was between 25% and 28%. The boundaries between "near"

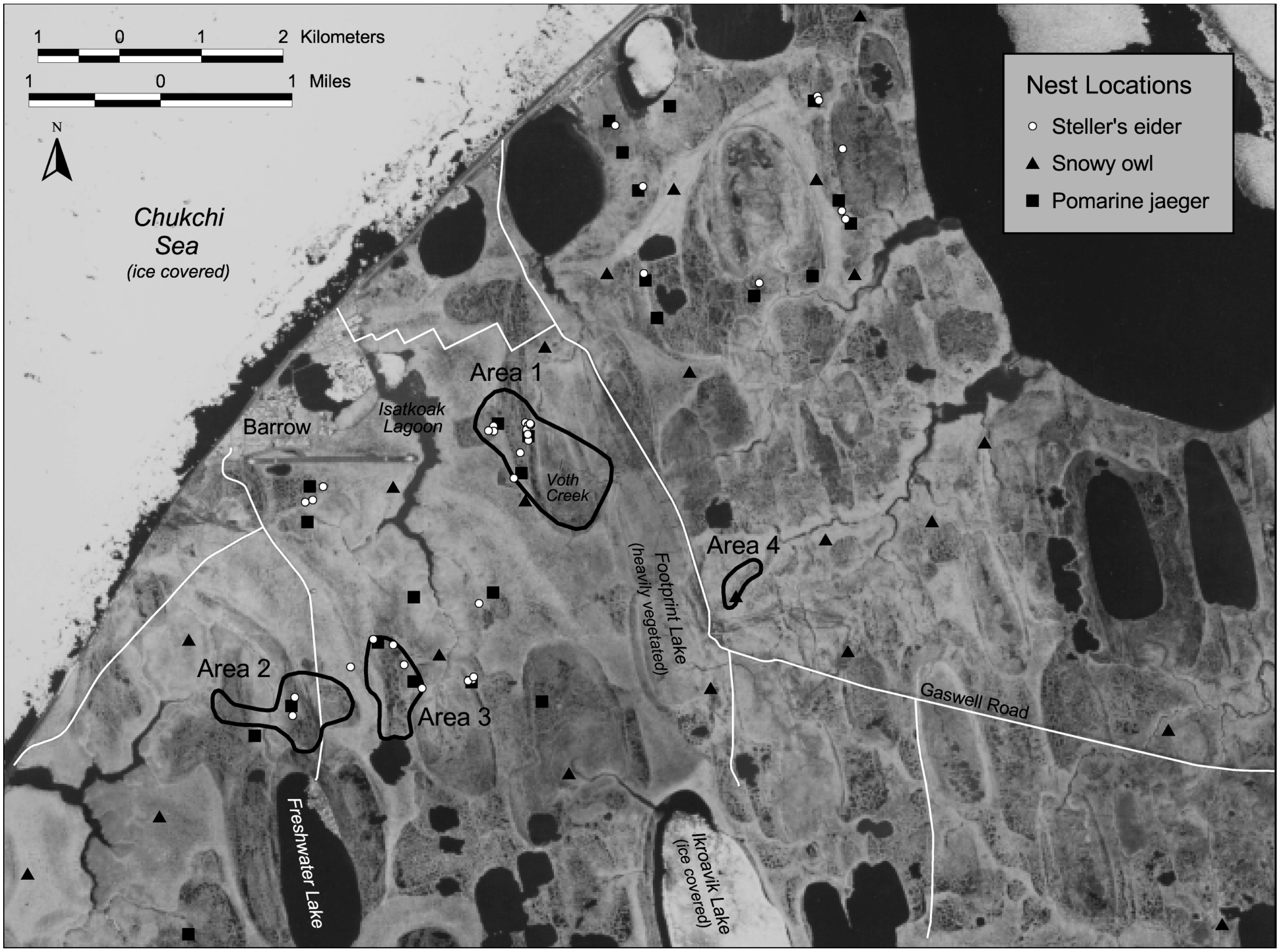

FIG. 3. Distribution of Steller's eider (○), snowy owl (▲), and pomarine jaeger (■) nests near Barrow, Alaska in 1999 relative to four general nesting areas.

and "far" were selected to be consistent with the closely defended territorial ranges of jaegers (Maher, 1974) and snowy owls (Pitelka et al., 1955; Parmelee, 1972). However, moving these boundaries somewhat did not alter the pattern of relatively low nest density and relatively low probability of nesting success for eiders far from an owl and far from a jaeger. That the observed probability of success when far from an owl was greater when near a jaeger than when far from a jaeger suggested the importance of a "distance-to-jaeger:distance-to-snowy owl" interaction term.

