

Kurt K. Burnham with William A. Burnham, Ian Newton,
Jeff A. Johnson and Andrew G. Gosler

The History and Range Expansion of Peregrine Falcons in the Thule Area, Northwest Greenland



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Abstract

Peregrine Falcons, *Falco peregrinus tundrius*, were historically unknown to Inuit and early explorers in the Pituffik (Thule) area, northwest Greenland (75.90–77.60° N). Here we provide information collected from 1993–2005 on what we believe is a recently established and expanding population of High Arctic nesting Peregrines in the area associated with climate change. From 1979 to 2005, the average of the mean monthly temperature, minimum monthly temperature, and maximum monthly temperature for the five-month period, May through September, increased 1.1, 0.5, and 1.6 °C, respectively. Forty-one breeding attempts were recorded at six sites from 1993 to 2005 for this new population. Satellite transmitters were used to determine the home ranges and seasonal movements of female Peregrines, with adults traveling an average of 10,794 km at a rate of 205 km/day on outward migration. During outward migration, the maximum distance traveled by any female on one day was 1,349 km with the maximum total outward and return migrations for single individuals 12,438 and 11,071 km, respectively, to and from South America. Comparisons with Peregrine populations in Greenland at 67° N and 60.5° N, approximately 1,100 (Kangerlussuaq) and 1,700 (South Greenland) km south of the Pituffik area, respectively, show differences in various aspects of ecology. Based on a lack of both morphological and genetic differences it appears the Pituffik area population is likely a result of the extension of more southern breeding Peregrines moving north and taking advantage of an ameliorating climate and lengthened breeding window. Should climatic amelioration continue, the species may eventually expand its range into the very northernmost land area, Peary Land.

Key Words: peregrine falcon, Greenland, satellite telemetry, migration, High Arctic, climate change, range expansion, Argos accuracy

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Introduction

Climate change

Changes in global climate are occurring at an alarming rate (Comiso & Parkinson 2004, Arctic Climate Impact Assessment 2004, Hansen *et al.* 2006, Richter-Menge *et al.* 2006, IPCC 2007), and over the past 10–20 years, climate change has emerged as one of the greatest purported worldwide threats to ecological communities, with the extinction of large numbers of species a possible result (Root *et al.* 2003, Thomas *et al.* 2004, Bellard *et al.* 2012). Throughout the world, species from most major taxa have been impacted by climate change (reviews in McCarty 2001, Walther *et al.* 2002, Parmesan & Galbraith 2004, Parmesan 2006, Chen *et al.* 2011), and recent extinctions both at the species and population levels have been attributed to climate change (Pounds & Crump 1994, Pounds *et al.* 1999, McLaughlin *et al.* 2002, Thomas *et al.* 2006).

The most significant and most rapid climatic changes have been documented throughout the Arctic (Overpeck *et al.* 1997, 2005, Serreze *et al.* 2000, Arctic Climate Impact Assessment 2004). Warming temperatures have caused both reduction in the extent (Stroeve *et al.* 2005) and thickness of sea ice (Rothrock *et al.* 2003), significant melting of the Greenland Ice Sheet (Chen *et al.* 2006), and reductions of snow cover in many areas (Serreze *et al.* 2000, Hanna *et al.* 2001). These changes have been associated with warmer and milder winters and springs throughout the Arctic and with warmer and longer summers (Mountain *et al.* 2001, Chapin *et al.* 2005, Schaefer *et al.* 2005).

The effects of weather and climate on bird populations have been well documented and discussed (Lack 1954, 1966, Newton 1998, 2003a, Møller *et al.* 2010). As a result of anthropogenically accelerated climate change, these effects have been significantly intensified, with an unprecedented number of bird species affected (for reviews see Møller *et al.* 2004, Wormworth & Mallon 2006). The effects of climate change on bird species have most frequently focused on changes in the timing of migration and breeding, breeding performance, population size and distribution, and the action of natural selection (see Crick 2004 for a review of each topic). Of the above-mentioned, changes in spring arrival, egg-laying (Crick *et al.* 1997, Dunn & Winkler 1999, Both *et al.* 2004) and geographical distribution are perhaps most common, in association with both altitudinal (Pounds *et al.* 1999,

2005) and latitudinal climatic shifts (Gibbons & Wotton 1996, Thomas & Lennon 1999, Hitch & Leburg 2006).

In the Arctic, the effect of climate change on bird species has been less studied. In the Canadian Arctic, the timing of breeding of Brünnich's Guillemots *Uria lomvia* at the southern (Coats Island, 62° N) and northern (Prince Leopold Island, 72° N) limit of their range has been found to be positively correlated with summer ice cover, with egg laying by the Coats Island population having advanced since 1981 simultaneously with a local decrease in summer ice (Gaston *et al.* 2005). No change was detected in laying dates or summer sea ice cover at Prince Leopold Island (Gaston *et al.* 2005). Documentations of a climate-related northern range expansion of bird species currently breeding in the Arctic are sparse or non-existent, with much of the available data based on future predictions and modeling (Huntley *et al.* 2006).

Peregrine Falcons

Peregrine Falcons *Falco Peregrinus* occur on every continent except Antarctica (Cade 1982). Beginning in the 1950s and continuing into the 1960s, their populations throughout Europe and North America crashed as a result of the use of organochlorine pesticides, notably DDT and dieldrin, with some local populations becoming extinct (for reviews see Cade 1982, Ratcliffe 1993, Cade & Burnham 2003). Following restrictions on the use and the ultimate ban of these organochlorines in most countries, Peregrine populations in both continents began to increase, partially as a result of large-scale captive propagation and release of individuals into the wild (Ratcliffe 1993, Cade & Burnham 2003). In association with massive reintroduction projects in both Europe and North America, large amounts of data were collected on both captive and wild Peregrines, making the Peregrine one of the best-studied raptor species in the world (e.g., Hickey 1969, Cade *et al.* 1988, Ratcliffe 1993).

