Periodic nonbreeding of Steller's Eiders near Barrow, Alaska, with speculations on possible causes

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Abstract

Steller's Eiders *Polysticta stelleri* nested near Barrow, Alaska, in 1991, 1993, and 1995, but not in 1992 or 1994. Available information indicated that this pattern was similar to that observed in one area on the Siberian nesting grounds during 1991–1995. Possible causes of periodic nonbreeding at Barrow include variability in 1) body condition, 2) weather, and 3) the numbers and species of predators present on the nesting grounds. We do not have annual data on body condition; however, nesting by Steller's Eiders in Barrow coincided with years in which lemming densities were high. It is not known whether Steller's Eiders travel elsewhere to nest when they do not nest near Barrow; aerial surveys conducted throughout potential nesting habitat elsewhere in Alaska did not locate nesting Steller's Eiders. Steller's Eiders are long-lived and may maximize individual fitness by foregoing breeding in years when reproductive success may be low and adult mortality high.

Résumé

Les Eiders de Steller (*Polysticta stelleri*) ont niché près de Barrow, en Alaska, en 1991, en 1993 et en 1995, mais pas en 1992, ni en 1994. Les renseignements disponibles ont indiqué que cette tendance était semblable à celle observée dans un secteur des lieux de nidification de Sibérie de 1991 à 1995. Les causes possibles de ces périodes de non-reproduction à Barrow comprennent les variations 1) de la condition physique, 2) du climat et 3) du nombre et des espèces de prédateurs présents sur les lieux de nidification. Nous ne disposons pas de données annuelles sur la condition physique. Toutefois, les années de nidification des Eiders de Steller à Barrow coïncidaient avec celles au cours desquelles la densité des populations de lemmings était élevée. On ignore si les Eiders de Steller vont nicher ailleurs quand ils ne nichent pas près de Barrow; des relevés aériens menés dans les habitats propices à la nidification ailleurs en Alaska n'ont pas permis de repérer des sites de nidification d'Eiders de Steller. Ces derniers vivent longtemps et peuvent se maintenir en bonne santé en évitant de se reproduire les années où les chances de succès sont faibles et la mortalité adulte est élevée.

1.0 Introduction

Steller's Eiders *Polysticta stelleri* currently nest in northern Alaska and Russia, wintering mainly along the Alaska Peninsula and Aleutian Islands. The primary breeding area is believed to be the coast of northern Russia, from the Chukotsk Peninsula (Bellrose 1976) in the east to the Yamal Peninsula (Yesou and Lappo 1992) in the west. Historically, the primary breeding area in Alaska was the Yukon-Kuskokwim Delta (Conover 1926; Brandt 1943; Kertell 1991); however, between 1975 and 1995, only one nest was found there (P. Flint, pers. commun.). Barrow, Alaska, is the only known nesting area in North America currently in consistent use by Steller's Eiders. Causes of a decline in the number of Steller's Eiders nesting in Alaska and a reduction in the breeding range of the species within the state are not known.

Every year within most waterfowl populations, some portion of breeding-age birds attempt to breed with varying degrees of success; these frequencies depend upon conditions in wintering, staging, and/or nesting areas (Barry 1962; Coulson 1984). Coulson (1984) studied a population of Common Eiders *Somateria mollissima* in which as many as 65% of the breeding-age adults did not attempt to nest in some years and suggested that periodic nonbreeding of long-lived birds may be widespread. Jaegers (*Stercorarius* spp.) and Snowy Owls *Nyctea scandiaca* are well-known examples of arctic birds that exhibit periodic nonbreeding when lemmings, their preferred prey, are scarce (Parmelee 1992). Other arctic birds, not dependent on lemmings for food, have also been reported as periodic nonbreeders. In Greenland, Bertram et al. (1934) and Bird and Bird (1940) found nonbreeding in King Eiders *Somateria spectabilis*, Red-throated Loons *Gavia stellata* (reported as *Colymbus stellata*), Pink-footed Geese *Anser brachyrhynchus*, and Oldsquaw *Clangula hyemalis*. In those years when waterbirds did not nest, passerines and shorebirds were observed to have nested normally (Bertram et al. 1934; Bird and Bird 1940).

