

A Tropical Volcano, High Predation Pressure, and the Breeding Biology of Arctic Waterbirds: A Circumpolar Review of Breeding Failure in the Summer of 1992

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ABSTRACT. Although periodic breeding failures of Arctic-nesting birds on a regional scale are common, a breeding failure encompassing almost the entire Arctic in the same year is exceptional. In the spring and summer of 1992, however, the aerosol cloud resulting from the 1991 eruption of Mount Pinatubo (Philippines) had reached the high northern latitudes and caused significant cooling in most of the Arctic, with widespread negative consequences for Arctic-breeding birds. At the same time, low abundance of small rodents and high abundance of predators presented additional problems for breeding birds in parts of the Palearctic. We compiled data on breeding biology of Arctic waterfowl and waders from more than 30 field studies to illuminate in what ways the circumpolar bad weather and predation influenced the breeding season of Arctic birds in 1992.

Most projects reported a higher proportion of nonbreeders and a delayed onset of nest initiation compared to other years. Hatching and fledging success of the low number of late breeders was reduced. In addition, some projects reported lower clutch sizes and increased adult mortality. Detailed data from field studies are complemented by data on overall reproductive success of waterfowl and wader populations collected from staging and wintering grounds. In total, there was an almost complete reproductive failure for waders and waterfowl throughout the Arctic in 1992, suggesting a short-term effect on global waterbird populations. This is an example of climatic fluctuations influencing reproductive biology of a group of species on a circumpolar scale.

Key words: Arctic-breeding birds, breeding failure, global climate signal, predation, spring temperatures, volcanic eruption, waders, waterfowl

RÉSUMÉ. Bien que des échecs périodiques de reproduction parmi les oiseaux nicheurs de l'Arctique soient communs à l'échelle régionale, un échec de reproduction qui englobe presque tout l'Arctique durant la même année est chose exceptionnelle. Au cours du printemps et de l'été de 1992 cependant, le nuage aérosol causé par l'éruption du mont Pinatubo, aux Philippines, qui avait eu lieu en 1991, avait atteint les latitudes les plus septentrionales et causé un refroidissement significatif dans la plus grande partie de l'Arctique, entraînant des conséquences négatives d'envergure pour les oiseaux nicheurs de l'Arctique. Parallèlement, une faible abondance de petits rongeurs et une grande abondance de prédateurs présentaient des problèmes supplémentaires pour les oiseaux nicheurs dans certaines parties du paléarctique. On a compilé les données sur la biologie de reproduction de la sauvagine et des échassiers arctiques provenant de plus de 30 études sur le terrain en vue de faire la lumière sur la façon dont le mauvais temps circumpolaire et la prédation ont influencé la saison de reproduction des oiseaux arctiques en 1992.

La majorité des études faisaient état d'une proportion plus élevée d'oiseaux qui ne poussaient pas et d'un retard du début de la couvaison par rapport aux autres années. Le succès d'éclosion et d'envol du faible nombre de reproducteurs tardifs était en baisse. De plus, certaines études rapportaient une diminution de la taille des pontes et une augmentation de la mortalité adulte. Des données détaillées provenant d'études menées sur le terrain sont complétées par des données, recueillies à des points d'escale ou des aires d'hivernage, sur le succès de la reproduction de populations de sauvagine et d'échassiers. En 1992, il y a eu dans l'ensemble un échec de reproduction presque complet pour les échassiers et la sauvagine dans tout l'Arctique, ce qui suggère une retombée à court terme sur la population de la sauvagine à l'échelle de la planète. Ceci représente un exemple des fluctuations climatiques qui influencent la biologie reproductive d'un groupe d'espèces à l'échelle circumpolaire.

Mots clés: oiseaux nicheurs de l'Arctique, échec de reproduction, signal climatique mondial, prédation, températures printanières, éruption volcanique, échassiers, sauvagine

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INTRODUCTION

Arctic summers are short, and therefore bird populations breeding in the Arctic are less buffered against unfavourable events than those breeding in temperate conditions.

Potential for re-nesting after an unsuccessful breeding attempt is low or absent in this extreme environment, and breeding failures in unfavourable years are therefore rather common. Weather and predation, the two environmental factors with greatest impact on breeding success of arctic

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birds, are both subject to pronounced, but partially independent, annual fluctuations. Sporadic episodes of severe weather are common in the Arctic, but such bad-weather events are usually local or regional, and do not affect the entire Arctic. The breeding ranges of most Arctic-nesting bird populations have a sufficient longitudinal spread so that only subsets of populations are affected. Similarly, fluctuations in predation pressure, which are often linked to cyclic changes in abundance of small rodents (lemmings and voles), usually occur at a local or regional scale, although they can affect annual reproductive success of entire populations of Arctic-breeding birds (Roselaar, 1979; Summers, 1986; Greenwood, 1987; Summers and Underhill, 1987).

Unfavourable weather events can negatively influence breeding success in a variety of ways. Depending on the nature and timing of severe weather, birds may opt out of breeding entirely (e.g., Mayfield, 1978) or suffer losses through decreased clutch size (Barry, 1962), reduced hatching success (Harvey, 1971), increased (up to 100%) juvenile mortality (Raveling, 1977), or even adult mortality (Barry, 1968; Morrison, 1975). General correlations between Arctic weather, particularly spring temperatures, and overall breeding success of Arctic bird populations have been well established (Boyd, 1982, 1992, 1996; Fox et al., 1989; Fox and Gitay, 1991; Skinner et al., 1998). However, much less is known about the relative importance of the various mechanisms that may depress breeding success. Because of the cost and logistical difficulties involved, long-term studies of the population ecology of Arctic birds that provide detailed information on breeding parameters and their relation to weather patterns are relatively scarce.

The summer of 1992 was unusual in that the Arctic was influenced by a global climatic event. In June 1991, the volcano Mount Pinatubo (on the island of Luzon in the Philippines, 15°N, 121°E) erupted numerous times, the main eruption taking place on 15 June. The stratospheric sulphuric acid aerosol clouds produced by explosive volcanic eruptions increase the optical depth of the stratosphere and can produce a decrease in surface air temperature of a few tenths of a degree Celsius averaged over the entire Northern Hemisphere (Kelly and Sear, 1984). This temperature decrease may result in significant weather anomalies: for example, the eruption of Tambora (8°S, 118°E) in 1815 was followed by a "year without a summer" in parts of the Northern Hemisphere in 1816 (Stommel and Stommel, 1979). After major eruptions in low latitudes, the cooling signal in high latitudes is most pronounced 8 to 10 months after the event (Bradley, 1988). The Pinatubo eruption was the largest on record so far this century in terms of gas and dust being injected into the stratosphere, and by early 1992, the optical depth of the stratosphere had increased by two orders of magnitude at all latitudes (McCormick et al., 1995). At high northern latitudes, the optical depth reached a peak value in early May 1992 (Stone et al., 1993), and temperatures in Arctic regions were generally

below normal throughout the summer of 1992 (McKinley, 1992). As a result of this temperature anomaly, snowmelt and vegetation development were considerably delayed in large parts of the Arctic in the 1992 spring and summer.

The exceptional nature of 1992, with its adverse weather conditions throughout large parts of the Arctic during the breeding season, offers the opportunity for a cross-sectional study to investigate more closely how unfavourable weather can influence breeding success of Arctic-nesting birds. Detailed information on the relationship between weather and reproduction is needed as input, for example, into scenarios for assessing the potential impact of global climate change on bird populations (e.g., Boyd and Diamond, 1994; Boyd and Madsen, 1997). In this paper, we investigate the extent and mechanisms of reproductive failure in Arctic-breeding waders and waterfowl during the summer of 1992. We document weather anomalies throughout the Arctic during the 1992 breeding season and present complementary information on predation pressure. We then review the influence of weather and predation on overall breeding success and specific breeding parameters of various waterbird populations throughout the Arctic. We chose waterfowl (Anatidae) and waders (Scolopacidae and Charadriidae) for the analysis for three reasons. First, these two groups of birds form a large part of the Arctic-breeding avifauna. Second, more field studies are carried out on the breeding biology of these two groups than on other groups of Arctic-breeding birds (such as passerines or raptors). Finally, for waterfowl and waders, ample information is available, both from the breeding grounds and on juvenile percentages on the wintering grounds, so that the breeding success in a given season can be assessed for many species and populations.

METHODS

Breeding Data of Arctic Waterbirds in 1992: Field Studies

We designed a survey sheet with questions about the breeding parameters of Arctic waterbirds in the summer of 1992. From June 1997 to January 1998, this sheet was distributed among researchers or research groups for whom fieldwork on breeding waterbirds in the Arctic in 1992 was part of a multiple-year study, so that they could assess possible peculiarities of the 1992 breeding season by comparison with other seasons. Specifically, we asked for information about the following aspects of the 1992 breeding season of intensively studied species: breeding phenology (timing of arrival and nest initiation), breeding population (number of breeding pairs or nests, nest density), clutch size, breeding success (hatching success, brood sizes, fledging success) and factors reducing breeding success (nest abandonment, predation, juvenile mortality), adult mortality, and any additional factors the respondents considered relevant. We also included a question about the abundance of both small rodents and

mammalian and avian predators in the study area. Furthermore, we asked for anecdotal information on bird species other than those that were intensively studied. Some basic questions on the location and nature of the study area and length of the study were included as well. We distributed a total of 42 survey sheets and received 26 responses. Most respondents had completed the sheets, while some sent data in other formats or provided copies of publications or reports.