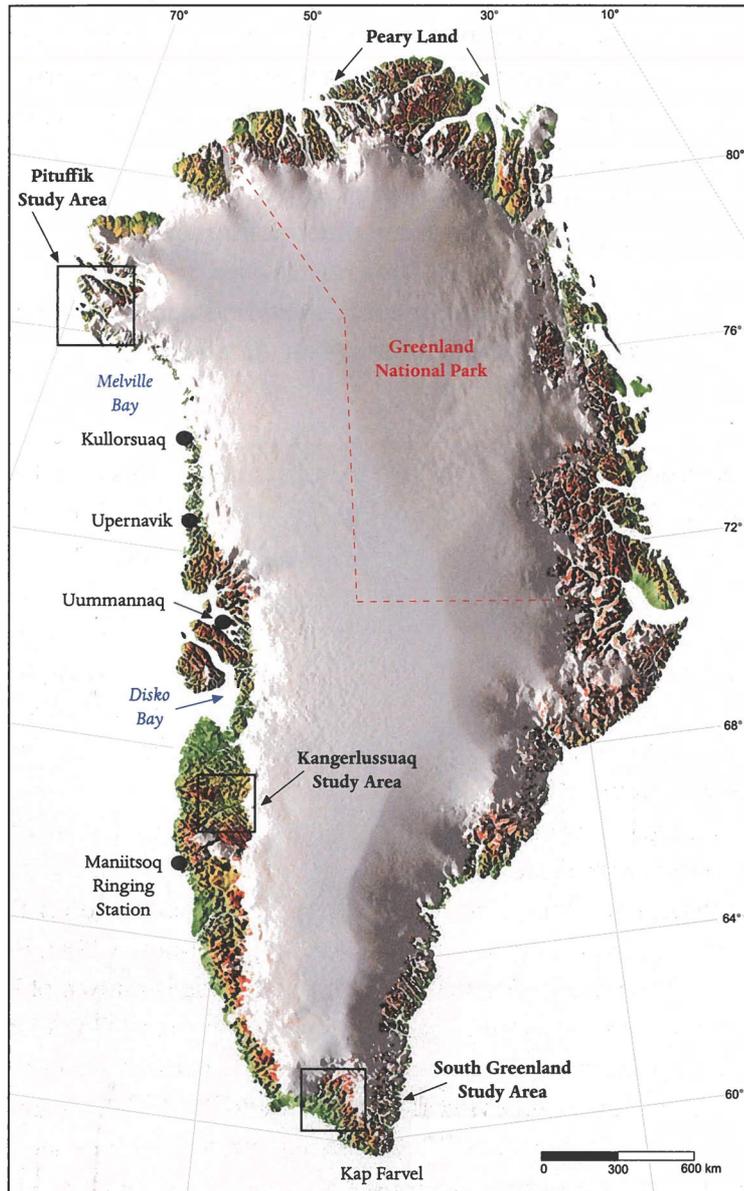
Peregrines breed throughout much of the Arctic, but do not breed in Iceland and islands north of the Aleutian chain (Cade 1982). With this wide geographic distribution, many long-term studies have been conducted on Peregrines breeding in the Low Arctic (e.g., Cade 1960, Burnham & Mattox 1984, Bromley 1988, Bromley & Matthews 1988, Franke *et al.* 2010), but little is known of Peregrines breeding in the High Arctic as they are far less common there. Greenland provides an opportunity to examine arctic nesting Peregrine Falcons along a geographical gradient extending from approximately 60.32° N to 77.59° N, a distance of ~2,123 km (Fig. 1). Over that latitudinal range, Peregrine populations are subjected to different ecological, environmental, climatic, and evolutionary pressures. Some influences

are short term and may vary somewhat over years and decades (e.g., prey density and weather), while others (e.g., prey species, nest sites, and longitudinal climate differences) remain roughly constant for centuries and millennia.

We examine how these populations have responded to short- and long-term pressures by emphasizing new information collected on a recently discovered High Arctic Peregrine population in the Pituffik area of northwest Greenland, existing long-term information and new data collected on Peregrines to the south

Figure 1

Map of Greenland showing study areas and pertinent place names. Base map from National Survey and Cadastre, Denmark.