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In this paper, we report on the breeding density, nest success, and periodic nonbreeding of Steller's Eiders during five consecutive summers near Barrow, Alaska. We then explore possible relationships among Steller's Eider reproductive performance, variation in lemming density, predator numbers, and weather.

2.0 Methods

2.1 Study area

The study was conducted at the extreme northwestern corner of the Alaska Coastal Plain near Barrow, Alaska (71°18'N, 156°40'W). A 19-km road (Gaswell Road) was used for road surveys and access to nesting areas. The Barrow area is underlain by continuous permafrost (Bunnell et al. 1975), and the landscape is dominated by ice-wedge polygons, shallow northwest–southeast-oriented lakes, and drained lake basins. Maximum topographical relief occurs with remnant beach ridges and shores of drained lakes, stream banks, and berms caused by repeated use of trails by heavy equipment. The remaining tundra is of low relief, mostly less than 2 m. Plant communities include upland meadow, wet meadow, and marshes with emergent vegetation and open water in numerous small ponds and lakes (Bunnell et al. 1975).

Terrestrial mammalian fauna in the Barrow area is less diverse than in other coastal and inland areas of northern Alaska. One species, the brown lemming *Lemmus trimucronatus*, undergoes large population fluctuations. Collared lemmings *Dicrostonyx groenlandicus* are also present, usually in lower numbers. When lemming numbers are high, they support breeding mammals (arctic foxes *Alopex lagopus*, least weasels *Mustela nivalis*, and short-tailed weasels *M. erminea*) and predatory birds (Snowy Owls, Pomarine Jaegers *Stercorarius pomarinus*, and Short-eared Owls *Asio flammeus*). Glaucous Gulls *Larus hyperboreus* are present in large numbers regardless of lemming numbers, although most appear to be nonbreeders.

2.2 Breeding pair densities

We conducted road surveys along Gaswell Road during June and July, 1991 through 1995, from all-terrain vehicles. Observers drove the length of the road, stopping frequently to scan for eiders using 10×40 binoculars. Both sides of the road were surveyed out to 300 m. Road surveys covered 11.5 km² and took approximately four hours to complete. Pair densities were calculated based on the assumption that each male represented a breeding pair. Twelve surveys were conducted between 15 June and 16 July 1991, five between 12 and 19 June 1992, 28 between 8 June and 7 August 1993, 10 between 18 June and 14 July 1994, and 15 between 12 June and 19 July 1995.

2.3 Spring chronology

Spring chronology from 1992 to 1995 was determined by using the dates at which nearby breeding bird study plots were snow-free (Suydam and Wesselmann 1993; Wesselmann and Suydam 1993; Johnson et al. 1994, 1995). In 1991, breeding bird plots were not surveyed; therefore, snowmelt data recorded by the Climate Diagnostics Monitoring Laboratory of the National Oceanic and Atmospheric Administration (NOAA) were used (E. Dutton, pers. commun.).

2.4 Nest searches

We found nests by observing female behaviour and by searching areas where pairs were consistently observed. Searches were not confined to the road survey area. Nest searching began on 19 June 1991, 17 June 1993, and 14 June 1995. In 1992, the only pair of Steller's Eiders observed was seen only once; therefore, no nest searches were conducted. In 1994, Steller's Eiders remained flocked on a lake. When pairs or small groups of birds were seen away from the flock, that area was searched for nests. Nest searches consisted of walking the margins of ponds and tundra in the area where birds had been observed. Nest searches continued throughout the season until well after hatch (August). Nests that failed before discovery were identified as those of Steller's Eiders by the presence of very dark down, characteristic contour feathers, and/or the presence of Steller's Eider eggs or eggshells; nests without down or eggs were excluded.

2.5 Nest success

We tried to avoid flushing females when nests were discovered, and nest data were recorded quickly to minimize disturbance. Nests were monitored approximately once a week to determine nest fate, although no regular schedule was used. As the expected hatching date approached, nests were monitored more frequently to accurately determine nest fate and incubation period. During revisits, nests were observed from a distance, and females usually were not flushed from nests. Nest success was calculated using the Mayfield method (Mayfield 1961, 1975).