Logistic regression models that included explanatory variables "distance-to-jaeger" and "distance-to-snowy owl" as well as the "distance-to-jaeger:distance-to-snowy owl" interaction term fit the observed patterns of nest distribution and nest success better than the same models without the interaction term (Fig. 4a, b). Whether the distance terms were included as discrete (i.e., "near" and "far") or as continuous explanatory variables, the likelihood ratio test showed the interaction term to be significant at the 92% and 98% confidence levels, respectively. In addition, model selection criteria for AIC (Akaike Information Criterion; Akaike, 1973), AICc (small sample size AIC; Hurvich and Tsai, 1989; Burnham and Anderson, 1998) and QAICc (dispersion-adjusted, small sample size AIC; Lebreton et al., 1992; Burnham and Anderson, 1998) all selected for the models with the interaction term. The fitted logistic regression model with continuous explanatory variables and the interaction term was:

$$\ln\left[\frac{\pi(x)}{1-\pi(x)}\right] = -2.9095 + 0.0173 \bullet X_1 + 0.0034 \bullet X_2 - 0.000036 \bullet X_1 \bullet X_2 \quad (1)$$

where $\pi(x)$ = probability of apparent nesting success, $X_1$ = distance to jaeger, $X_2$ = distance to snowy owl, and $X_1 \bullet X_2$ = distance-to-jaeger:distance-to-snowy owl interaction term.

Models that included the interaction term predicted values for the probability of nest success that were much more consistent with observed values than those predicted by models without the interaction term. For example, the models with discrete covariate terms predicted values for nest success far from both jaegers and snowy owls of 11% without the interaction term and nearly zero with the interaction term, the latter value nearly identical to that

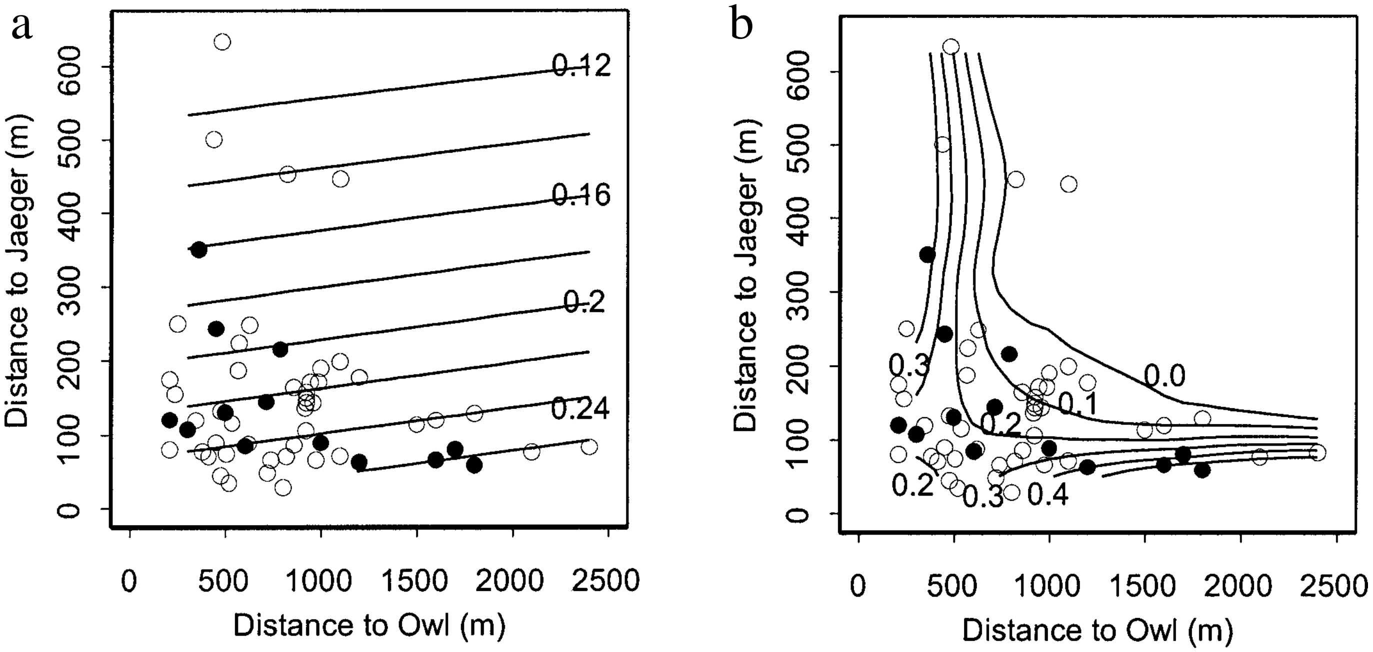

FIG. 4. Steller's eider nesting success relative to distance to pomarine jaeger and snowy owl nests. Closed circles represent successful nests; open circles represent unsuccessful nests. (a) Contour lines represent the probability of apparent nesting success as determined by fitting a logistic regression model with "distance-to-jaeger" and "distance-to-snowy owl" as explanatory variables. (b) Contour lines represent the probability of apparent nesting success as determined by the same model with an additional term representing the interaction between the "distance-to-jaeger" and "distance-to-snowy owl" variables. In (a) and (b), the model was used to predict the probability of apparent nesting success at each nest location, and these values were contoured to generate the lines.

observed. The results from the logistic regression models with continuous covariate terms both including and not including the interaction term (Figs. 4a and 4b) show a similar pattern. Model equation (1) was used to predict the probability of apparent nesting success at each nest location, and these values were contoured.