In addition to the survey sheets, we scanned recent ornithological literature for publications on multiple-year studies of Arctic waterbird breeding biology that included data from 1992. Additional information about rodent and predator abundances and overall breeding success in the Russian Arctic in 1992 was extracted from Tomkovich (1994).

Breeding Success of Arctic Waterbirds in 1992: Surveys from Staging and Wintering Areas

To complement the direct information on breeding success from the field study surveys, we searched the literature for long-term data on abundance of juvenile waterfowl and waders on staging and wintering grounds. In addition, we approached organizations and individuals involved in long-term monitoring of Arctic-breeding waterbirds with a request for unpublished material that would allow us to evaluate overall breeding performance in 1992 as compared to other years. Data consisted mostly of counts (sight records) of juvenile percentages of geese and waders in the field; for waders, absolute numbers of passing juveniles at one site (Helgoland, Germany) and data from annual mass catches in Australia were also used to assess population-wide breeding performance.

Weather During the 1992 Breeding Season

Although maps of temperature anomalies in 1992 have been published (McKinley, 1992; Jones and Kelly, 1996), these show only large-scale temporal and geographical patterns. We were interested more specifically in the conditions in the breeding areas of arctic waterbirds during the 1992 breeding season. Therefore, we extracted weather data for May–August 1992 from published meteorological reports (McKinley, 1992) of weather stations throughout the Arctic. We selected 36 stations located at or near major waterbird breeding areas from which data were available for 1992. We used monthly temperature means as an indication for overall weather, comparing the 1992 values to long-term standards. For 59 stations and months, the standard was the 30-year mean of 1961–90; where this was not available, we used the 10-year mean of 1986–95 for comparison (62 stations and months); where this was not available either, we used the mean of a shorter run of years between 1986 and 1995 (23 stations and months; Appendix 2).

In the survey sheets mentioned above, researchers were also asked to provide their personal assessment of weather

in their study area during the 1992 breeding season, to compare the 1992 situation to that of other study years, and to comment on the effect of weather on the breeding success of their study species in 1992. Some additional information about weather in the Russian Arctic was gained from Tomkovich (1994).

Nomenclature

In the text, only English names of bird species will be given; all Latin names can be found in Appendix 3. Where English and North American species names differ, English names are used throughout the text, even when referring to North American populations; North American names are given in Appendix 3. Similarly, we use the general term “waders” rather than “shorebirds” throughout the text.

RESULTS

Field Studies Included in the Review

We obtained data from a total of 35 multiple-year field studies of waterfowl and waders carried out at 30 sites throughout the Arctic (Fig. 1, Appendix 1). Single studies covered between 2 and 29 breeding seasons each, with an average of 8.6 seasons. Throughout the following text, numbers in parentheses refer to field sites shown in Figure 1 and listed in Table 1. To facilitate reading, we have omitted sources of information for each site and species from the text and listed them instead in Table 1. Data from 28 of the 35 studies reached us through direct correspondence with the field scientists; for the remaining 7 studies, data were extracted from published scientific papers and reports, without personal contact with the authors. The main body of information compiled from these studies is presented in Table 1. In the text we also include certain additional information reported by field workers that is not included in Table 1.

Arctic Weather During the 1992 Breeding Season

Monthly Mean Temperatures: Throughout the 1992 breeding season (May to August), temperatures were considerably lower than normal in many areas of the Holarctic, although the pattern differed between the Nearctic and Palearctic (Fig. 2). Only in Svalbard, northern Scandinavia, the Far East of Russia, and eastern Greenland were temperatures close to or slightly above the long-term mean throughout the breeding season. In May (time of arrival and nest initiation for most species in the Low Arctic and some species in the High Arctic), monthly mean temperatures were several degrees below normal in western Alaska, in most of the Canadian Arctic, and in Greenland, whereas they were slightly above normal in most of the Russian Arctic. In June (arrival and nest initiation for most High Arctic species), monthly mean temperatures in Canada

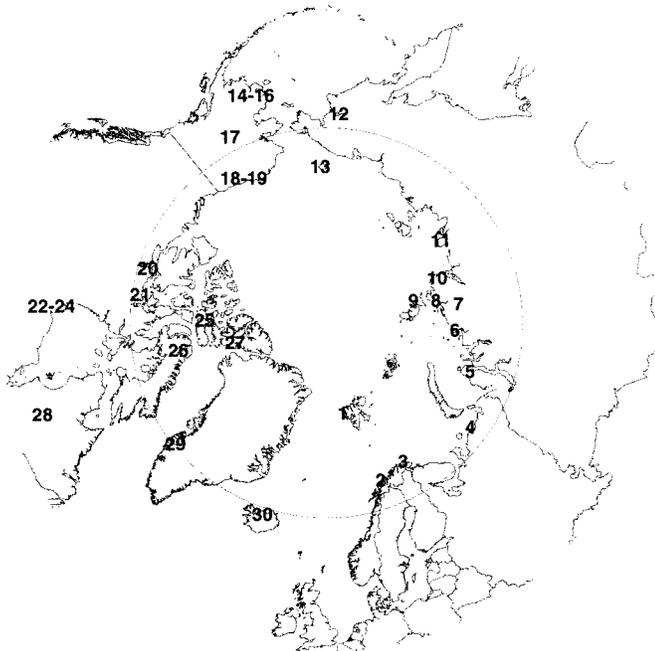


FIG. 1. Location of field studies, ordered by longitude, moving east from the Greenwich meridian. For exact locations see Appendix 1.

Norway 1: Ny Ålesund, 2: Tromsø, 3: Gamvik; **Russia** 4: Russkiy Zavorot, 5: Yamal, 6: Pyasina-Delta, 7: Malaya Logata, 8: Knipovich Bay, 9: Severnaya Zemlya, 10: Pronchishcheva Lake, 11: Lena-Delta, 12: Anadyr Gulf, 13: Wrangel Island; **U.S.A.** 14: Yukon-Kuskokwim Delta (Tutakoke), 15: Yukon-Kuskokwim Delta (Kashunuk River), 16: Yukon-Kuskokwim Delta, 17: Koyukuk National Wildlife Refuge, 18: Prudhoe Bay, 19: Howe Island; **Canada** 20: Kent Peninsula, 21: Karrak Lake, 22: Churchill, 23: La Pérouse Bay, 24: Cape Churchill, 25: Cardigan Strait, 26: Bylot Island, 27: Alexandra Fjord, 28: Laforge I; **Greenland** 29: Isungua; **Iceland** 30: Lake Myvatn.

and western Greenland stayed low, and those in the Russian Arctic (on and to the west of the Taymyr Peninsula) also dropped to values considerably lower than long-term means. In July (time of brood-rearing for most species), monthly mean temperatures in the northern Canadian Arctic and Greenland returned to normal, but it was still much colder than normal around Hudson Bay and in the western half of the Russian Arctic, and also colder in Iceland. The monthly mean temperatures in August (end of brood rearing and departure) no longer showed a consistent deviation from long-term means throughout the Arctic.

Additional Information from Field Workers: In his compilation of information on breeding conditions in the Russian Arctic in 1992, Tomkovich (1994) reports unfavourable weather conditions (cold and late spring, cold summer, or both) from most sites. Some of the field researchers we contacted also included information about 1992 summer weather on their survey sheets. This information remains anecdotal, but it adds to the rough picture that can be gained from monthly mean temperatures. Snow cover in spring was reported to be unusually heavy in Knipovich Bay (8), on Wrangel Island (13), in Koyukuk National Wildlife Refuge (17), and at Karrak Lake (21). By contrast, spring snow cover was unusually light in

Russkiy Zavorot (4) and at Anadyr Gulf (12). Spring temperatures were unusually cold at Knipovich Bay (8), at Anadyr Gulf (12), on Wrangel Island (13), at Koyukuk National Wildlife Refuge (17), on Howe Island (19), at Karrak Lake (21) and at La Pérouse Bay (23). Accordingly, snowmelt at these sites was (much) later than normal, except at Anadyr Gulf (12), where snow cover was light to start with. In contrast to the general pattern, early snow disappearance was reported from Russkiy Zavorot (4), where temperatures were unusually high in May (but not in June-July, cf. Fig. 2), and from Prudhoe Bay (18). Major snowfalls during spring and summer were reported from Yamal (5) for May and June; Malaya Logata (7) for May, June and early July; Knipovich Bay (8) for June and July; Howe Island (19) for May and June; La Pérouse Bay (23) for June; and Laforge I (28) for June. At all of these sites, the amount of snowfall (or frequency of snowstorms) during those months was considered to be unusually high. At Anadyr Gulf (12), by contrast, the entire breeding season was unusually dry, with neither snow nor rain. An unusually early onset of winter was reported from Russkiy Zavorot (4) and from Wrangel Island (13), where a major snowstorm on 20 August marked the beginning of the winter season. At Malaya Logata (7), temperatures rose suddenly by 15° on 19 July, which underscores that monthly mean temperatures convey only part of the temperature pattern that may have biological importance. Unusually severe spring flooding was reported from Koyukuk National Wildlife Refuge (17) and from La Pérouse Bay (23), where sheet ice blocking the local river led to flooded areas in parts of the river delta and dry areas in other parts. Persistent ice bridges to breeding islands, resulting in easy access for predators to these islands, were reported from Howe Island (19) and La Pérouse Bay (23). Slow and unusually brief daytime warming during the entire summer was reported at Kent Peninsula (20) and La Pérouse Bay (23).