2.6 Nest predation

The cause of nest failure was determined whenever possible by direct observation of nest predation or was interpreted from characteristic evidence left by avian and mammalian predators. Arctic foxes generally remove all eggs, leaving no eggshells (Quinlan and Lehnhausen 1982; Burgess 1984); if eggshells remain, they are usually broken and licked clean (this study). In contrast, jaegers scatter eggshells and down about the nest site, and eggshells are usually found with holes poked through them and with some residual contents (this study). Common Ravens *Corvus corax* have been observed to remove whole Steller's Eider eggs from nests (this study). The degree to which weasels and Glaucous Gulls may be predators of Steller's Eider eggs is unknown, as is any characteristic evidence implicating them

2.7 Lemming densities

Snowy Owl nest density was used as an index of relative lemming density (R. Suydam and D. Norton, unpubl data; D. Holt, unpubl. data). Large numbers of Snowy Owls nest only when lemmings are abundant, although a few owls may nest when lemmings are moderately abundant (Parmelee 1992).

Table 1
Lemming densities, breeding densities of Steller's Eiders and predatory birds, and weather parameters near Barrow, Alaska, 1958, 1975–1980, and 1991–1995

Year	Lemming density	Steller's Eiders	Snowy Owls	Pomarine Jaegers	Snowmelt date	Deviation from normal June (°C)[a]
1958[b]	Low	None	No	No	15 June[c]	+0.1
1975[d]	Moderate (5–10)	Moderate	Yes	Yes	12–19 June	+0.4
1976[e]	High (50–60)	High	Yes	Yes	14–17 June	+0.1
1977[f]	Low (<1)	None	No	No	9 June	+0.6
1978[g]	Low (<5)	Low	Low	Yes	12 June	0.0
1979[h]	Low	Low	No	No	9–14 June	-0.3
1980[i]	Low	Low	No	No	10–12 June	+2.2
1991	0	High[j]	0.47[k]	Yes[j]	15 June[j]	+2.0
1992	Low	None[j]	No[m]	No[j]	8 June[n]	+1.4
1993	+	High[j]	0.11[m]	Yes[j]	11 June[o]	+1.3
1994	Low	None[j]	No[m]	No[j]	24–28 June[p]	-0.8
1995	0	High[j]	0.11[m]	Yes[j]	16 June[q]	+1.4

[a] National Weather Service, Barrow, Alaska.
[b] Myres (1958).
[c] Dutton and Enders (1991).
[d] Myers and Pitelka (1975a, 1975b) (estimated lemmings per hectare).
[e] Myers et al. (1977a, 1977b) (estimated lemmings per hectare).
[f] Myers et al. (1978a, 1978b) (estimated lemmings per hectare).
[g] Myers et al. (1979a, 1979b, 1979c) (estimated lemmings per hectare).
[h] Myers et al. (1980a, 1980b) (lemmings too low to support avian predators).
[i] Myers et al. (1981a, 1981b, 1981c) (lemmings too low to support avian predators).
[j] This study.
[k] R. Suydam and D. Norton, unpubl. data (Snowy Owl nests per square kilometre).
[l] E. Dutton, pers. commun.
[m] D. Holt, unpubl. data (Snowy Owl nests per square kilometre).
[n] Suydam and Wesselmann (1993); Wesselmann and Suydam (1993).
[o] Suydam et al. (1994); Johnson et al. (1994).
[p] Johnson et al. (1995); MacLean et al. (1995).
[q] R. Suydam, unpubl. data.

3.0 Results

3.1 Breeding pair densities

We estimated the breeding pair density of Steller's Eiders to be 1.5 pairs/km² in 1991, 3.0 pairs/km² in 1993, and 1.6 pairs/km² in 1995. During 1992 and 1994, no evidence of nesting was observed. In 1992, only one pair was present for only one day (pair density of 0.1 pairs/km²). In 1994, smaller groups and a few pairs were observed, but no nests were found (pair density of 1.9 pairs/km²). No broods were seen during the normal brood-rearing period in 1992 or 1994. Researchers studying Snowy Owls and shorebirds spent a good deal of time in our study area and often reported Steller's Eider nests and broods; no nests or broods were found by them in 1992 or 1994.