### *Brood Rearing and Fledging Success*

In 1995, we monitored the movements of eight broods. All stayed within 650 m of their nest sites for up to 32 days after hatching. Broods were located a total of 39 times and most (79.5%) of those times they were found in ponds and canals with emergent *Arctophila fulva*. Similarly, in 1996, five broods stayed within 700 m of their nest sites for up to 35 days after hatching and were located 20 times—17 times (85%) in water bodies with emergent *Arctophila fulva*. Water bodies with emergent sedges were the habitat next most used by broods in both years.

Fledging success appeared to be low throughout the study. In the sample of broods that were marked and monitored in 1995 (n = 8) and 1996 (n = 5), only one brood was thought to have fledged each year. In 1995, seven broods were located multiple times using radio-telemetry. In six cases, the broods were known to have perished, but the causes could not be determined. Only 33% of these broods survived longer than one week. One moribund duckling was found near loose dogs and presumably was killed by them. Snowy owls killed at least two adult female Steller's eiders, each with a brood. Two brood adoptions were documented during this study. In one case, a female Steller's eider was killed by a snowy owl, after which her ducklings were adopted into a nearby brood. The combined brood had seven ducklings. In another case, a radio-tagged female abandoned two ducklings, and another female with three ducklings adopted them. Ducklings of known age were first observed flying 36 days after hatch; however, they may have been capable of flight a few days earlier.

### *Habitat Use*

Most nests (78%) were found clustered in four general areas (Fig. 5). Area 1 was used most in all nesting years (Table 1). Areas 2 and 3 were used approximately equally within years, and Area 4 was used the least and was not used at all in 1999. Single nests or several nests together were also found in areas away from the main clusters in every year (Fig. 5).

More Steller's eider nests (53%) were found on the rims of low-centered polygons than in other terrestrial habitat types (Table 4). More than half (52%) of all nests found were nearer to ponds and canals with emergent *Arctophila fulva* than to other types of permanent water bodies with other types of emergent vegetation (Table 5). Ponds and canals with emergent sedges (mostly *Carex aquatilis*) were almost as important for nesting, with 44% of all nests found there (Table 5).

In terrestrial habitats, the highest percentage of successful nests (42%) was found on the rims of low-centered polygons and a similar habitat type (low polygons; Table 4). In aquatic habitats, the most successful nests (54%) were