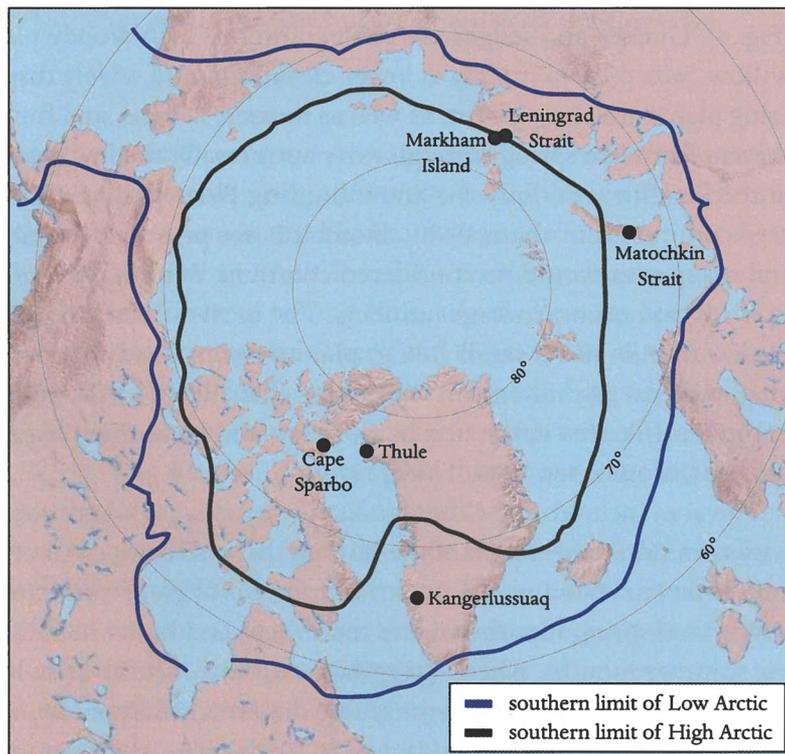
in the Kangerlussuaq area in central-west Greenland, and previously collected information on Peregrines in southern Greenland (Fig. 1). Data are compared and contrasted between populations, and the effect of climate change on the Pituffik area population is discussed.

From 1972 to 1997, under the leadership of W. Mattox, the first in-depth study of Peregrines in Greenland (Burnham & Mattox 1984) was accomplished in a large ice-free land mass centered around Søndre Strømfjord Air Base, now re-named Kangerlussuaq, 67.02° N, 50.71° W (Fig. 1). That study was continued by K. Burnham and W. Burnham through to 2005, with 178 sites where territorial Peregrines were documented. In 1981, surveys and data collection began on Peregrines in the most southwestern part of Greenland, 60.32 – 61.00° N (Fig. 1, Falk & Møller 1988). K. Burnham and W. Burnham collected data on Peregrine Falcons in the High Arctic centered around Pituffik (Thule Air Base), northwest Greenland, 75.90 – 77.60° N from 1993 to 2005 (Fig. 1).

Study areas

The Arctic has commonly been classified into different regions or zones, such as Tundra, Rock Desert, and Ice Desert (Porsild 1951) or Low, Mid, and High Arctic (Polunin 1951), leading to confusion amongst researchers and the frequent misuse of terms, such as Low and High Arctic. Of the various classifications, Bliss's (1975, 1979, Bliss *et al.* 1973) division into Low and High Arctic, based on temperature, flora, and fauna, is perhaps the most widely used in biology. The Low Arctic is defined as having a mean July temperature in the range of 8 to 11 °C with the High Arctic starting in areas with mean July temperatures in the area of 4–6 °C, with more temperate areas to the south frequently referred to as Subarctic (Fig. 2, Bliss *et al.* 1973). The temperature gap between areas (7 °C) is a transitional region, where descriptions based on plants, herbivore species, and other characteristics (as described by Bliss 1975, 1979, Bliss *et al.* 1973) are further used to describe and

Figure 2
Boundary lines of the Low and High Arctic as defined by a mean July temperature of 8–11 °C and 4–6 °C, respectively (Bliss 1979). Map modified and based on map from Bliss (1979). Dots show locations of most northern known breeding populations of Peregrine Falcons and the Kangerlussuaq study area.



identify the area. Throughout this monograph the use of the terms Low and High Arctic are based on these definitions.

The Pituffik area is considered High Arctic and is known for its severe weather and harsh environment. Snowfall and strong winds (>160 km/h) may occur in any month. Between 1951 and 1986 at 76.5 m elevation (76.50° N, 68.70° W), mean monthly temperatures were -18° in April, -6° in May, 2° in June, 5° in July, 4° in August, and -2° in September (centigrade; Thule Air Base Weather Service 1994). Temperature noticeably decreases, snow accumulates, and wind velocity increases with even 50 m increase in elevation. Typically, snowfall that occurs after mid-August does not melt at elevations above 300 m. Near Pituffik, pack ice usually breaks up in June or July and the ocean freezes over again by mid-October. Glaciers calving along the coast during summer months create large numbers of icebergs. Even under the best weather conditions, ambient temperatures are cool, and unattended eggs or small young birds could easily die.

The limited ice-free land consists of rolling hills and valleys with streams emanating from the Greenland Ice Sheet or smaller glaciers. The ice margin lies up to 26 km from the sea but reaches the sea in some locations (Fig. 3). Most cliffs are adjacent to fjords, bays, or glaciers and have extensive talus slopes below (Fig. 4). Ice-free land usually occurs below 600 m. Higher elevations are frequently ice covered. Vegetation is sparse and prostrate, typically no higher than ten centimeters (Fig. 4). Grasses and sedges are most common, with woody plant species such as willow *Salix* present mainly at lower elevations, and widely dispersed. Some flowering plants are also present, as well as mosses, lichens, and fungi. Bird species are present from late spring through early autumn. Of the few small passerine species in the Pituffik area, only the Snow Bunting *Plectrophenax nivalis* could be considered common (Burnham 1996). Shorebirds are present, albeit in limited numbers, and no species would be considered common. Sea cliffs support gulls and other seabirds, sometimes in large numbers. The most numerous of all bird species is the Little Auk *Alle alle*, a small (160 g) planktivorous alcid that breeds in the Pituffik area, with ca. 33 million pairs (Egevang *et al.* 2003). Little Auks arrive at colonies in the Pituffik area in the first half of May, and leave them before the start of September (Salomonsen 1950, Thing 1976).