Abundance of Predators and Small Rodents in 1992

We did not receive specific information about numbers of predators or small rodents from field sites on Svalbard and in Norway (1–3), but field workers at those sites considered predation pressure to have been “normal” or “average” in 1992. As reported by Tomkovich (1994), lemmings and voles across the entire Russian tundra either had reached a population low point or were decreasing during the summer of 1992 except on Wrangel Island (13), where lemmings were increasing. At the same time, numbers of predators, mainly arctic foxes *Alopex lagopus*, were high throughout the area, except on southern Yamal (5) and Severnaya Zemlya (9). This pattern was confirmed by information we received from Russkiy Zavorot (4), Yamal (5), Pyasina Delta (6), Malaya Logata (7), Knipovich Bay (8), Pronchishcheva Lake (10), Anadyr Gulf (12), and Wrangel Island (13). All those sites reported low numbers of lemmings/voles (except at Russkiy Zavorot (4) and Wrangel Island (13), from which we did not receive

TABLE 1. Overview of weather and breeding parameters of waterfowl and waders at field sites throughout the Arctic in 1992. Field sites are ordered by longitude, moving east from the Greenwich meridian.

Site number and name ¹	Study years (# years)	Weather summary ²	Species ³	Arrival time	Initiation time	# Pairs/Density	Clutch size	Hatch success	Predation ⁴	Overall success	Cause of failure	Sources ⁵
1. Ny Ålesund	92-97 (6)	Normal	<i>Branta leucopsis</i>		Average	Average	Average	Low	Average	Average	-	1-2
2. Tromsø	86-95 (10)	Normal	<i>Somateria mollissima</i>		Average	Average	Average	Average	Average	Average	-	3
3. Gamvik	91-97 (7)	Normal	<i>Calidris alpina</i>		Average	Average	Average	Low	Average	Average	-	4
4. Russkiy Zavorot	91-97 (7)	Early	<i>Cygnus columbianus bewickii</i>		Earliest ever	Average	Highest ever	Very low	Very high	Very low	Weather + Predation	5-9
5. Yamal	89-95 (7)	Late Cold	<i>Pivovialis squatarola</i>	Very late	Latest ever	Low	Highest ever	Lowest ever	Highest ever	Very low	Weather + Predation	10-11
6. Pyasina-Delta	89-95 (6)	Late Cold	<i>Branta bernicla bernicla</i>	Normal	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	12
7. Malaya Logata	89-92 (4)	Late Cold	<i>Anser albifrons albifrons</i>	Late	Late	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	13-14
	89-92 (4)		<i>Anser fabalis rossicus</i>	Late	Late	Low	Lowest ever	Low	Very high	Total failure	Weather	13-14
	89-92 (4)		<i>Branta rufficollis</i>	Late	Late	Lowest ever	Lowest ever	Low	Very high	Total failure	Weather + Predation	13-14
8. Knipovich Bay	90-92 (3)	Late Cold	<i>Pivovialis squatarola</i>	Latest ever	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	15-17
	90-92 (3)		<i>Calidris canutus</i>	Latest ever	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	15-17
	90-92 (3)		<i>Calidris alba</i>	Late	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	15-17
	90-92 (3)		<i>Calidris ferruginea</i>	Late	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	15-17
	90-92 (3)		<i>Calidris minima</i>	Latest ever	Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather + Predation	15-17
9. Severnaya Zemlya	91-96 (6)	Late Cold	<i>Branta bernicla bernicla</i>		Latest ever	Lowest ever	Lowest ever	Lowest ever	Very high	Total failure	Weather	18-20
	91-96 (6)		<i>Calidris maritima</i>			Average				Average	-	18-20
	91-96 (6)		<i>Calidris alba</i>			Average				Average	-	18-20
10. Pronchishcheva Lake	91-92 (2)	Late Cold	<i>Branta bernicla bernicla</i>		Very late	Very low	Low	Very low (0)	Very high	Total failure	Predation	21
	91-92 (2)		10 wader species			Average				Very low	Predation	21
11. Lena-Delta	92, 94 (2)	Late Cold	<i>Branta bernicla nigricans</i>			Very low		Lowest ever	Very high	Total failure	Weather + Predation	22
12. Anadyr Gulf	91-94 (4)	Early	<i>Branta bernicla nigricans</i>	Average	Average	Very low	Lowest ever	Very low	Very high	Very low	Predation	23
	91-94 (4)		<i>Anser canagicus</i>	Average	Average	Very low	Lowest ever	Lowest ever	Very high	Very low	Predation	23
	91-94 (4)		<i>Anser albifrons</i>	Average	Early	Average	Average	Average	High	Very low	Weather + Predation	24-26
13. Wrangel Island	69-97 (29)	Late	<i>Anser caerulescens caerulescens</i>	Latest ever	Average	Average	Very high	High	Low	High	-	27
14. Yukon-Kuskokwim Delta (Tuakoke)	86-93 (8)	Late	<i>Anser caerulescens nigricans</i>		Latest ever	Average	Average	High	Low	High	-	28-29
15. Yukon-Kuskokwim Delta (Kashumuk River)	85-92 (8)	Late Cold	<i>Branta canadensis minima</i>	Late	Late	Highest ever	High	High	Low	High	-	28-29
	85-92 (8)		<i>Anser albifrons frontalis</i>	Late	Late	High	Average	High	Low	High	-	28-29
	85-92 (8)		<i>Anser canagicus</i>	Late	Late	Low	Average	Average	Low	High	-	28-29
	91-95 (5)		<i>Somateria fischeri</i>	Late	Late	Average	High	Average	Low	High	-	30
16. Yukon-Kuskokwim Delta	86-97 (12)	Late	<i>Branta canadensis minima</i>		Very late	Average	Average	High	Low	High	-	31
	86-97 (12)		<i>Anser albifrons frontalis</i>		Late	Average	Average	High	Low	High	-	31
	86-97 (12)		<i>Anser canagicus</i>		Late	Low	Very high	Average	High	Very low	Weather	32-33
17. Koyukuk National Wildlife Refuge	86-97 (12)	Late Cold	<i>Branta canadensis</i>		Late	Very low	Average	Average	High	Very low	Weather	32-33
	86-97 (12)		<i>Anser albifrons frontalis</i>		Early	Lowest ever	Lowest ever	Low	High	Very low	Predation	34
18. Prudhoe Bay	81-82, 84, 86-92 (10)	Early Cold	14 wader species			Average		Very low	High	Very low	Predation	34
19. Howe Island	80-97 (18)	Late	<i>Anser caerulescens caerulescens</i>	Very late	Very late	Low	High	Very low	Very high	Total failure	Weather + Predation	35-36
20. Kent Peninsula	87-97 (11)	Late Cold	<i>Anser albifrons frontalis</i>	Late	Very late	Average	High	Low	Very high	High	-	37
	87-97 (11)		<i>Branta canadensis hutchinsii</i>	Late	Very late	Average	High	Low	Very high	High	-	37
21. Karak Lake	91-96 (6)	Late	<i>Anser rossii</i>		Very late	Very low	Average	Very low	Very high	Very low	Weather	38
	88, 92-95 (5)	Late Cold	<i>Anser caerulescens caerulescens</i>		Very late	Very low	High	Lowest ever	Very high	Very low	Weather	38
22. Churchill	92-98 (7)		<i>Charadrius semipalmatus</i>	Latest ever	Latest ever	Lowest ever	Lowest ever	Lowest ever	High	Very low	Weather	39
	68-93 (26)	Late Cold	<i>Calidris alpina</i>		Latest ever	Very low	Very low	Very low	Average	Very low	Weather	40
23. La Pérouse Bay	91-93 (3)	Late Cold	<i>Anser caerulescens caerulescens</i>	Very late	Latest ever	Lowest ever	Lowest ever	Lowest ever	Highest ever	Total failure	Weather + Predation	41-43
	76-97 (22)	Late Cold	<i>Somateria mollissima</i>	Latest ever	Very late	Very low	Very low	Very low	Highest ever	Total failure	Weather + Predation	44-45
24. Cape Churchill	84, 92 (2)	Late Cold	<i>Branta canadensis interior</i>	Very late	Very late	Very low	Very low	Very low	Highest ever	Very low	Predation	46
25. Cardigan Strait	89-97 (9)	Late Cold	<i>Somateria mollissima</i>	Average	Latest ever	Lowest ever	Lowest ever	Average	High	Very low	Weather + Predation	47
26. Bjølot Island	86-92 (7)	Late Cold	<i>Anser caerulescens atlantica</i>			Lowest ever	Lowest ever	Average	High	Very low	Weather	48-50
27. Alexandra Fjord	86-92 (7)	Late Cold	<i>Somateria mollissima</i>			Average		Average	High	Very low	Weather + Predation	51
			<i>Clangula hyemalis</i>							Very low	Weather + Predation	51

TABLE 1. Overview of weather and breeding parameters of waterfowl and waders at field sites throughout the Arctic in 1992. Field sites are ordered by longitude, moving east from the Greenwich meridian – continued.