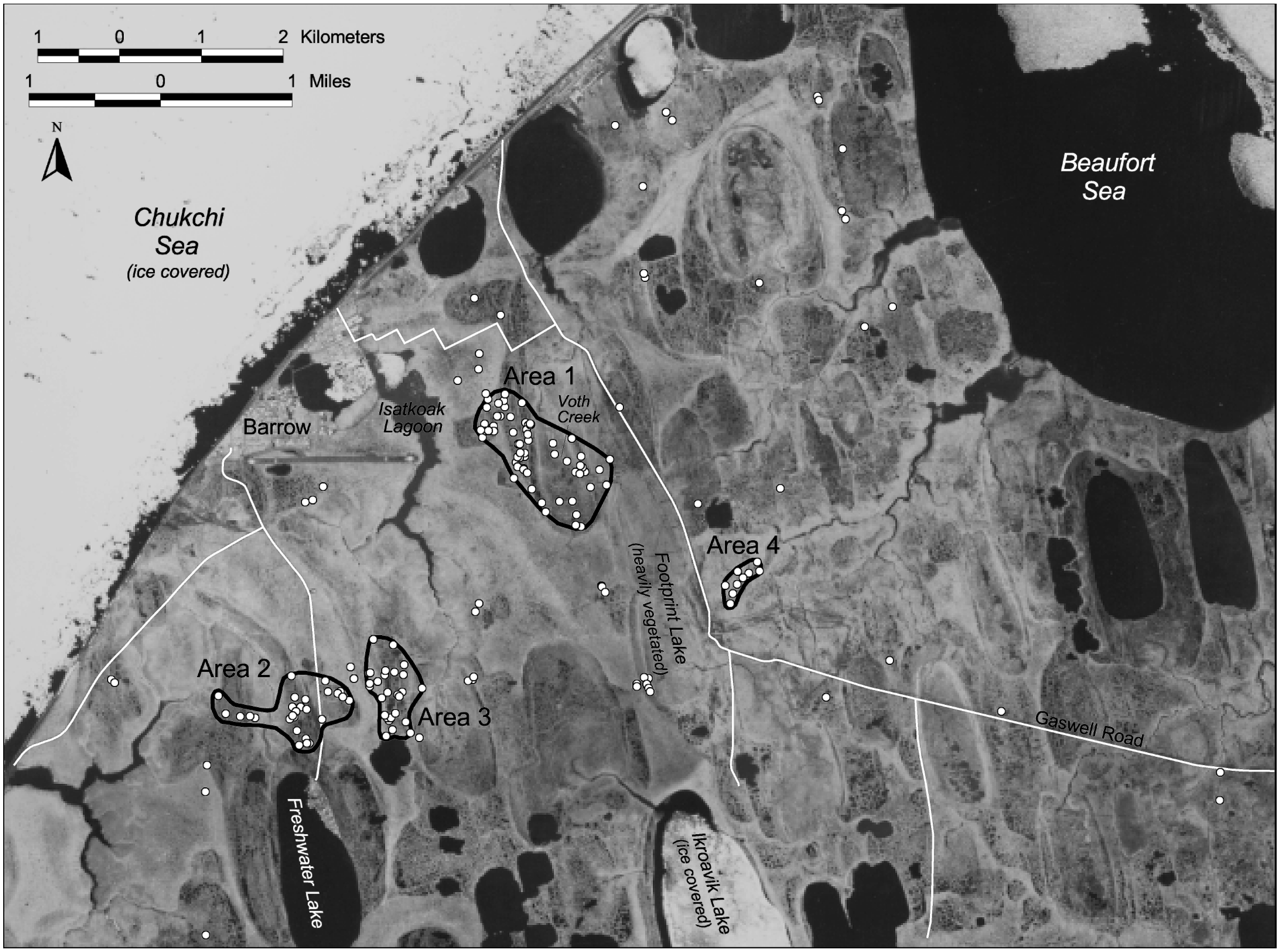

FIG. 5. Aerial photograph of the study area, depicting four general nesting areas and nest locations used by Steller's eiders in 1992–99.

found nearest to permanent water bodies with emergent *Arctophila fulva*, but ponds with emergent *Carex aquatilis* were also important, with 42% of all successful nests found there (Table 5). Few Steller's eider nests were found on islands; however, few islands are present in the study area. The average distance from nest site to nearest permanent water body was 7 m (range 0.6–33.0, SD = 3.9, n = 20) in 1993, 21 m (range 0.3–110, SD = 5.2, n = 79) in 1995, 28 m (range 1.0–115, n = 22) in 1996, and 45 m (range 0.3–272, SD = 68, n = 36) in 1999.

## DISCUSSION

### *Arrival and Nest Initiation*

Arctic breeding waterfowl must begin nesting as soon as conditions allow in order for young to fledge before freeze-up. Steller's eiders are seen during May in leads in the sea ice just offshore from Barrow (Suydam et al., 2000). They appear at breeding areas as the tundra begins to show through the melting snow, usually during early June. It is likely that Steller's eiders stage in open water on the ocean, perhaps flying over the tundra regularly to monitor snowmelt. King eiders in northwestern Canada follow a similar pattern, staging in leads off the west coast of Banks Island in May before moving to nesting areas on Banks and Victoria Islands in early June (Manning et al., 1956; Barry and Barry, 1982; Alexander et al., 1993, 1994).

Steller's eiders arrived on the tundra in flocks and spent approximately a week in these flocks before dispersing in pairs to nesting sites. Similar observations have been made on the Lena Delta in Russia, where nest building begins one to five days after arrival (Solovieva, 1997). Within flocks, birds appeared to be paired when they arrived at Barrow. Pair formation begins in wintering areas (Laubhan and Metzner, 1999), but courtship behavior and copulations were observed in our study area in years in which nests were found. Nest initiation usually occurred soon after the tundra became snow-free, usually in mid-June (Fig. 2).

In non-nesting years (see Nesting Associations and Periodic Non-Nesting below), Steller's eiders remained in mixed-sex flocks. Although sex ratios indicate they may have been paired within the flocks, few isolated pairs were

TABLE 4. Number of nests and successful nests of Steller's eiders in each terrestrial habitat type in 1993, 1995, 1996, 1997, and 1999, showing percentages of annual total (in parentheses). There were no successful nests in 1997.

| | 1993 | | 1995 | | 1996 | | 1997 | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Habitat Type | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | Total Nests All Years | Succesful Nests All Years |
| Polygons | | | | | | | | | | | | |
| Low-centered | 9(45) | 1(25) | 38(51) | 4(44.5) | 12(55) | 4(67) | 3(100) | – | 20(56) | 1(20) | 82(53) | 10(42) |
| Low | 2(10) | 2(50) | 20(27) | 4(44.5) | 4(18) | 2(33) | 0 | – | 11(31) | 2(40) | 37(24) | 10(42) |
| High-centered | 3(15) | 0 | 9(12) | 1(11) | 5(23) | 0 | 0 | – | 3(8) | 1(20) | 20(13) | 2(8) |
| Sedge meadow | 2(10) | 1(25) | 4(5) | 0 | 1(4) | 0 | 0 | – | 0 | 0 | 7(5) | 1(4) |
| Other (banks, islands) | 4(20) | 0 | 3(4) | 0 | 0 | 0 | 0 | – | 2(6) | 1(20) | 9(6) | 1(4) |
| Total Nests | 20 | 4(20) | 74 | 9(12) | 22 | 6(27) | 3 | – | 36 | 5(14) | 155 | 24(15) |

observed in the non-nesting years. In 1997, a few isolated pairs were observed and four nests were found.