The area includes five Greenlandic towns/villages where subsistence hunting is very common, with much of the human diet still comprised of marine mammals and birds harvested in the area. Hunting takes place year round, by dogsled in winter and spring months and by motorboat and kayak in summer months. During summer months, when Peregrines are in the Pituffik area, hunters spend large amounts of time hunting throughout the area. Additionally, travel between the five local towns/villages commonly occurs by boat in the summer, with the coast-

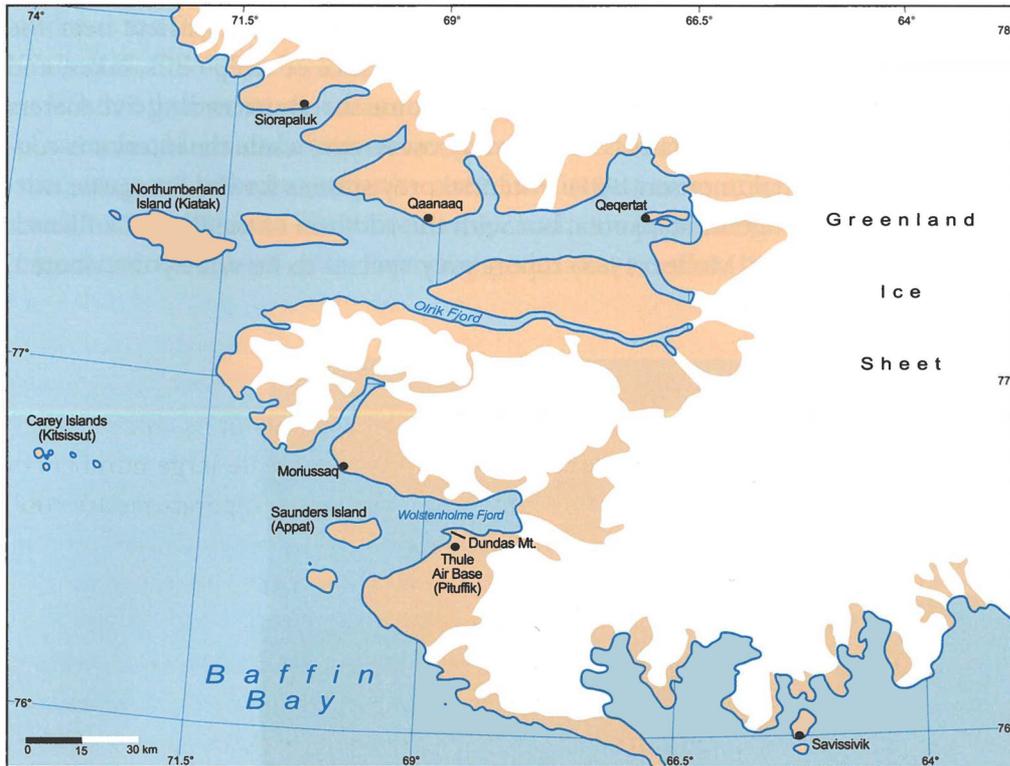


Figure 3 Map of the Thule study area in the Avanersuaq District, northwest Greenland.

line usually providing the most direct route of travel. For these reasons the native Pituffik people have an excellent knowledge of the local wildlife (see Berthelsen *et al.* (1993) for additional information on the Thule culture).

Approximately 1,170 km to the south of Pituffik, the Kangerlussuaq area is a large Low Arctic ice-free land area of rolling hills, which contains hundreds of lakes and valleys and is divided by Søndre Strømfjord (Figs. 1, 2 & 4). Glacial outflow rivers traverse the area. As in North Greenland, sedges and grasses dominate the tundra vegetation but grow more densely and higher, with willow growing up to two meters tall (Fig. 4). The weather is more stable than in the Pituffik area and warmer during the spring and summer months. Small passerines occur in abundance during the summer months and form the primary prey base for breeding Peregrines (Restani & Mattox 2000). Rock Ptarmigan *Lagopus mutus* are also present and utilized by Peregrines along with shorebirds and waterfowl. For further description of this study area see Burnham & Mattox (1984).

South Greenland, with approximately 650 km separating the northern boundary of the study area and the southern boundary of the Kangerlussuaq study area,

is mountainous with long fjords, some of which terminate at glaciers near the Greenland Ice Sheet (Fig. 1). The area has an abundance of steep cliffs, lakes, and marshes. Grasses and shrubs cover the ground, some shrubs exceeding five meters tall. Along the coast the climate is considered Low Arctic, while the interior is considered Subarctic (Salomonsen 1981). Potential prey species for the Peregrine mirror those in the Kangerlussuaq area, but with the addition of the Black Guillemot *Cepphus grylle*. Falk & Møller (1988) report prey species to be widely distributed,



and that the Peregrine feeds almost exclusively on passerines and Rock Ptarmigan (Falk *et al.* 1986). For further details of this study area see Falk *et al.* (1986).