Site number and name ¹	Study years (# years)	Weather summary ²	Species ³	Arrival time	Initiation time	# Pairs/Density	Clutch size	Hatch success	Predation ⁴	Overall success	Cause of failure	Sources ⁵
28. Laforge I	92–96 (5)	Late Cold	<i>Branta canadensis interior</i>	Late	Late	Lowest ever	Low	Lowest ever	Average	Very low	Weather	52
29. Isungua	89, 92, 97 (3)	Late	<i>Anser albifrons flavirostris</i>	Late	Late					Very low	Weather	53
30. Lake Myvatn	75–95 (21)	Normal Cold	<i>Anas penelope</i>							Very low	Weather	54

¹ For site locations see Figure 1.

² Timing of melt, temperature during the breeding season

³ For English names see Appendix 3.

⁴ Proportion of nests or broods lost to predation.

⁵ Sources: 1: Tombre et al., 1998; 2: I. Tombre, pers. comm. 1997; 3: J.O. Bustnes and K.E. Erikstad, pers. comm. 1997; 4: H.–U. Rösner, pers. comm. 1997; 5: Bowler et al., 1993; 6: Bowler et al., 1994; 7: Bowler et al., 1995; 8: J.M. Bowler, pers. comm. 1997; 9: J.H. Beekman, pers. comm. 1997; 10: Ryabitshev, 1995; 11: V.K. Ryabitshev, pers. comm. 1997; 12: B. Spaans and B.S. Ebbinge, pers. comm. 1997; 13: Mooij et al., 1995; 14: J.H. Mooij, pers. comm. 1997; 15: Tomkovich and Soloviev, 1996; 16: Soloviev and Tomkovich, 1997; 17: P.S. Tomkovich and M. Yu. Soloviev, pers. comm. 1997; 18: Korte et al., 1995; 19: Volkov et al., 1997; 20: J. de Korte and A. Volkov, pers. comm. 1997; 21: Underhill et al., 1993; 22: P. Prokosh, pers. comm. 1997; 23: A.V. Kondratyev, pers. comm. 1997; 24: Bousfield and Syroechkovskiy, 1985; 25: Baranyuk and Takekawa, 1998; 26: V.V. Baranyuk, pers. comm. 1998; 27: Lindberg et al., 1997; 28: Ely et al., 1993; 29: C.R. Ely, pers. comm. 1997; 30: Grand and Flint, 1997; 31: Bowman et al., 1997; 32: Lowe and Spindler, 1996; 33: M.A. Spindler, pers. comm. 1998; 34: TERA, 1993; 35: Johnson, 1993; 36: S.R. Johnson, pers. comm. 1997; 37: R.G. Bromley, pers. comm. 1998; 38: R.T. Alisauskas, pers. comm. 1998; 39: Nol et al., 1997; 40: J. Jehl Jr., pers. comm. 1999; 41: Ganter and Cooke, 1996; 42: F. Cooke, pers. comm. 1997; 43: B. Ganter, pers. obs.; 44: Robertson, 1995a; 45: Robertson, 1995b; 46: S.E. Walter, pers. comm. 1998; 47: S. Smith, pers. comm. 1992; 48: Gauthier and Lepage, 1992; 49: Lepage et al., 1996; 50: Gauthier et al., 1997; 51: J. Whitney, pers. comm. 1992; 52: J. Hughes and A. Reed, pers. comm. 1992; 53: Wright and Mitchell, 1993; 54: Gardarsson and Einarsson, 1997.

information on rodent numbers) and high numbers of predators. The predators were mainly arctic foxes, which were roaming widely; but nonbreeding, nomadic avian predators, namely snowy owls and skuas, were also reported to have occurred in large numbers in 1992 at Yamal (5), Pyasina Delta (6), and Pronchishcheva Lake (10). We received less information on numbers of rodents and predators from the Nearctic; apparently the striking uniformity of very high predator and very low rodent abundances reported from Russia was absent here. However, many foxes were reported from Howe Island (19) and Alexandra Fjord (27), and at the latter site there was also a lack of lemmings. Northeast Greenland also experienced a deep lemming depression and high abundance of predators (Sittler, 1995). A special effect was reported from Kent Peninsula (20) in Canada: an uncommonly high number of pomarine skuas was present at this site in 1992, presumably because of the cold weather in their usual breeding areas farther north. Because all skuas are aggressive, even against other skua species (Furness, 1987), the dominant pomarine skuas (Ryabitshev, 1995) kept the arctic skuas (usually numerous on the Kent Peninsula) out of the area. While arctic skuas are opportunistic predators and pose a threat to breeding waterbirds, the pomarine skuas are rodent specialists, and thus predation pressure on waterbirds was reduced at this site in 1992 (R.G. Bromley, pers. comm. 1998).

Breeding Data of Arctic Waterbirds in 1992

Information on overall breeding success as well as different breeding parameters in 1992 relative to other breeding seasons is listed in Table 1. Below, we summarize the information according to geographic patterns of overall breeding success, interspecific differences in overall breeding success, relative importance of weather and predation, and patterns in different breeding parameters. At Severnaya Zemlya (9) and Pronchishcheva Lake (10), the same research teams studied both waterfowl and waders. However, since the two groups of birds differed in success at both sites, waterfowl and wader results are treated as separate studies and depicted with separate symbols in Figures 3 and 4.

Of the 35 field studies included in this review, 16 reported very low breeding success of the study species in 1992 and an additional eight reported total breeding failure. In contrast, only four studies reported average breeding success and two studies high breeding success (Fig. 3). The remaining five studies reported only information on some breeding parameters; no information on overall breeding success was available. Breeding failures were reported from High and Low Arctic locations, both in the Palearctic and in the Nearctic regions. Three of the four study sites with

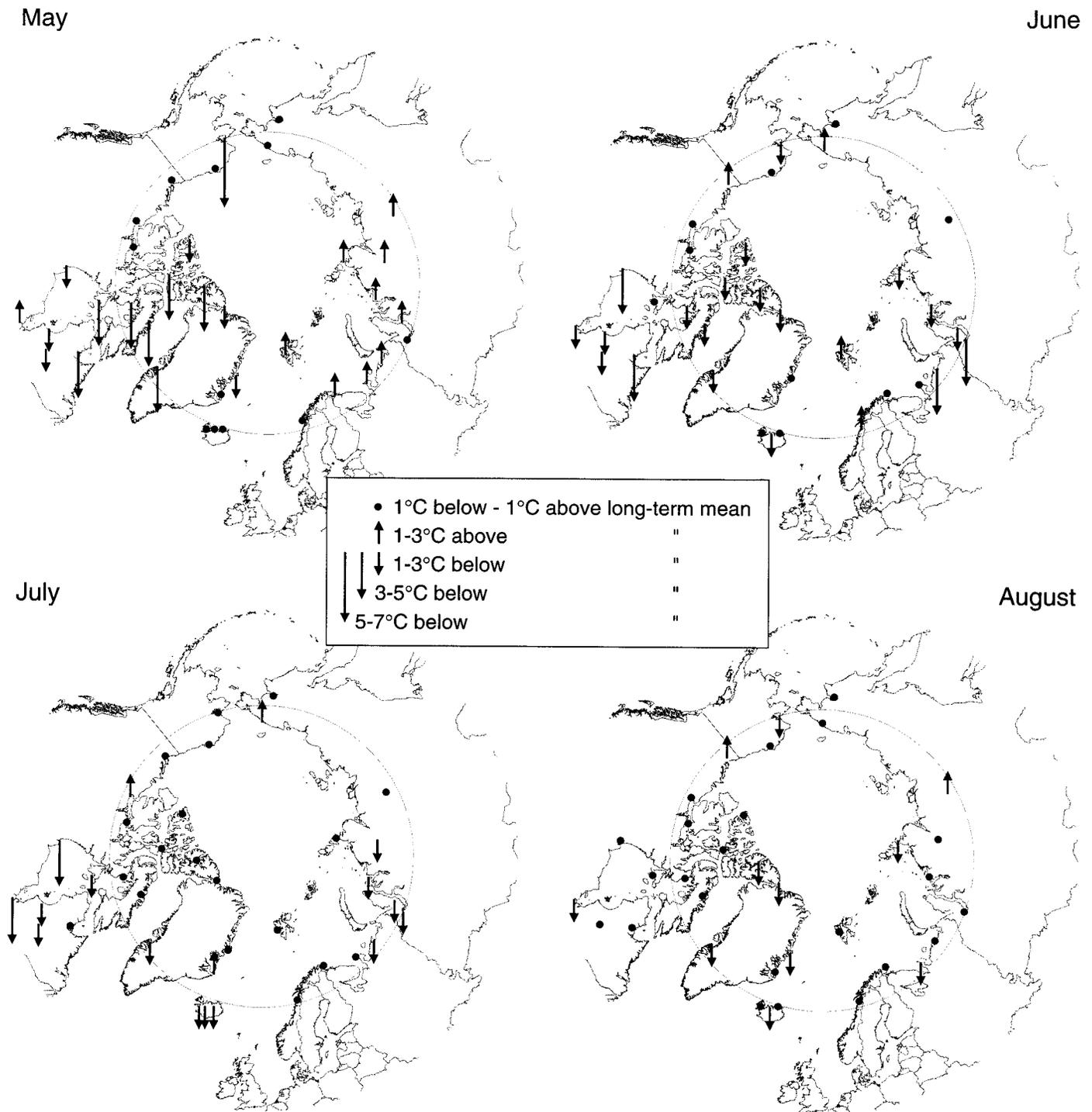


FIG. 2. Deviation of May-August 1992 monthly mean temperatures from long-term monthly means. For names of weather stations and availability of long-term standards, see Appendix 2.

average breeding success were located on Svalbard (1) and in northern Scandinavia (2, 3), where weather patterns did not deviate greatly from normal in the 1992 summer. The fourth site was on the High Arctic islands of Severnaya Zemlya (9) in central Siberia, where waders could achieve average breeding success despite low temperatures. High breeding success was reported from the Yukon-Kuskokwim Delta (15) in western Alaska, a site that is located rela-

tively far south, and from the Kent Peninsula (20) in the central Canadian Arctic. Six of the eight studies with total breeding failure were concentrated in the central Russian Arctic (sites 6 to 11); the other two were located in northern Alaska and on west Hudson Bay (sites 19 and 23).