Nest initiation near Barrow began in mid-June, in contrast to other nesting locations, where initiation began in mid to late June (Solovieva, 1997; Deygtyarev et al., 1999). In most years, nests near Barrow must be initiated no later than the last week of June in order for the young to fledge before freeze-up on the tundra.

### *Clutch Size*

The clutch sizes we observed at Barrow were similar to those reported on the Lena Delta in Russia, where the mean was 6.1 eggs (range 5–8; Solovieva, 1997). We observed several instances of partial depredation during laying or incubation; thus, true clutch sizes were likely larger than we observed. Many factors can affect clutch size in waterfowl, including female age and body condition (Johnson et al., 1992). Intraspecific nest parasitism has been documented, or suspected, in other eider species (Palmer, 1976; Kellett and Alisauskas, 1997), and may occur in Steller's eiders, although our data do not lead us to suspect that it occurs frequently.

Clutch sizes of Steller's eiders in this study declined significantly with later initiation dates. The same relationship has been observed for king eiders (Kellett and Alisauskas, 1997), spectacled eiders (Dau, 1976; Grand and Flint, 1997), and common eiders (Gorman, 1970; Milne, 1974). Waning nutrient reserves are a possible explanation (Alisauskas and Ankney, 1992). If later nests represent second nesting attempts, females would likely have less energy to invest in egg production (Newton and Cambell, 1975). Younger females take longer to build up nutrient reserves and may nest later and lay fewer eggs per clutch (Dau, 1976).

### *Incubation and Incubation Constancy*

The incubation period of Steller's eiders nesting in North America has not been documented previously. Our finding of 24 days was shorter than the 26–27 day period reported by Solovieva (1997) for Steller's eiders nesting on the Lena Delta, Russia, but was similar to periods reported for king eiders (22–24 days; Parmelee et al., 1967; Cotter et al., 1997; Kellett and Alisauskas, 1997) and spectacled eiders (20–25 days; Dau, 1974; Kondratev and Zadorina, 1992; Harwood and Moran, 1993; Moran and Harwood, 1994; Moran, 1995). Common eiders had a slightly longer incubation period (26 days; Korschgen, 1977). Consecutive eggs were laid approximately 24 hours apart, which was similar to intervals reported for ducks, including eiders (Lamothe, 1973; Dau, 1974; Milne, 1974; Mickelson, 1975; Alisauskas and Ankney, 1992).

Incubation constancy for Steller's eiders was 81%. This was lower than the mean (88%, SD = 1) but within the range (73–99%) for 34 species of waterfowl in which only the female incubates (Afton and Paulus, 1992). In our study, an average Steller's eider egg represented approximately 8% of the mass of the average adult female. Egg mass relative to female mass was higher for Steller's eiders than for the other larger-bodied eider species (range 4.3–6.0%) but lower than five species of smaller sea ducks (range 8.7–10.9%; Alisauskas and Ankney, 1992). Steller's eiders took twice as many recesses per day and spent more time per day off the nest than other related species; however, the length of each recess was typically shorter (Afton and Paulus, 1992). Because Steller's eiders have a smaller body size than other eider species, they may need to forage more during incubation to meet energetic demands. More time away from the nest likely increases the risk of avian nest depredation. Steller's eiders may save energy, however, by leaving their nests unattended most during midday, when air temperatures are warmest.

### *Nesting Success*

In this study, annual nesting success was low (0–35% Mayfield; 0–27% apparent) but within the range reported for other eider species. For king eiders, apparent nesting success ranged from 0% to 69% (Lamothe, 1973; Warnock and Troy, 1992; Kellett and Alisauskas, 1997). For common eiders, apparent nesting success ranged from 33% to 37% (Choate, 1967; Schamel, 1977). For spectacled eiders, apparent nesting success ranged from 10% to 71% (Dau, 1974; Kistchinski and Flint, 1974; Warnock and Troy, 1992; Anderson et al., 2001) and Mayfield nesting success ranged from 18% to 80% (U.S. Fish and Wildlife Service, 1996; Grand and Flint, 1997).

TABLE 5. Number and percentage (in parentheses) of all nests and successful nests of Steller's eiders relative to the nearest permanent water body in 1993, 1995–97, and 1999. There were no successful nests in 1997.