While all three study areas are along the west coast of Greenland, the amount of open land between them varies greatly. The South Greenland and Kangerlussuaq areas are linked together by one of the largest areas of ice-free land in Greenland, with Peregrines likely occurring continuously between the two areas both on coastal and inland cliffs. From Kangerlussuaq north to Pituffik, the amount of



Figure 4
Representative photographs of the Kangerlussuaq (opposite page) and Pituffik study areas and photos showing variation in typical tundra vegetation between areas.

ice-free land decreases, with Peregrines only nesting on coastal cliffs starting in the Disko Bay area and with the density decreasing northwards. In 2000, during an 18-day bird survey of the Uummannaq area (just north of Disko Bay, see Fig. 1), which is primarily made up of a very large system of fjords, over 2,900 km of coastline were surveyed by boat and an additional 350 km by helicopter, with only one territorial pair of Peregrines found and an additional adult observed flying at another location (Burnham *et al.* 2005). North of the Uummannaq area the amount of ice-free land and coastal cliffs decreases further, with Melville Bay, between Kullorsuaq and the Pituffik area, providing an approximate 300 km barrier of coastal cliffs and ocean-calving glaciers. While no one has surveyed the area, it is likely that no Peregrines breed in the Melville Bay area, and probably occur in extremely limited numbers to the south between Upernavik and Kullorsuaq.

For additional information on the flora and fauna of Greenland see Fredskild (1973) and Salomonsen (1982), respectively, and Born & Böcher (2001) for a review of the ecology.

Methods

Survey, capture, and breeding biology

While working out of Thule Air Base, from 1993 to 2005, researchers interviewed Greenlandic and Danish workers with local knowledge and experience traveling throughout the Pituffik area. Interviewees were asked about observations of both Gyrfalcons *Falco rusticolus* and Peregrine Falcons. Additionally, during the summer of 1998, researchers visited the largest local Greenlandic community, Qaanaaq, for five days and using a local Greenlandic interpreter, who spoke Greenlandic, Danish, and English, interviewed as many local hunters and families as possible. Both while at Thule Air Base and in Qaanaaq, photographs of both falcon species were also shown during interviews and maps were provided so those being interviewed could show locations where falcons were observed.

When local hunters were encountered in the field and an interpreter was not present interviews were conducted using a combination of gesturing and photos (e.g., holding up a pair of binoculars to our eyes, showing close up photographs of Peregrine Falcons and Gyrfalcons, and then showing a map of the area).

Falcon surveys were carried out from mid-July to early September from 1993 to 2005 along the coast and off-shore islands of Pituffik, with approximately 984 linear km of coastline and islands surveyed between 75.90° N, 66.50° W and 77.60° N, 71.17° W. Although the entire area was not traveled every year, almost all locations were visited multiple times over the 13 years. An attempt was made to search all reported locations for territorial falcons every year in addition to other likely unreported locations. Nest sites were frequently only visited once each year and because of this it was not possible to use the Mayfield (1961) method to calculate daily nest survival probability, as has been done for other raptor studies (e.g., Barber *et al.* 1998, Griffin *et al.* 1998).

Initial surveys were conducted using a small aircraft to overfly the area to identify possible falcon nesting locations. Boats (motorized and kayak) and helicopters were used to observe cliffs and to gain access to areas more inland for walking surveys. When Peregrines were encountered, observations were made to determine whether they were breeding, territorial, behaviorally attached to a cliff or area but not defensive, or just using a cliff as a perch for hunting or resting. If birds were breeding, nests were rappelled or climbed into, prey remains collected,

physical nest and cliff features recorded, and young ringed and bled. Whenever weather conditions allowed, nests with breeding Peregrines were visited more than once per season to record brood sizes. However, remote locations and inclement weather frequently precluded follow-up visits. Whenever possible, breeding adult Peregrines were captured, measured, ringed and bled, and satellite-received transmitters (platform transmitter terminals, PTTs) were placed on adult females (the males being considered too small to carry PTTs). Peregrines were ringed with a standard Danish numbered lock-on ring on one leg and an alpha-numeric ring (ACRAFT, Edmonton, Canada) on the other.

In the Kangerlussuaq area, only known Peregrine nest sites were visited, except for new sites discovered incidentally while surveying for breeding Gyrfalcons. Although data were routinely collected on reproduction at Peregrine nest sites, emphasis was placed on obtaining blood samples from nestlings and adults and obtaining morphometric measurements and attaching PTTs (for adults). Blood samples were used for DNA analyses and sexing.

All falcons were captured and released unharmed. Various capture methods were used depending upon the time of year and physical situation, most of which are described in Meredith (1961), Webster & Beebe (1964), and Bub (1978).

Nest site characteristics

Ten measurements were collected from active Peregrine breeding sites when possible. Measurements were taken as described by Falk *et al.* (1986) and Wightman & Fuller (2005) for the South Greenland and Kangerlussuaq area, respectively. All degrees were corrected to True North and circular data were analyzed as described by Zar (2004) and by Fisher (1996). Any given nest may be represented more than once if occupied in multiple years (Falk *et al.* 1986).

Morphometrics

For fully-feathered Peregrines, measurements of beak length, tarsus length, tail length, wing cord, and mass were taken as described by Baldwin *et al.* (1931) and Gosler (2004). Nineteen adult Peregrines (12 females and seven males) were captured from 15 June 2001 to 3 September 2004 in the Kangerlussuaq area, and nine adults (females) in the Pituffik area from 25 July 2001 to 25 September 2004. If individuals had food in their crops, the volume was estimated as 0.25, 0.5, 0.75, or full. Sex of adults, juveniles, and nestlings was determined in the field and later confirmed using genetic methods (Ito *et al.* 2003).