3.2 Spring chronology

Dates when plots became snow-free indicated that the onset of spring was similar in 1991 (15 June), 1993 (11 June), and 1995 (16 June). The snow-free date in 1992 was earlier than in other years (8 June), albeit not much earlier than in 1993, but in 1994 it was much later (approximately 26 June) (Table 1). In 1992, the sea ice conditions were severe, with few nearshore leads open near Barrow during May (Philo et al. 1994). Aerial surveys of the wintering grounds near the Alaska Peninsula found Steller's Eiders unusually concentrated during May 1992 because of heavy ice conditions there as well (Larned et al. 1994). The same survey in 1993 found no such concentration, indicating an early breakup with no perceived obstructions to spring migration (Larned et al. 1994). Extensive sea ice along the spring migration route may have delayed migration in 1992 and precluded nesting that year; however, King and Common eiders migrated past Barrow on schedule (R. Suydam, unpubl. data).

In 1994, Steller's Eiders were present on the nesting grounds prior to 18 June, more than a week earlier than the snow-free date. Some nesting habitat was available during the normal nest initiation period; however, no nests were found. Passerines and shorebirds that could have been similarly affected by late snowmelt were observed to nest. Shorebird nest densities were lower on one plot, probably because of the effects of unusually late snow and standing water (MacLean et al. 1995).

3.3 Nest success

For nesting years, nest success ranged from 14.6% (n = 13) in 1993 to 71.3% (n = 6) in 1991 (Table 2). Nest search effort was lower in 1991, and some nests were missed, as indicated by the number of broods seen in August. Even though the sample sizes were low, 1991 appeared to have the highest nest success of any year during this study.

3.4 Predation

Although we do not know how fox numbers varied with fluctuations in lemming numbers, avian numbers varied widely among years (Table 1). Arctic foxes were assumed to be responsible for nest predation in cases where entire

Table 2
Fate of Steller's Eider nests near Barrow, Alaska, 1991–1995

	1991	1992	1993	1994	1995
Nests found	6	0	20	0	78
Nests found active	6		13		25
Successful nests	5[a]		4		9
% success (Mayfield)	71.3	0	14.6	0	15.3
Unsuccessful nests	1		16		69
Failed after found	1		9		17
Abandoned	0		2		2
Avian predation	1		1		5
Fox predation (suspected)	0		5		7
Hen mortality	0		0		1[b]
Unknown predator	0		1		2
Unknown cause	0		0		0
Failed before found	0		7		52
With no eggs[c]	–		6		35
With egg(s)[d]	–		1		17

[a] Two and possibly three of these nests were partially depredated by Common Ravens.
[b] The hen was killed by a Snowy Owl, causing the nest to fail.
[c] No eggs or eggshells were associated with these nests when found, but eggs could have been removed by predators.
[d] Whole or broken eggs were found in or near the nest bowl.

clutches disappeared at once and were suspected to have caused the failure of 44% (n = 27) of Steller's Eider nests in all years (Table 2). We found that the primary avian predators of Steller's Eider eggs were Pomarine Jaegers. Common Ravens were observed removing whole eggs from attended and unattended Steller's Eider nests. Common Ravens may be capable of removing an entire clutch of eggs in several trips and therefore could be responsible for some predation attributed to arctic foxes. Glaucous Gulls may be predators of Steller's Eider eggs as well; however, this has not been documented. For nests that failed after we discovered them, avian or mammalian predators were implicated in the single nest failure in 1991, seven of nine nest failures in 1993, and 15 of 17 nest failures in 1995 (Table 2).

Avian predators have been the predominant natural cause of adult Steller's Eider mortality on the breeding grounds. Of eight Steller's Eider carcasses where an avian predator was suspected, Snowy Owls were responsible for three of the deaths, Peregrine Falcons *Falco peregrinus* for two, and a Gyrfalcon *F. rusticolus* for one; for two others, the species of the avian predator was unknown.

4.0 Discussion

4.1 Explanations for nonbreeding at Barrow

Steller's Eiders nested near Barrow in 1991, 1993, and 1995, but not in 1992 or 1994. Little is known about nest site fidelity of Steller's Eiders, so it is not known whether those eiders nesting near Barrow in some years nest elsewhere in other years. Few Steller's Eiders have been seen on the Arctic Coastal Plain outside of Barrow during aerial surveys conducted between 1992 and 1995 (W. Larned and G. Balogh, pers. commun.; R. King, unpubl. data). In 1992 and 1994, Steller's Eiders were not found nesting elsewhere in northern Alaska.