| | 1993 | | 1995 | | 1996 | | 1997 | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nearest Permanent Water Body | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | All Nests | Successful Nests | Total Nests All Years | Succesful Nests All Years |
| Shallow-*Arctophila* | 8(40) | 3(75) | 21(28) | 2(22) | 4(18) | 1(17) | 1(33) | – | 19(53) | 2(40) | 53(34) | 8(33) |
| Deep-*Arctophila* | 2(10) | 0 | 6(8) | 1(11) | 7(32) | 3(50) | 0 | – | 0 | 0 | 15(10) | 4(17) |
| *Arctophila* canal | 4(20) | 0 | 6(8) | 0 | 0 | 0 | 0 | – | 3(8) | 1(20) | 13(8) | 1(4) |
| Total *Arctophila* | 14(70) | 3(75) | 33(45) | 3(33) | 11(50) | 4(67) | 1(33.5) | – | 22(61) | 3(60) | 81(52) | 13(54) |
| *Carex* pond | 5(25) | 1(25) | 35(47) | 5(56) | 9(41) | 2(33) | 2(66.5) | – | 12(33) | 2(40) | 63(41) | 10(42) |
| *Carex* canal | 1(5) | 0 | 3(4) | 0 | 1(4.5) | 0 | 0 | – | 0 | 0 | 5(3) | 0 |
| Total *Carex* | 6(30) | 1(25) | 38(52) | 5(56) | 10(45) | 2(33) | 2(66.5) | – | 12(33) | 2(40) | 68(44) | 10(42) |
| Deep open lake | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 | 0 | 0 | 0 |
| Other (troughs) | 0 | 0 | 3(4) | 1(11) | 1(4.5) | 0 | 0 | – | 2(6) | 0 | 6(4) | 1(4) |
| Totals | 20 | 4(20) | 74 | 9(12) | 22 | 6(27) | 3 | – | 36 | 5(14) | 155 | 24(15) |

Predation was the major cause of Steller's eider egg and duckling mortality. Pomarine jaegers and common ravens appeared to be responsible for much of the egg loss we observed, but avian predators often failed to remove the entire clutch, and many of the eggs left by predators hatched. In many failed nests, all eggs disappeared with no trace of eggshells, implicating arctic foxes or ravens, which remove and cache whole eggs. Although we did not directly observe arctic foxes preying on Steller's eider eggs, foxes are efficient predators of adults and eggs of geese and other eider species (Larson, 1960; Ryder, 1969; Quinlan and Lehnhausen, 1982; Elander and Blomqvist, 1986; Anthony et al., 1991; Stickney, 1991). Arctic foxes are known to have a major influence on the breeding success and distribution of ground-nesting birds in the Arctic (Larson, 1960). When foxes were removed from Kigigak Island in the Y–K Delta, spectacled eider nesting success (Mayfield method) reached 95% (Harwood and Moran, 1993). Similarly, when mew gull (*Larus canus*) numbers were reduced, spectacled eider nesting success more than doubled (J.B. Grand, pers. comm. in U.S. Fish and Wildlife Service, 1996). Since waterfowl smaller than medium-sized geese are not capable of defending their nests from arctic foxes (Mickelson, 1975; Thompson and Raveling, 1987), they may need other protective strategies—such as nesting on islands, in colonies, or near species that exhibit territorial defense—to reproduce successfully.

### *Habitat Use*

The rims of low-centered polygons near water bodies with emergent vegetation, primarily *Arctophila fulva* and secondarily *Carex aquatilis*, were important for nest sites. Polygon tundra was also important nest habitat on the Lena Delta, Russia (Solovieva, 1997), and in Yakutia, Siberia (Deygtyarev et al., 1999). Although the species is not considered colonial, many Steller's eider nests were found in clusters. Low-centered polygon habitat is common in the Barrow area; therefore, the concentration of Steller's eiders within specific areas is poorly understood. The attraction may be related only partially or indirectly to physical habitat characteristics.

Brood rearing occurred in the same habitats as nesting, a finding similar to observations in the Lena Delta, Russia (Solovieva, 1997). Ponds with emergent *Arctophila fulva* within 700 m of the nest site were important for broods. Ponds of this type appeared to provide abundant food and cover for young. Steller's eider fledging occurred on freshwater ponds, unlike that of king eider broods, which move from tundra ponds toward salt water for fledging (Sutton, 1932; Parmelee et al., 1967; Suydam, 2000).

### *Nesting Associations and Periodic Non-Nesting*

Periodic non-nesting to the extent that we have seen in this study has been documented only rarely for waterfowl species (Bertram et al., 1934; Bird and Bird, 1940; Litvin et al., 1985; Dorogoi, 1990). There are examples of large-scale reproductive failures in waterfowl populations due to food scarcity caused by drought (Davies and Cooke, 1983; Krapu et al., 1983) and cold weather (Barry, 1962; Ganter and Boyd, 2000), but few examples of entire breeding populations that regularly forego breeding independent of weather conditions (Litvin et al., 1985; Dorogoi, 1990).

During this study, Steller's eiders nested only in years when lemming numbers were high (Table 6). Numerous lemmings allowed for nesting snowy owls and pomarine jaegers (Pitelka et al., 1955; Maher, 1974). Evidence of the relationship between Steller's eider nesting and lemming density was recorded in 1958 (Myres, 1958) and from 1975 through 1980 (Myers and Pitelka, 1975a, b; Myers et al., 1977a, b, 1978a, b, 1979a, b, c; Myers et al., 1981 summarized in Quakenbush and Suydam, 1999; Table 6). Similar relationships between ground-nesting Arctic birds and lemming densities have been recorded elsewhere (Summers, 1986; Summers and Underhill, 1987; Ebbinge, 1989; Underhill et al., 1989; Syroechkovskiy et al., 1991; Underhill et al., 1993; Van Impe, 1996; Sittler et al., 2000).