The 30 studies for which data on overall breeding success are available included 14 species of waterfowl at 25 sites and 20 species of waders at 7 sites. Patterns of

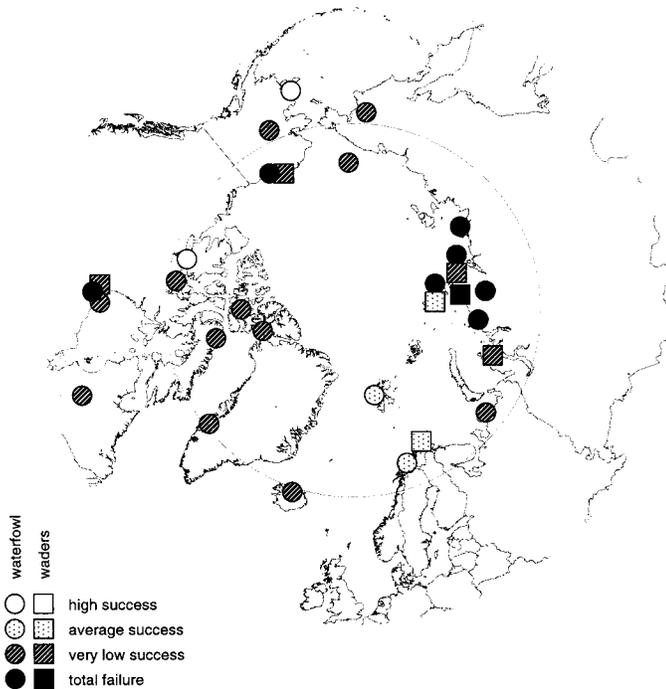


FIG. 3. Breeding success of arctic waterfowl and waders in 1992, as reported from field studies. One symbol may represent one or more species per field site.

success or failure were similar across species and species groups and seemed to be determined mainly by geographic location (Fig. 3). One exception was waders on Severnaya Zemlya, where purple sandpipers and sanderlings bred in average densities and with average success.

In 9 of the 24 studies that reported very low breeding success or total breeding failure, field researchers attributed the failure to unfavourable weather conditions. In five other studies, only predation was named as the source of breeding failure, and in the remaining ten cases, a combination of bad weather and high predation pressure was thought to have caused the breeding failure. In accordance with the high abundance of predators in the entire Russian Arctic in 1992, predation appears to have been more significant in the Palearctic than in the Nearctic (Fig. 3), whereas bad weather influenced breeding success in almost all parts of the Arctic (Fig. 3).

Breeding Parameters in 1992

Timing of Breeding: Where timing of nest initiation was reported, it was either late, very late, or the latest recorded for the duration of the studies, except at sites 1–4, 12, 13, and 18, where spring (in contrast with the majority of sites) was normal or early. Wrangel Island (13) was exceptional: timing of nest initiation was average despite a late spring. At Knipovich Bay (8), the late start of the breeding season prevented waders from laying replacement clutches when their first clutches were lost. Late nest initiation almost always followed late arrival of birds in the study area in the cases where both factors were

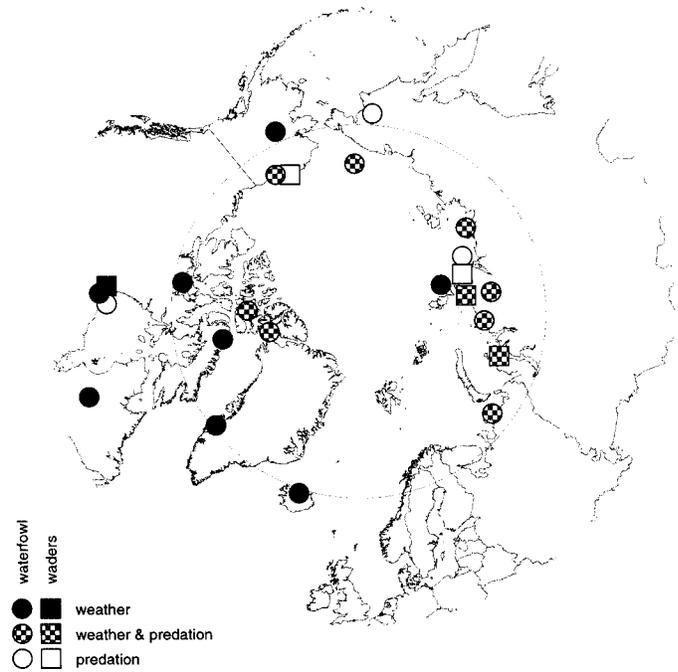


FIG. 4. Causes of breeding failure of arctic waterfowl and waders in 1992, as reported from field studies. One symbol may represent one or more species per field site.

recorded. The only exceptions were the Pyasina Delta (6) and Bylot Island (26), where geese arrived at the usual time but then delayed nest initiation.

Breeding Population: The size of the breeding population in the study areas was reported either as the number of breeding birds in a fixed area, as nest density, or as proportion of nonbreeders in the population. For most species and at most sites, breeding populations in 1992 were low, very low, or the lowest recorded during the studies. Exceptions were again sites 1–4 and 18, where spring was normal or early. Further exceptions were the waders at sites 9 and 10, which bred in average densities, white-fronted geese (but not emperor geese) at site 12, snow geese at site 13, geese (but not spectacled eiders) at sites 15 and 16, and Canada geese (but not white-fronted geese) at site 20. Thus many, but not all, species reacted to a delayed spring with an increased tendency to opt out of breeding (or to leave the area to breed elsewhere), and at some sites different species reacted in different ways. As far as we can tell from the studies included in this review, the breeding propensity of waders appears to be less affected by a late spring than that of waterfowl.

Clutch Size: Information on clutch size is available from only about half of the studies, and the picture is very heterogeneous (Table 1). From sites 1 to 4, which had an early or normal spring, average or high mean clutch sizes were reported; but at site 12, where spring was also early, mean clutch sizes in 1992 were the lowest ever recorded. Similarly, mean clutch sizes at sites with late springs ranged from the lowest ever recorded to very high. In waterfowl, low clutch sizes may occur in late springs

because females' body reserves are lower (Barry, 1962); on the other hand, increased clutch sizes may be attributable in part to increased rates of intraspecific nest parasitism (ISNP) in late years with a shortage of nest sites (Bousfield and Syroechkovskiy, 1985). Only very little information on nest parasitism reached us: in black-bellied brent geese in the Yukon-Kuskokwim Delta (14), high clutch sizes were not thought to be a result of ISNP; at Karrak Lake (21), ISNP and egg dumping (laying of eggs on the bare tundra outside nests) were high among geese; in common eiders at La Pérouse Bay (23), ISNP was lower than usual, which was attributed to the low nest density. In waders, mean clutch sizes usually show very little fluctuation: clutch size is fixed at three or four eggs, depending on the species. However, a remarkable reduction in clutch size was reported for semipalmated plovers at Churchill (22), where 25% of all females laid less than four eggs, and was attributed to the very cold and late spring. Overall low mean clutch sizes were also reported for the ten wader species at Pronchishcheva Lake (10); however, this result was considered to be an artifact because many nests were taken by predators before clutches were complete.

Hatching Success: Where hatching success was reported, it was low, very low, or the lowest recorded during the studies for most species and at most sites. Exceptions were common eiders at Tromsø (2), all species at sites 13 to 16, Canada geese at Koyukuk National Wildlife Refuge (17), and snow geese at Bylot Island (26). In those cases where rates of nest predation were reported, there was a direct relationship between predation and hatching success: sites with high predation had low hatching success, and vice versa. Only at La Pérouse Bay (23) and at Laforge I (28) was the hatching success of geese very low, though nest predation rates were average. At La Pérouse Bay (23), the rate of nest failure during incubation was the highest ever recorded during the 26-year study of snow geese, and most of the nest failures were due to abandonment by incubating females.