The possibility that Steller's Eiders move between Russia and Alaska can be addressed indirectly by comparing nesting on the Lena River Delta with that in Barrow. In 1995, the number of pairs was low in Russia (D. Solovieva, pers. commun.) and high in Barrow. However, 1991 and 1993 were good nesting years and 1992 and 1994 were poor nesting years in both locations. Although the evidence is limited, it does not support a movement of Steller's Eiders between Russian and Alaskan nesting areas.

Weather may have prevented Steller's Eiders from nesting in Barrow during some years, but no pattern emerges when comparing snowmelt dates or June temperatures for Barrow with the presence or absence of nesting Steller's Eiders (Table 1). In 1992, only one pair of Steller's Eiders was observed on the tundra and for only one day. Severe sea ice conditions, resulting in scant open water offshore of Barrow during May 1992 (Philo et al. 1994), may have prevented Steller's Eiders from reaching the breeding grounds, although these conditions did not preclude migration of other eider species. In 1994, when Steller's Eiders were present on the breeding grounds but did not nest, snowmelt was the latest recorded during our and other studies near Barrow (Table 1). The late snow melt-off may have prevented access to some suitable nesting areas; however, passerines and shorebirds nested normally. Poor body condition resulting from inadequate food on the wintering grounds in some years may also be a factor in determining whether or not Steller's Eiders breed. We have no data to address this possibility.

During this study, Steller's Eiders nested only in years when lemming numbers were high, as indicated by the number of nesting Snowy Owls. Nesting Steller's Eiders were absent from Barrow during two years when lemming populations were low, but weather conditions during migration in 1992 and upon arrival in 1994 were extreme.

Arctic foxes were present on the breeding grounds every year and are known to flush incubating female waterfowl to depredate nests (Quinlan and Lehnhausen 1982; Burgess 1984). Arctic foxes are also capable of killing and eating adult eiders (Elander and Blomqvist 1986) and probably have the greatest influence on the breeding success of ground-nesting arctic birds (Larson 1960), including Steller's Eiders. Indeed, we believe foxes may have caused more total nest failures than any other predator during this study. It is likely that there has been strong selective pressure for Steller's Eiders to develop strategies to decrease nest predation by foxes. If fox predation has exerted strong selective pressure on Steller's Eider nesting behaviour, possible strategies to avoid fox predation may include 1) nesting only when and where sufficient other prey (i.e., lemmings) are present and 2) nesting in association with species that exhibit effective antipredator defences.

4.2 Evaluation of nesting strategies

4.2.1 Nest only when and where alternative prey are present

Arctic foxes are dependent on lemmings (Larson 1960); however, when lemmings are not abundant (and sometimes even when they are), foxes prey on birds, their eggs, and other items opportunistically (Chesemore 1968; Stickney 1991). Larson (1960) concluded that predation pressure by arctic foxes was a major influence in the distribution of arctic breeding birds. Species that did not possess adaptations to avoid fox predation were absent or low in numbers in areas without lemmings. Barrow is well-known

Table 3
Some reported cases of waterbirds nesting in association with bird species that exhibit antipredator defence

Protected species	Predator providing protection	Reference
Red-breasted Goose *Branta ruficollis*	Peregrine Falcon *Falco peregrinus* and Rough-legged Hawk *Buteo lagopus*	Kostin and Mooij (1995)
Brant *B. bernicla*	Snowy Owl *Nyctea scandiaca*	Underhill et al. (1993)
King Eider *S. spectabilis*	Long-tailed Jaeger *Stercorarius longicaudus*	Blomqvist and Elander (1988)
	Snowy Owl *Nyctea scandiaca*	Summers et al. (1994)
Eurasian Curlew *Numenius arquata*	Eurasian Kestrel *Falco tinnunculus*	Norrdahl et al. (1995)
Bristle-thighed Curlew *N. tahitiensis*	Long-tailed Jaeger	McCaffery and Gill (1992)
Bar-tailed Godwit *Limosa lapponica*	Long-tailed Jaeger	Maher (1959)