For individuals with partial or full crops, masses were adjusted according to

observations made on captive Peregrine Falcons at The Peregrine Fund's World Center for Birds of Prey in Boise, Idaho. According to C. Sandfort (pers. comm.), who has overseen the captive production of more than two thousand Peregrines, captive adult female Peregrines on an unlimited food supply of Japanese Quail *Coturnix japonica* eat on average 1.25 per day while adult males eat 0.75. Typically the adults feed once daily until they have a full crop; all parts of the quail are eaten except for a portion of the feathers. To estimate weight added by food in the crop and stomach of wild Peregrines, we used a quail mass of 128 g, the mean of 26 individuals examined prior to being fed to captive Peregrines. Using this figure, adult female and male Peregrines in captivity consumed approximately 161 and 97 g of food each day, respectively. These numbers were divided according to estimated crop size (e.g., 0.5 crop for female = 80.5 g) of individual wild-caught Peregrines and subtracted from the total body mass.

To test for morphological differences between Peregrines caught in different areas, a principal components analysis (PCA) was used (Rising & Somers 1989, Bollmer *et al.* 2003). PCA provides a more accurate and better overall way to analyze body size than testing individual measurements alone, combining multiple measurements together to identify one or more measurements that when combined give the best possible description of "true" body size (Rising & Somers 1989, Freeman & Jackson 1990). Components with eigenvalues greater than one were used, and males and females were analyzed separately to avoid differences due to sexual size dimorphism, with males weighing approximately 33% less than females (White 1968). Mass among adult females varied over 34% from the lowest to highest (compared to an average of 14% of the mean for the other four variables) and was not included in the PCA. Two PCAs were conducted: an analysis on adult females from the Kangerlussuaq and Pituffik areas, and adult males from the Kangerlussuaq area. For the analysis on females, sub-adults (falcons more than one year old molting into "blue" adult plumage) were included with adults. For females, t-tests were run between the means of individuals from the Kangerlussuaq and Pituffik areas for PC1 to test for a significant difference between the two populations. Linear regression was used to test the significance of PC1 as a predictor of mass. MINITAB Version 14 was used for all analyses.

Genetics

Tissue collection and DNA extractions

Blood samples were collected from all Peregrine Falcons captured or ringed in the nest in the Pituffik and Kangerlussuaq areas from 2001 to 2005 to test for genetic differences between study areas. Additionally, an autumn capture and ringing station was established for migrant falcons in 2002 near the town of Maniitsoq (Fig. 1), southwest of Kangerlussuaq, and Peregrines captured there were analyzed separately. A total of 47 unrelated blood samples were collected from the three areas, Kangerlussuaq ($n = 27$), Pituffik ($n = 15$), and Maniitsoq ($n = 5$).

From each bird, between 0.1 and 0.3 cc of blood was collected from the brachial vein and preserved in lysis buffer (Tris, NaCl, EDTA, and SDS). If nests were clearly occupied and it was not possible to capture adults and/or reach the nest to ring/bleed young, molted feather samples were collected. Feathers from previous years were easily identified by bleaching from the sun and wear and distinguished from current year feathers. In both study areas, only one individual from each nest site per year was used; unrelated individuals sampled from the same nest site from different years were distinguished by unique mitochondrial haplotypes. Related individuals are defined as either siblings, including young from the same pair in different years, or parents and offspring, as it is impossible to trace more distant relationships. DNA was extracted from both blood and feather tissues using a DNeasy Tissue Extraction Kit (QIAGEN Inc.) and diluted to approximately 50 ng/mL prior to PCR.

Genotyping, sequencing, and statistical analysis

Eight microsatellite loci originally developed for Peregrine Falcons (Fp13, Fp31, Fp54, Fp79-4, Fp82-2, Fp89, Fp92-1, and Fp107; Nesje *et al.* 2000) were used for the microsatellite analyses. All microsatellite loci were dinucleotide repeats, and locus Fp107 had an imperfect core repeat. For the mitochondrial DNA (mtDNA) analyses, 1,540 base pairs (bp) of continuous sequence consisting of 397 bp of cytochrome b (cytb) and tRNAt_{thr} and 1,143 bp of the 5' end of the control region was obtained using primers 14532L/15646H and 15573L/16090H (Johnson *et al.* 2007). Microsatellite and mtDNA PCR amplifications were performed as described by Johnson *et al.* (2007), and resolved on an ABI 3730 automated sequencer (Applied Biosystems). All mtDNA sequences were aligned using SEQUENCHER™ 4.2.2, and verified for accuracy.

Microsatellite genotypes were tested for linkage equilibrium and departure from the Hardy–Weinberg equilibrium within each population at each locus using the computer program GDA (Lewis & Zaykin 2001). Sequential Bonferroni correc-

tions were applied to correct for multiple simultaneous comparisons (Rice 1989). Mean number of alleles per locus (allelic diversity) and mean heterozygosity were also calculated using GDA. Measures of allelic richness were included to control for differences in the number of alleles among sampling locations that differ in sample size (Leberg 2002) and were calculated using the program FSTAT v. 2.9.3.2 (Goudet 1995). To investigate differences between populations in mean number of alleles, allelic richness, and observed heterozygosity, a Wilcoxon signed rank test for each population pair was conducted. Mitochondrial DNA control region diversity was investigated by comparing population estimates of haplotype diversity (h), nucleotide diversity (π), and Tajima's D using the program DNAsp v. 4.00 (Rozas *et al.* 2003).