Hatching to Fledging: Only limited information is available on brood-rearing success of the studied species in 1992. The assessments of overall breeding success (or production of fledglings in the study areas) generally correspond to the previous breeding parameters (breeding population, clutch size and hatching success). At La Pérouse Bay (23), very high gosling mortality occurred during a snowstorm and cold weather just after hatch. At the sites with high abundance of predators and high nest predation rates, it is likely that predation rates on juvenile birds were also high.

Adult Body Condition and Mortality: Information on adult body condition is available only from a few sites. At Knipovich Bay (8), adult waders (knots, sanderlings, curlew sandpipers and little stints) were lighter during the 1992 pre-breeding period than in other years, which was attributed to the late and cold spring. At Howe Island (19), adult snow geese were in poor condition in spring, and this may have caused low clutch sizes. At Laforge I (28),

female Canada geese captured during late incubation were in poorer condition than in other years, and one female captured in two years weighed 2700 g in 1992 as opposed to 2930 g in 1993. Adult mortality during the breeding season is rarely observed directly. However, from Knipovich Bay (8) a high number of adult little stints were reported to be taken by arctic skuas; some mortality of adult snow geese was reported from Howe Island (19); and at La Pérouse Bay (23), several female snow geese were found dead and intact near their nests. Although the cause of mortality is not known, it appears likely that at least some of them died of starvation.

Observations of Nontarget Species: All nonsystematic observations on breeding data of species other than the main study species that were reported on the survey sheets referred to low numbers of breeding birds in 1992, or very poor breeding success, or both. The following observations were mentioned: very poor success and low numbers of long-tailed ducks and bean geese at Russkiy Zavorot (4); no nesting of white-fronted geese and king eiders and very low numbers of long-tailed ducks at Yamal (5); very low numbers of king eiders and long-tailed ducks at Malaya Logata (7); large numbers of nonbreeders or failed breeders of brent geese, long-tailed ducks, and bar-tailed godwits at Knipovich Bay (8); low numbers of nesting black-bellied brent geese and common eiders at Howe Island (19); very low nesting density of green-winged teal, black duck, common scoter, and surf scoter at Laforge I (28).

Unusual Movements of Birds

Several cases were reported of birds on reverse migration and of birds (target and nontarget species) that shifted their breeding area or appeared in unusual numbers at sites outside the usual range of the species. Reverse migration was reported for geese over the Kent Peninsula (20) in spring and for waders (predominantly turnstones, grey phalaropes and white-rumped sandpipers) over Churchill (22) in mid-June (J. Jehl, Jr., pers. comm. 1999). In Gamvik (3), uncommonly high numbers of little stints appeared, most of them breeding (Strann, 1996), and sightings of snowy owls and Steller's eiders were unusually common, possibly because bad weather prevented these birds from reaching their usual breeding areas in the Russian Arctic. At Knipovich Bay (8), many males of grey plover and knot (species in which males are more site-faithful than females) were unable to find mates because the less site-faithful females had preferred to go elsewhere. At Prudhoe Bay (18), many post-breeding western sandpipers, which are rare in other years, appeared in the study area. At Churchill, La Pérouse Bay, and Cape Churchill (22–24), thousands of grey phalaropes, which are usually only passing migrants en route to breeding areas farther north, spent large parts of the summer (but did not breed). Pectoral sandpipers occurred and attempted to breed in the Churchill area, a phenomenon observed only in years with extremely severe weather and poor breeding

conditions farther north in the Arctic (J. Jehl Jr., pers. comm. 1997). On Bylot Island (26), very few snow geese nested in the usual area of the main colony, whereas a large concentration of nests was found in a different valley about 30 km distant.

Overall Breeding Success of Arctic Waterfowl and Wader Populations in 1992

Monitoring of breeding success of some Arctic-breeding goose populations by field counts of juvenile proportions in autumn and winter goes as far back as the 1940s (Lynch and Singleton, 1964); however, regular data collection for many populations only started much later. We have therefore confined our compilation of data to the period 1980–97, for which annual data on productivity are available for 22 populations, with very few gaps (Table 2). Nearly all regions of the Arctic are represented by these populations, which include 10 not covered by our breeding area survey. Years of low success for these 22 populations, and the rank of 1992 in terms of breeding success among the 18 years, are shown in Table 2. For 19 of the populations (86%), 1992 was among the five years with lowest breeding success during the 1980–97 period, and for 9 populations (47%), it was the year of lowest productivity. The three populations with better breeding success in 1992 were Russian barnacle geese, black-bellied brent geese, and Tule white-fronted geese, the latter two breeding in Alaska. For most populations where data both from our breeding ground survey and from staging/wintering ground surveys are available, there is concordance between the two concerning the overall breeding output. Exceptions are barnacle geese from Svalbard (1) and greater white-fronted geese from the Yukon-Kuskokwim Delta (15) and Kent Peninsula (20): for these populations, average or high success was reported from breeding ground studies, whereas overall success was low. No other year was as globally unsuccessful as 1992; the second worst was 1986, when 14 out of 22 populations (64%) had low success (Table 2).

For Arctic-breeding waders, data from staging and wintering grounds on population-wide breeding success are scarcer than for geese, and methods of determining breeding success are more varied, but some long-term data sets do exist. For 10 populations (belonging to eight species) of waders with breeding areas between eastern Canada and eastern Russia/Alaska, breeding success in 1992 ranked low among the years studied (Table 3). These populations include dunlins breeding in northern Scandinavia/Russia and sanderlings breeding in Russia; for both of these, single breeding ground studies had reported average success.

DISCUSSION

There can be no doubt that, from a circumpolar perspective, 1992 was a poor breeding season for Arctic-nesting waterfowl and waders. In contrast to other years, when

breeding success differs among regions of the Arctic, the poor reproductive performance of Arctic waterbirds in 1992 was unusually uniform. Low breeding success was largely a consequence of below-normal spring and summer temperatures prevailing throughout most of the Arctic, which were in turn caused by aerosols emitted during the Mount Pinatubo eruption in 1991 (Jones and Kelly, 1996). The effect of this unfavourable circumpolar weather pattern was exacerbated by high predation pressure in large parts of the Palearctic and some areas of the Nearctic.

Exceptional Nature of the 1992 Breeding Season

How exceptional was 1992 in terms of weather, predation, and breeding success of Arctic waterbirds? Cool Arctic summers have occurred before: 1978 and 1986, for instance, showed widespread cooling (although unrelated to volcanic eruptions) throughout the Arctic (Jones and Mörth, 1978; Jones, 1986). Volcanic eruptions, although infrequent in the magnitude of the 1991 Pinatubo explosion, have certainly also occurred before. Bradley (1988) lists eight major eruptions (of a sufficient strength to inject large amounts of material into the stratosphere) between 1851 and 1981, although detailed information on subsequent temperatures in Arctic waterbird breeding areas is not available to us. Monthly mean temperatures, which we used as the main indicator of weather patterns, are good indicators of overall general conditions during the Arctic summer, but they do not convey the full picture of weather events that may be relevant to the breeding biology of birds (Skinner et al., 1998). Thus, although preceding summers (1978, 1986) may have been on average as cool as 1992, other factors, such as depth of snow at the beginning of spring or frequency and timing of spring and summer snowstorms, may have made the 1992 season even less favourable.

Predation pressure, according to Tomkovich (1994), was unusual in 1992 in that it was uniformly high across a very wide area. The co-occurrence of bad weather and low rodent/high predator levels in the Palearctic may have been coincidental: rodents follow more or less regular cycles that are generally thought to be independent of summer weather (Stenseth and Ims, 1993). However, it is possible that weather influences the cycle to some extent by contributing to a particularly high or low year. Whether such an interaction between weather and rodent cycles took place in 1992 is unknown to us, but cannot be entirely ruled out. In the absence of detailed investigations on the impact of weather on small rodent populations in that particular year, a causal relationship between the two remains speculative.

Looking at the circumpolar reproductive success of Arctic waterbirds, 1992 appears to have been an exceptionally poor year. While a number of researchers returned our survey sheet with the remark that “1992 was bad, but 19xx was just as bad/even worse,” the alternative years mentioned were by no means the same across the sites

TABLE 2. Years of low breeding success (determined from counts of the proportion of juveniles in autumn or winter flocks) for 22 Arctic-breeding goose populations during the period 1980–97.