TABLE 6. Nest densities of Steller's eiders, snowy owls, and pomarine jaegers relative to lemming densities near Barrow, Alaska, in 1958, 1975–80, and 1990–99.

| Year | Lemming Density | Steller's Eider | Snowy Owl | Pomarine Jaeger | Reference |
|---|---|---|---|---|---|
| 1958 | low | none | none | none | Myres, 1958 |
| 1975 | moderate (5–10) | moderate | yes | yes | Myers and Pitelta, 1975a, b; estimated lemmings per hectare |
| 1976 | high (50–60) | high | yes | yes | Myers et al., 1977a, b; estimated lemmings per hectare |
| 1977 | low (< 1) | none | none | none | Myers et al., 1978a, b; estimated lemmings per hectare |
| 1978 | low (< 5) | low | low | yes | Myers et al., 1979a, b; estimated lemmings per hectare |
| 1979 | low | low | none | none | Myers et al., 1980a, b; lemming numbers too low to support avian predators |
| 1980 | low | low | none | none | Myers et al., 1981a, b, c; lemming numbers too low to support avian predators |
| 1991 | present | high | 0.47[1] | yes | this study |
| 1992 | low | none | none[2] | none | this study |
| 1993 | present | high | 0.11[2] | yes | this study |
| 1994 | low | none | none[2] | none | this study |
| 1995 | present | high | 0.31[2] | yes | this study |
| 1996 | present | high | 0.11[2] | yes | this study |
| 1997 | low | low | none[2] | none | this study |
| 1998 | low | none | none[2] | none | this study |
| 1999 | present | high | 0.16[2] | yes | this study |

[1] R. Suydam and D. Norton, unpubl. data; snowy owl nests per km$^2$.

[2] D. Holt, unpubl. data; snowy owl nests per km$^2$.

In most cases, nesting occurred annually, although often at reduced levels and with reduced success when lemming numbers were low. On Wrangel Island, Russia, black brant (*Branta b. nigricans*) did not attempt to nest in years when lemming abundance was too low to support snowy owls (Litvin et al., 1985; Dorogoi, 1990).

Arctic foxes prefer lemmings when they are abundant, but will eat birds and eggs when lemmings are rare (Larson, 1960; Chesemore, 1968; Strand et al., 1999). Thus, predation by foxes on eggs may be very high in years following lemming highs, when owls and jaegers are mostly absent and foxes are abundant because of high reproductive success during the previous year. The pattern of low predation and high nest success in a year with a lemming high and high predation and low nest success in the post-high year has been called the Roselaar-Summers Hypothesis (Roselaar, 1979; Summers, 1986; Dhondt, 1987). The year following a lemming peak has been called a predator year (Dhondt, 1987; Ebbinge, 1989). Black-bellied brent geese (*Branta b. bernicla*) were found to have low reproductive success in predator years over more than 30 years of study (Dhondt, 1987; Ebbinge, 1989). Such predation pressure on Steller's eiders would select for an ability to predict breeding success before laying eggs. Birds that could evaluate their chances of success before expending the energy required for breeding could experience greater lifetime breeding success.

Steller's eiders may "choose" to nest during high lemming years because nest predation by foxes is predictably lower in those years, either because alternative prey are abundant or because jaegers and owls defending their own nest territories also protect eiders. Brown lemming populations near Barrow undergo large fluctuations (Rausch, 1950; Pitelka et al., 1955; Thompson, 1955a, b; MacLean et al., 1974; Batzli and Pitelka, 1983). Two major predators of Steller's eiders or their eggs (pomarine jaegers and snowy owls) are typically much less abundant in low-lemming years, yet few or no Steller's eiders nest in those years. Owls and jaegers vigorously defend their nests and territories against arctic foxes and other predators (Pitleka et al., 1955; Parmelee, 1992). While under attack, foxes are likely to forage less effectively and may avoid owl and jaeger territories. Spaans et al. (1998) found that if foxes were present on an island when brent geese arrived to nest, the geese would forego breeding in that year. Foxes are not usually tolerated within 1000 m of snowy owl nests (Pitelka et al., 1955; Parmelee, 1972) and several studies have suggested a nesting association between waterfowl and snowy owls (Litvin et al., 1985; Dorogoi, 1990; Tremblay et al., 1997). Brent geese and king eiders were clustered around two snowy owl nests at distances of 40 to 400 m on the Taimyr Peninsula, Russia (Summers et al., 1994). Snowy owls typically defend territories out to 1000 m (Parmelee, 1972; Pitelka et al., 1955), and pomarine jaegers defend out to 150 m (Maher, 1974). Steller's eiders may place their nests within the territories of jaegers or owls (or both) for protection.