for its brown lemming cycles, and numerous studies have been conducted there (Rausch 1950; Pitelka et al. 1955; Thompson 1955a, 1955b; MacLean et al. 1974; Batzli and Pitelka 1983). The Inupiat Eskimo name for Barrow is Ukpeagvik, which means "place to hunt Snowy Owls," implying that Snowy Owls have occurred regularly near Barrow for many years, likely in response to lemming availability. It may be that years of lemming abundance occur with greater frequency and amplitude near Barrow than at other places on the Alaska Coastal Plain. The Prudhoe Bay oilfield, another Arctic Coastal Plain location where the fauna has been studied, had one year when lemmings were high (D. Troy, pers. commun.) within the five-year period when Barrow had three years of lemming highs.

In years when records are available for both Steller's Eider nests and lemming numbers, nesting by Steller's Eiders near Barrow has been correlated with lemming numbers (Table 1). Although high lemming numbers may attract more foxes and avian predators, they may also decrease predation pressure on Steller's Eiders and their eggs by providing abundant primary prey. On the Lena Delta, lemmings were at moderate levels in 1993, a good nesting year for Steller's Eiders, and at low levels in 1994 and 1995, which were poor nesting years for breeding Steller's Eiders (D. Solovieva, pers. commun.). Observations elsewhere on other species support this explanation as well. Summers and Underhill (1987) concluded that the breeding success of Brant *Branta bernicla bernicla* in arctic Russia was more strongly correlated with lemming abundance than with spring feeding conditions or with weather on the breeding grounds. In a review of six incidences of nonbreeding in several species of waterbirds in eastern Greenland, all were found to coincide with poor lemming years; these same species bred during good lemming years (Bertram et al. 1934). Another study conducted from 1936 to 1938 in northeast Greenland (Bird and Bird 1940) found waterbirds nesting in 1936 and 1937, but not in 1938, which was a poor lemming year. Pehrsson (1986) found that peaks in Oldsquaw duckling production in northern Sweden were better correlated with microtine abundance than with weather parameters. Underhill et al. (1993) studied Brant and shorebirds in 1991 and 1992. Spring arrived late in both years, but 1991 was a good nesting year and 1992 was a poor nesting year, corresponding with high lemming densities in 1991 and decreasing lemming densities in 1992.

4.2.2 *Nest in association with species that exhibit effective antipredator defences*

Pomarine Jaegers are known predators of Steller's Eider eggs (this study), but jaegers are not known to displace females from their nests to prey on eggs. When the nest is unattended (such as during the laying period), jaegers often remove some eggs without destroying the entire nest. Pomarine Jaegers and Snowy and Short-eared owls are aggressive in defence of their nest territories and harass all intruders that are potential predators of their eggs and young. This may cause foxes to avoid the territories of owls and jaegers, or the foxes may be so distracted by the attacks that their effectiveness as predators on Steller's Eider nests is reduced. Thus, species with no antipredator defences of their own may gain protection from foxes by nesting in association with species that exhibit these defences (Table 3). Therefore, nesting in association with Pomarine Jaegers and/or owls may result in greater nest success for Steller's Eiders, even if they lose some eggs to jaegers. Koskimies (1957) argued that such a relationship could become established if young raised in association with a certain species recognized the presence of that species as a critical component of nest site selection.

5.0 Conclusion

Steller's Eiders are long-lived sea ducks that may maximize their individual fitness by foregoing breeding in years when reproductive success may be low and adult mortality high. In years when lemming numbers are low and avian predators do not nest, Steller's Eiders and their nests likely become more vulnerable to fox predation. This study and data from previous studies (Table 1) suggest a relationship between lemming numbers and nesting Steller's Eiders at Barrow. Although we cannot rule out the possible influences of environmental factors and body condition on nest success and periodic nonbreeding, we conclude that abundant lemmings may benefit Steller's Eiders by providing foxes with an easy or preferred prey alternative to Steller's Eider eggs and/or by attracting species that defend their territories from arctic foxes. Although Steller's Eiders probably do not evaluate lemming abundance directly, they may respond to the presence or absence of territorial jaegers and/or owls.

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