Species/Subspecies	Breeding area ²	Years with low breeding success ¹																		rank ³	Source
		80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97		
Pink-footed Goose	Svalbard	•																		1	Madsen et al., 1998
Barnacle Goose	Svalbard	•	•										•							2	Madsen et al., 1998
Light-bellied Brent Goose	Svalbard	•	•	•																5	Madsen et al., 1998
Tundra Bean Goose	Russian Arctic W-C																		×	2	van den Bergh, 1999
European White-fronted Goose	Russian Arctic W-C																		×	1	Mooij et al., 1999
Barnacle Goose	Russian Arctic W																		×	7*	Ganter et al., 1999
Dark-bellied Brent Goose	Russian Arctic C																		×	1*	Ebbinge et al., 1999
Lesser Snow Goose	Russian Arctic E (Wrangel I.)																			3	Walter, 1993, 1998
Black-bellied Brent Goose	Russian Arctic E to Canadian Arctic C																			6	Walter, 1993, 1998
Greater White-fronted Goose	Alaska S-W																			2	Walter, 1993, 1998
Tule White-fronted Goose	Alaska S-C																			2	Walter, 1993, 1998
Greater White-fronted Goose	Alaska C-N to Canadian Arctic C																			10*	Walter, 1993, 1998
Ross's Goose	Canadian Arctic C																			1	Walter, 1993, 1998
Lesser Snow Goose	Canadian Arctic W																			2	Walter, 1993, 1998
Lesser Snow Goose	Canadian Arctic C, Hudson Bay																			4	Walter, 1993, 1998
Light-bellied Brent Goose	Canadian Arctic E																			1	Walter, 1993, 1998
Greater Snow Goose	Canadian Arctic E																			1	Walter, 1993, 1998
Light-bellied Brent Goose	Canadian High Arctic E																			2	Walter, 1993, 1998
Greenland White-fronted Goose	Greenland W																			5	Merne et al., 1999
Barnacle Goose	Greenland E																			1	Fox et al., 1999
Pink-footed Goose	Iceland, Greenland E																			1	Ogilvie et al., 1999
Greylag Goose	Iceland																			1	Mitchell et al., 1999
																				1	Mitchell & Sigfusson, 1999
N populations with low success		3	6	5	3	4	5	14	5	2	9	6	2	19	0	9	10	4	4		
N populations with data available		22	22	22	21	21	22	22	22	22	22	22	22	22	22	21	21	19	15		
% populations with low success		14	27	23	14	19	24	64	23	9	41	27	9	86	0	43	48	21	27		

¹ For each population, the five years with lowest proportions of juveniles during the 1980–97 period are marked with a •; • denote the year of lowest success of period. X = no data.

² Breeding areas sorted by longitude, moving east from the Greenwich meridian. N = north, E = east, S = south, W = west, C = central.

³ Rank of 1992 breeding success in period 1980–97: ranks from 1 (lowest success of period) to 18 (highest success of period). Tied ranks are marked with an asterisk.

studied, but varied widely. The exceptional homogeneity of poor success in 1992 is also supported by the long-term data on overall breeding success of Arctic-nesting geese (Table 2), which show that while there were other unfavourable years, no other single year had reproductive failures in as many populations as 1992. Our survey of field studies showed that there were some exceptions to the general pattern, and some waterbird species at some sites had average or high breeding success. In many cases, however, these local results were in contrast to low overall breeding success of the populations studied (Tables 2 and 3). In these instances, small-scale patterns of predation pressure or climate may have led to local conditions that were not representative of the overall breeding range of the populations.

Weather or Predation?

In the areas where unfavourable weather conditions and high predation pressure coincided in 1992 (as in most of the Russian Arctic except the Far East), the relative role of the two factors is difficult to assess. When asked whether reduced breeding success was caused mainly by weather or by predation, most field researchers in those areas answered “both”; only at one site, Pronchishcheva Lake on the Taymyr Peninsula, was predation clearly held responsible for breeding failure (Fig. 4). Because both factors were very unfavourable at many sites, it could be argued that each factor alone would have been sufficient to greatly reduce reproductive output in 1992. Indeed, at Anadyr Gulf, one of the few sites with favourable weather, predation alone was sufficient to prevent geese from breeding successfully. And on Severnaya Zemlya, where predators were scarce, weather alone

TABLE 3. Results of multiple-year staging and wintering ground studies of breeding success of Arctic-nesting wader populations.

Species	Breeding area ¹	Years between	Range of values	1992 value	1992 rank ²	Method / Source ³
Dunlin	Scandinavia N/Russian Arctic W-C	91–97	4.4 – 23.8	9.7	2 (7)	1
		72–92	6 – 100	7	2 (21)	2
Bar-tailed godwit	Scandinavia N/Russian Arctic W-C	91–96	0.1 – 31.2	0.1	1 (6)	1
Little stint	Scandinavia N/Russian Arctic W-C	72–92	3 – 100	4	3 (21)	2
Grey plover	Russian Arctic W-C	90–97	3.4 – 63.9	3.4	1 (8)	1
Knot	Russian Arctic C	72–92	1 – 100	4	5 (21)	2
Curlew sandpiper	Russian Arctic C	91–97	11.7 – 74.8	11.7	1 (6)	1
		72–92	0 – 100	1	6 (21)	2
Sanderling	Russian Arctic C	72–92	7 – 100	13	2 (21)	2
Curlew sandpiper	Russian Arctic C-E	78–97	0.1 – 44.0	0.1	1 (20)	3
Red-necked stint	Russian Arctic C-E / NW Alaska			3.9*		3
Knot	Canadian Arctic NE / Greenland N	91–95	2.5 – 23.4	2.5	1 (4)	1

¹ Breeding areas sorted by longitude, moving east from the Greenwich meridian. N = north, E = east, S = south, W = west, C = central.

² Rank of 1992 breeding success: ranks from 1 (lowest success during study) to n (highest success during study). In parentheses: n (number of years with data).

³ Method of determining breeding success:

1: proportion of juveniles determined by field counts during staging in the Schleswig-Holstein Wadden Sea, Germany (H.-U. Rösner and K. Günther, pers. comm. 1998).

2: index of number of juveniles observed on passage on Helgoland, North Sea; maximum value = 100. 1992 values are approximated from figures. After Dierschke (1994).

3: proportion of juveniles in mass catches in Victoria, SE Australia (C.D.T. Minton, pers. comm. 1999).

* Data from other years not available, but breeding success very poor in 1992 (C.D.T. Minton pers. comm. 1999).

prevented brent geese from breeding. Interactions between weather and predation occurred as well. These included changes favourable to geese in the predator community at the Kent Peninsula and the occurrence of persistent ice bridges, facilitating predator access to breeding islands (a phenomenon previously reported by, e.g., Madsen et al., 1989, 1992). For wader species, which are usually able to lay replacement clutches, the delayed onset of the 1992 breeding season meant that after predation of the first clutch, not enough time remained to start a second breeding attempt (P.S. Tomkovich and M.Yu. Soloviev, pers. comm. 1997). This was a further example of weather and predation interacting.

Breeding Parameters Affected by Weather

Looking more closely at the breeding parameters that were negatively affected by weather in 1992, we find that negative effects on every single parameter were reported. The two most important effects, however, were reduced numbers (or densities) of breeding pairs and delayed clutch initiation dates. Observations of reverse migration of Arctic-breeding birds in spring may be seen as further indication of birds opting out of breeding early, although some of them may have subsequently returned north for late breeding attempts. Unfavourable weather is the most likely cause of widespread nonbreeding and delayed clutch initiation; however, nonbreeding can also be caused by the mere presence of large numbers of predators (Spaans et al., 1998). Certainly nonbreeding and delayed breeding were widespread in the Nearctic, where predation pressure was not unusually high in 1992. Late breeding is generally

associated with lower breeding success, and in the Arctic this association is particularly pronounced because of the short summer and early end to the breeding season. For breeding parameters other than breeding densities and nest initiation dates, not quite as many data are available. Clutch sizes, although depressed for some species at some sites, showed no uniform pattern in relation to unfavourable weather in 1992. Hatching and fledging success tended to be low, although this may have been primarily a function of predation; however, reduced hatching success due to weather was also reported (high nest abandonment rates by geese in poor condition in La Pérouse Bay). Adult mortality does not appear to have been particularly prevalent during the 1992 breeding season. Some cases were reported, however, and in view of the general scarcity of such observations, this by itself seems noteworthy.

A few populations of birds seem to have responded to unfavourable weather by shifting their breeding range in 1992; this was especially true for species with low breeding-site fidelity, such as little stints. However, in most cases where large numbers of birds were observed out of their usual ranges during the breeding season, they did not breed. This indicates that a simple shift of breeding range in response to poor weather is not an option for most Arctic-breeding waterbird populations.

Global Implications of Breeding Failure in 1992

A year of nearly circumpolar breeding failure of Arctic waterfowl and waders must have had an effect on global population sizes of these birds. However, as Sargeant and Raveling (1992:412) point out, “sporadic, severe oscillations

in reproductive success of Arctic-nesting waterfowl are common natural occurrences that, in the main, have only temporary effects on populations.” Indeed, there are examples of 1992 creating a short-term “dip” in population numbers without changing the overall trend. This was the case for winter indices of some waders in Britain (Cranswick et al., 1997), population numbers of dunlin on the East-Atlantic Flyway (Rösner, 1997), and population indices of some North American geese (Abraham and Jefferies, 1997). Even though the 1992 summer probably had no long-term effect on population sizes, the mere fact that a single climatic event can cause such a dramatic temporary reduction in breeding success around the Arctic should remind us of the great sensitivity of Arctic waterbirds to climatic fluctuations. In view of global climate change, a number of recent publications have dealt with the influence of climatic fluctuations on ecological processes, particularly the annual timing of reproduction (e.g., Crick et al., 1997; Forchhammer et al., 1998). In the present study, some uncertainties remain concerning the relative contribution of weather and predation to breeding failure in parts of the Arctic in 1992. Nevertheless, our investigation of the indirect effect of a tropical volcanic eruption on Arctic waterbird reproduction is another case study that can contribute to this growing body of literature. We show that a global climate signal affected primarily breeding densities and timing of reproduction of Arctic waterfowl and waders, but that all other breeding parameters were affected as well.

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Appendix 1. Location of field sites reported on in this study.