To investigate population genetic structure with both microsatellite and mitochondrial DNA among sampling locations, pairwise F_{ST} values were calculated following Weir & Cockerham (1984), as implemented in Arlequin v. 2.0 (Schneider *et al.* 2000). Differences in population structure between sampling locations were tested using permutations (10,000) among populations with Fisher's exact test. Spatial genetic structure was also investigated, using the Bayesian method of Pritchard *et al.* (2000) and Falush *et al.* (2003), implemented in the program STRUCTURE v. 2.0. This method identifies genetically distinct clusters (K) based on allele frequencies across loci. The most likely value of K is assessed by comparing the likelihood of the data for different values of K . Calculations were conducted with a burn-in period of 100,000, followed by 500,000 iterations. Each simulation was performed four times using an ancestry model incorporating admixture, individual alphas for each population, and a model of correlated allele frequencies that did not include prior information on population origin (see Falush *et al.* 2003). To better comprehend the genetic relationships among sampling locations, the relationships between mtDNA haplotypes were visualized with a minimum spanning cladogram, or parsimony network, estimated using the program TCS v. 1.17 (Clement *et al.* 2000) that provides the 95% parsimoniously plausible branch connections between haplotypes.

Satellite-received telemetry

Transmitters

Between 2001 and 2003, 18 satellite-received transmitters (PTTs; Microwave Telemetry Inc., Columbia, MD, USA, and North Star Science and Technology, LLC, Baltimore, MD, USA) were placed on female Peregrines in the Kangerlussuaq and Pituffik areas (Table 1). Units weighed between 18 and 30 g and were solar- or

battery-powered and attached as backpacks using Teflon ribbon (Fuller *et al.* 1995). Duty cycles were programmed to transmit according to the power source and battery life (Table 1). GPS locations were taken at all nest sites or capture locations where birds were tagged. From each PTT, information was recorded on location, temperature, battery voltage, and activity. Location data were used for tracking falcons, while temperature, battery voltage, and activity sensor data were used to determine whether the PTT was functioning correctly. See Table 1 for summary information for each PTT.

Table 1.

Year	Region	ID numbers	No. of PTTs	Manufacturer	Duty cycle (on/off)	Weight	Power source
2001	Pituffik	10212, 10217, 10292	3	NS	daily (24h)	20 g	solar
	Kanger.	10219	1	NS	daily (24h)	20 g	solar
2002	Pituffik	35234, 35240	2	MT	10 h/24 h	18 g	solar
	Pituffik	35255, 36321	2	MT	5 h/38 h	30 g	battery
	Kanger.	35235–37	3	MT	10 h/24 h	18 g	solar
2003	Pituffik	36014–17	4	MT	7 h/106 h	20 g	battery
	Kanger.	32948, 35238, 41437–38	4	MT	4 h/61 h	20 g	battery

MT = Microwave Telemetry; NS = North Star

Information on satellite transmitters placed on Peregrine Falcons from 2001 to 2003 in the Kangerlussuaq and Pituffik areas, Greenland, and a single stationary PTT (36321) deployed at Thule Air Base.

Of the 18 females tagged, six adults, two sub-adults, and two juveniles were marked in the Pituffik area, while in the Kangerlussuaq area seven adults and one juvenile were marked. Nine adults began migration with functioning PTTs (six from the Pituffik area and three from the Kangerlussuaq area) along with a single juvenile from the Pituffik area. The fate of the other eight females with tags is unknown. However, in some cases PTTs continued to function well into winter near locations where birds were tagged, with sensors on the PTT (movement and temperature) indicating the unit was clearly not on a live bird and that the PTT had either fallen off the falcon or the bird had died with the unit attached. In other cases the units clearly failed as no signals were received shortly after attachment yet adult females were found present, with units still attached, in future years at

the nest where they were initially captured and tagged. PTTs weighed less than 3% of the body weight of Peregrines tagged. Individual Peregrines are identified by their five-digit Argos PTT ID numbers.

Falcon movements were tracked using the Argos satellite system which provides locations and accuracy estimates, called location class (LC) 3, 2, 1, 0, A, B, and Z. LC 3, 2, 1, and 0 are claimed to provide accuracy estimates of ≤ 150 m, ≤ 350 m, ≤ 1 km, and >1 km of the actual location, respectively (Service Argos, Inc.). Further location classes A, B, and Z are considered less reliable, but may be accurate to within <1 km. For LC Z, Argos commonly does not calculate a location estimate. For additional information on the Argos system and accuracy see <http://www.argosinc.com/>, Keating *et al.* (1991), Britten *et al.* (1999), and Hays *et al.* (2001).

To calculate the home range areas and routes of migration, it is important to understand the inherent level of inaccuracy of PTT-derived data. Although Argos estimates locations for LC 3–1 using location classes with an associated distance or error of accuracy, this error is commonly under-reported (Britten *et al.* 1999). Variation can be caused by many factors, e.g., environmental conditions, altitude, PTT power, and position of the tracked animal (Walton *et al.* 2001, Liaubet & Malarde 2003). In some studies, location classes ranging from 0 to B are used (White & Sjoberg 2002) in order to provide sufficient data on which to base home range estimates, because there are often only limited numbers of locations in LC 3–1 (Britten *et al.* 1999, Austin *et al.* 2003). Researchers may use filters based on a combination of distance, time, and LC to validate the use of locations with LC 0–B (Vincent *et al.* 2002, Austin *et al.* 2003). Despite filtering, using locations with coarser location classes, specifically A and B, may artificially inflate home range size. Such positions, if used, may be appropriate for descriptions of migratory movement over long distances and time intervals, but not for home range estimation (Britten *et al.* 1999, Green *et al.* 2002).