The logistic regression models showed that the "distance-to-jaeger:distance-to-owl" interaction term was necessary to yield predictions that matched the general pattern of Steller's eider nesting success. At distances far from an owl nest, Steller's eider nesting success was strongly dependent on proximity to a pomarine jaeger, with successful eider nests occurring within 80 m of a pomarine jaeger nest (Fig. 4b). At distances close to an owl, however, Steller's eider nesting success was much less dependent upon proximity to a pomarine jaeger, with successful nests occurring at distances up to 350 m from jaegers. Nesting close to an owl (< 400 m) and a jaeger (< 75 m) may seem like a good strategy for a Steller's eider, but since pomarine jaegers and snowy owls do not often nest in close proximity (Fig. 3), the opportunity for eiders to nest near both species may rarely exist. Steller's eiders did not nest in areas that were more than 200 m from jaegers and 1200 m from snowy owls, even though these areas were available and the habitat appeared similar to that of areas used for nesting (See Fig. 3).

The model was presented as a means to explore a mechanism that may help explain the observed pattern of nest distribution and nesting success—a mechanism that could serve as a hypothesis to be tested in a future study. Current model predictions have relatively high associated uncertainty that may be improved with additional observations. Especially if additional data support its use, the model may also be refined to account for the lack of nests very near either jaegers or owls, and model fit could be improved by accounting for spatial correlations in the probability of nesting success (Ver Hoef et al., 2001).

The common raven has recently begun to breed in the study area, and egg predation by ravens may have a significant impact on Steller's eider productivity, even in years of abundant lemmings. Territorial jaegers and owls do not appear to be effective at protecting Steller's eider nests from raven depredation.

We have considered other factors that could have explained periodic non-nesting by Steller's eiders, such as poor weather, severe sea ice conditions, competition, and early nest failure. Steller's eiders nested in years with both early and late snowmelt (Fig. 2). Spring sea ice conditions were severe only in 1992. Steller's eiders are the most abundant nesting waterfowl in the Barrow area (Pitelka, 1974), and no other species appeared to compete with Steller's eiders for food or nest sites. When nests fail early in incubation, waterfowl pairs can appear to be nonbreeders, when in fact they have failed in a breeding attempt. However, we found no evidence of nesting (eggs, eggshells, or fresh nest scrapes) in non-nesting years. Our best explanation for non-nesting by Steller's eiders is the absence of abundant lemmings. Abundant lemmings may benefit Steller's eiders by providing arctic foxes and other predators with a preferred prey source. In addition, vigorous nest defense by pomarine jaegers and snowy owls during lemming highs may confer protection on Steller's eiders nesting nearby.

Steller's eiders may live 20 years or more (Dunning, 1997), and adult female annual survival is high (~0.90; Flint et al., 2000). While Steller's eiders probably do not breed before their third year of life (Palmer, 1976), their longevity and high adult survival rate suggest they can likely afford to miss some breeding seasons. Steller's eiders may be able to assess the likelihood of nesting success in a given year and forego breeding in "bad" years. In a high lemming year near Barrow, the presence of snowy owls in May (Pitelka et al., 1955), before the arrival of Steller's eiders, may signal a potentially good breeding year. Pomarine jaegers initiate their nests at about the same time as Steller's eiders (Maher, 1974, Obritschkewitsch et al., 2001) but spend time prior to nesting in territorial defense and display. In the absence of territorial jaegers and snowy owls, the presence of arctic foxes during nest initiation may be a clear signal to Steller's eiders that breeding would not be worthwhile that year (e.g., Spaans et al., 1998).

Nesting and fledging success for Steller's eiders was low in all nesting years. This low success, coupled with periodic non-nesting, causes Steller's eiders near Barrow to exhibit extremely low productivity. Long-lived species, however, may depend on one grand year of productivity every decade or so to maintain the population. Factors likely to cause such a population to decline include a decrease in adult female survival, changes in the predator regime (e.g., the addition of ravens), and changes in the prey regime (e.g., a change in the amplitude or timing (or both) of lemming cycles).

## CONCLUSION

The breeding biology of Steller's eiders is mostly similar to that of other species of sea ducks. The greatest difference occurs in their periodic non-nesting behavior. We have speculated that lemmings affect when Steller's eiders nest near Barrow, but habitat, weather, and the persistence of sea ice may contribute in some years. Snowmelt was not a consistent indicator of nesting in any year (Fig. 2). Thus, we contend that Steller's eiders choose when and where to nest because of various factors: chief among them is pomarine jaeger and snowy owl distribution, which is based on lemming abundance. It appears that Steller's eiders have evolved a strategy that may minimize predation by foxes, either by nesting in association with species that exhibit territorial defense behavior or by nesting in years when alternative prey species are abundant.

The results of our study provide basic information on the breeding biology and ecology of Steller's eiders that will assist managers in evaluating and improving the status of this breeding population. The relationships of Steller's eiders with lemmings, pomarine jaegers, snowy owls, and arctic foxes, as well as the effect of raven predation, will require more attention before they are fully understood, but may hold some promise for enhancing this breeding population in the future.

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