Site Number	Site Name	Country	Latitude	Longitude	Nearest Weather Station
1	Ny Ålesund	Norway	78°55' N	12°15' E	Svalbard
2	Tromsø (Grindøya)	Norway	69°49' N	18°50' E	Bodø
3	Gamvik	Norway	71°05' N	28°25' E	Vardø
4	Russkiy Zavorot	Russia	68°30' N	53°50' E	Naryan Mar
5	Yamal	Russia	71°04' N	72°20' E	Dikson/Mys Kammenyi
6	Pyasina-Delta, Taymyr	Russia	74°07' N	86°50' E	Dikson
7	Malaya Logata, Taymyr	Russia	73°24' N	98°30' E	Dikson/Khatanga/Chelyuskin
8	Knipovich Bay, Taymyr	Russia	76°04' N	98°32' E	Chelyuskin
9	Severnaya Zemlya	Russia	79°00' N	102°00' E	Chelyuskin
10	Pronchishcheva Lake, Taymyr	Russia	75°16' N	112°28' E	Chelyuskin
11	Lena-Delta	Russia	73°30' N	124°00' E	Olenek
12	Anadyr Gulf	Russia	64°10' N	178°15' E	Anadyr
13	Wrangel Island	Russia	71°10' N	180°00' E	Mys Schmidta
14	Yukon-Kuskokwim Delta (Tutakoke)	U.S.A.	61°15' N	165°35' W	-
15	Yukon-Kuskokwim Delta (Kashunuk River)	U.S.A.	61°30' N	165°30' W	-
16	Yukon-Kuskokwim Delta	U.S.A.	61°00' N	165°40' W	-
17	Koyukuk National Wildlife Refuge	U.S.A.	65°50' N	156°30' W	Barrow/Kotzebue
18	Prudhoe Bay	U.S.A.	70°00' N	148°30' W	Barrow
19	Howe Island	U.S.A.	70°00' N	148°00' W	Barrow
20	Kent Peninsula	Canada	68°22' N	108°04' W	Cambridge Bay
21	Karrak Lake	Canada	67°14' N	100°15' W	Cambridge Bay
22	Churchill	Canada	58°45' N	95°04' W	Churchill
23	La Pérouse Bay	Canada	58°43' N	94°27' W	Churchill
24	Cape Churchill	Canada	58°44' N	93°49' W	Churchill
25	Cardigan Strait	Canada	76°38' N	90°40' W	Eureka
26	Bylot Island	Canada	73°08' N	80°00' W	Clyde
27	Alexandra Fjord	Canada	78°55' N	75°30' W	Eureka
28	Laforge I, N Quebec	Canada	54°00' N	72°00' W	La Grande IV
29	Isungua, W Greenland	Greenland	67°00' N	50°30' W	Egedesminde
30	Lake Myvatn	Iceland	65°35' N	17°00' W	Akureyri

Appendix 2. Location of circumpolar weather stations used in this study.

Station name	Country	Latitude	Longitude	Standard			
				May	June	July	August ¹
Bodø	Norway	67°18' N	14°24' E	B	B	B	B
Longyearbyen, Svalbard	Norway	78°18' N	15°30' E	A	A	A	A
Vardø	Norway	70°24' N	31°06' E	B	B	B	B
Kanin Nos	Russia	68°42' N	43°18' E	B	B	B	B
Naryan Mar	Russia	67°42' N	53°00' E	B	C	B	B
Salekhard	Russia	66°30' N	66°30' E	B	B	B	B
Mys Kammenyi	Russia	68°30' N	73°42' E	C	C	C	C
Ostrov Dikson	Russia	73°30' N	80°24' E	B	B	B	B
Khatanga	Russia	72°00' N	102°30' E	B	C	B	B
Mys Chelyuskin	Russia	77°42' N	104°18' E	B	B	C	C
Olenek	Russia	68°30' N	112°24' E	C	C	B	C
Anadyr	Russia	64°48' N	177°48' E	C	B	C	B
Mys Schmidta	Russia	68°54' N	179°30' E	B	C	B	B
Kotzebue	U.S.A.	66°54' N	162°36' W	B	B	B	B
Barrow	U.S.A.	71°24' N	156°18' W	B	B	B	B
Inuvik	Canada	68°18' N	133°30' W	A	A	A	A
Mould Bay	Canada	76°18' N	119°30' W	C	C	B	C
Coppermine	Canada	67°48' N	115°12' W	A	B	A	C
Cambridge Bay	Canada	69°06' N	105°00' W	A	A	A	A
Churchill	Canada	58°45' N	95°04' W	A	A	A	A
Resolute	Canada	74°42' N	94°54' W	A	A	A	A
Eureka	Canada	80°00' N	85°54' W	A	A	A	A
Coral Harbour	Canada	64°12' N	83°24' W	A	A	A	A
Hall Beach	Canada	68°47' N	81°13' W	A	A	A	A
Moosonee	Canada	51°18' N	80°48' W	A	A	A	A
Kuujuarapik	Canada	55°18' N	76°48' W	A	A	A	A
La Grande IV	Canada	54°00' N	76°00' W	C	C	C	C
Kuujuuaq	Canada	58°48' N	69°30' W	A	A	A	A
Clyde	Canada	70°30' N	68°36' W	A	A	A	A
Alert	Canada	82°30' N	63°12' W	A	B	B	B
Egedesminde	Greenland	68°42' N	52°54' W	B	B	B	B
Stykkisholmur	Iceland	65°00' N	22°42' W	A	A	A	A
Kap Tobin	Greenland	70°30' N	22°00' W	B	C	B	B
Hveravellir	Iceland	65°30' N	19°30' W	B	B	B	B
Danmarkshavn	Greenland	76°48' N	18°48' W	B	B	B	B
Akureyri	Iceland	65°42' N	18°06' W	A	A	A	A

¹ Long-term standard for monthly temperature means. A: 1961–90, B: 1986–95, C: shorter run of data 1986–95.

Appendix 3. Latin and English/North American names of bird taxa mentioned in the text and in Table 1.

Latin Name	English/North American Name	Latin Name	English/North American Name
<i>Cygnus columbianus bewickii</i>	Bewick's Swan	<i>Somateria fischeri</i>	Spectacled Eider
<i>Anser fabalis rossicus</i>	Tundra Bean Goose	<i>Polysticta stelleri</i>	Steller's Eider
<i>Anser brachyrhynchus</i>	Pink-footed Goose	<i>Clangula hyemalis</i>	Long-tailed Duck/Oldsquaw
<i>Anser albifrons albifrons</i>	(European) White-fronted Goose	<i>Melanitta nigra</i>	Common Scoter/Black Scoter
<i>Anser a. frontalis</i>	(Greater) White-fronted Goose	<i>Melanitta perspicillata</i>	Surf Scoter
<i>Anser a. gambeli</i>	Tule White-fronted Goose	<i>Pluvialis squatarola</i>	Grey Plover/Black-bellied Plover
<i>Anser a. flavirostris</i>	Greenland White-fronted Goose	<i>Charadrius semipalmatus</i>	Semipalmated Plover
<i>Anser anser</i>	Greylag Goose	<i>Limosa lapponica</i>	Bar-tailed Godwit
<i>Anser caerulescens caerulescens</i>	Lesser Snow Goose	<i>Arenaria interpres</i>	(Ruddy) Turnstone
<i>Anser c. atlantica</i>	Greater Snow Goose	<i>Phalaropus fulicaria</i>	Grey Phalarope/Red Phalarope
<i>Anser rossii</i>	Ross's Goose	<i>Calidris canutus</i>	(Red) Knot
<i>Anser canagicus</i>	Emperor Goose	<i>Calidris alba</i>	Sanderling
<i>Branta canadensis interior</i>	Interior Canada Goose	<i>Calidris minuta</i>	Little Stint
<i>Branta c. hutchinsii</i>	Richardson's Canada Goose	<i>Calidris mauri</i>	Western Sandpiper
<i>Branta c. minima</i>	Cackling Canada Goose	<i>Calidris ruficollis</i>	Red-necked Stint/Rufous-necked Stint
<i>Branta leucopsis</i>	Barnacle Goose	<i>Calidris fuscicollis</i>	White-rumped Sandpiper
<i>Branta bernicla bernicla</i>	Dark-bellied Brent Goose	<i>Calidris maritima</i>	Purple Sandpiper
<i>Branta b. nigricans</i>	Black-bellied Brent Goose/Black Brant	<i>Calidris alpina</i>	Dunlin
<i>Branta b. hrota</i>	Light-bellied Brent Goose/Atlantic Brant	<i>Calidris ferruginea</i>	Curlew Sandpiper
<i>Branta ruficollis</i>	Red-breasted Goose	<i>Calidris melanotos</i>	Pectoral Sandpiper
<i>Anas rubripes</i>	Black Duck	<i>Stercorarius pomarinus</i>	Pomarine Skua/Pomarine Jaeger
<i>Anas penelope</i>	(European) Wigeon	<i>Stercorarius parasiticus</i>	Arctic Skua/Parasitic Jaeger
<i>Anas crecca</i>	(Green-winged) Teal	<i>Stercorarius longicaudus</i>	Long-tailed Skua/Long-tailed Jaeger
<i>Somateria mollissima</i>	Common Eider	<i>Nyctea scandiaca</i>	Snowy Owl
<i>Somateria spectabilis</i>	King Eider		