To test the accuracy of Argos location estimates, a single stationary battery-powered PTT (36321) was placed on top of a prominent building at Thule Air Base, Greenland. The unit operated for the entire life of the battery (approximately 14 months). PTT 36321 was randomly selected from units intended for falcons and was mounted on a large brick with the unit facing up. Periodically the PTT was checked for snow cover, etc., and several times during the winter it was covered by <5 cm of snow. Accuracy results from this PTT can be found in Appendix A.

Statistical analysis

The start of outward migration was defined as when Peregrines began continuous movement in the general direction of wintering areas (Berthold 2001). Migration

distances were measured as Great Circle Distances (GCD). The total length of routes taken by Peregrines was calculated by summing the lengths of the individual flight segments along the migration route, beginning at the location of the nest, capture site, or pre-migration area, depending upon individual birds. The starting points for flight segments were chosen by taking the location with the highest quality location class, LC 3–0, from each duty cycle/transmission period (Fuller *et al.* 1998). If multiple locations with the same LC were available, the first to occur in the transmission cycle was used (Fuller *et al.* 1998). The overall speed of outward and return migration was determined by dividing the total of the segment lengths by the number of days on migration, providing an average speed of km/day. A range of distances traveled per day, from minimum to maximum, was calculated by using lengths of segments from locations on successive days. When flight segments included more than one day, the total distance of the segment was divided by the number of days encompassed in the segment and the mean value was used for those respective days. For all ranges of distances traveled, individual Peregrines may have traveled distances both farther than the maximum estimated range and shorter than the minimum estimated range, but without locations from each individual day this variability remained unknown.

The start of return migration was defined as when Peregrines began continuous movement in the direction of the breeding home range (Berthold 2001). Arrival and departure dates from the wintering area were determined by using the median date of the last and first location, respectively, >75 km from the harmonic mean of the wintering territory. All locations used to calculate migration were visually inspected in ArcView GIS (Environmental Systems Research Institute, Redlands, CA, USA) to verify accuracy based on other locations from the same day (Fuller *et al.* 1998).

Disagreement exists on methods to use when calculating breeding and winter home range area for large and mobile mammals and birds (for discussion see Seaman *et al.* 1999, Kenward 2001, Blundell *et al.* 2001, Kenward *et al.* 2001). We calculated breeding and winter range sizes in multiple ways to allow direct comparisons with published data on Peregrines and for a more informative estimate of range size. Range area was calculated as 90% minimum convex polygons (MCP) (McGrady *et al.* 2002, McGrady *et al.* 2003, Ganusevich *et al.* 2004) and fixed 95% and 50% kernels (Reynolds 2004). For 90% MCP, area was calculated using locations with both LC 3–0 and LC 3–1, and will from now on be referred to as 90% MCP LC 3–0 and 90% MCP LC 3–1. The 90% levels were used to reduce potential effects of using LC 1 and 0. The 95% and 50% fixed kernel areas are presented twice, first calculated using locations with LC 3–0 and second with LC 3–1, from now on referred to as 95% kernel LC 3–0, 95% kernel LC 3–1, 50% kernel LC 3–0,

and 50% kernel LC 3–1. For kernel range estimates, least square cross validation was applied (Seaman *et al.* 1999, Reynolds 2004).

At nest sites, size of falcon breeding home ranges included all points obtained from PTT attachment, usually from the middle of incubation through early young rearing, until departure for an outward pre-migration home range or for outward migration (McGrady *et al.* 2003, Ganusevich *et al.* 2004). In some instances, units operated and collected data but failed shortly before the falcon would have likely departed on outward migration. In these cases, if more than 30 locations with LC 3–0 had been received and over 25 days had lapsed from placement of unit on the falcon to failure, a breeding home range was calculated and has been included. In all cases where this occurred, the minimum 25-day period fell within the period when nestlings were within 10 days of fledging, the time of maximum activity and movement by adult female Peregrines (Ratcliffe 1993). When adult falcons left the breeding territory and did not begin outward migration but instead set up a home range more than 40 km from the nest, these areas were called pre-migration home ranges. Winter home range size was calculated from all the appropriate points received between arrival and departure from the wintering area, from which a harmonic mean was calculated. Calculations of area were done using a Lambert equal-area azimuthal projection of the globe (Ganusevich *et al.* 2004). Data from units that continued to function were excluded if patterns of locations, “body” temperature, or activity suggested that the bird had died or the unit had become detached.

For analysis of migration, home range area, and PTT performance, ArcView GIS and Spatial Analyst, and the Animal Movement Extension designed for it by Hooge & Eichenlaub (2000) were used. Argos data were imported into ArcView using the Argos-Tools extension designed for ArcView by E. Potapov & M. Dubinin. Locations with LC 3–0 were used to calculate distance, area, and mapping of travel paths. MINITAB and JMP were used for statistical analyses.

Climatic trends

Data collection

Previously unpublished weather data were obtained from Thule Air Base, Greenland, from a 27-year period spanning 1979–2005. Mean monthly temperatures, minimum monthly temperatures, and maximum monthly temperatures (all °C) from the months May through September, months when Peregrines have been shown to be in the Pituffik area (see results of PTT work below), were used for analysis. Data for September 1988 were not available.

Statistical analysis

Simple linear regression was used to analyze the mean monthly temperature, minimum monthly temperature, and maximum monthly temperature for each individual month, May through September, and for the five-month period averaged together. All data were tested for auto-correlation using Durban-Watson and data were normally distributed. To avoid type-1 error, Holm's Sequential Bonferoni corrections were used with p values, with analyzes being grouped together as mean monthly temperatures, minimum monthly temperatures, and maximum monthly temperatures.

Results

Surveys and breeding biology

Local hunters

From 1993 to 2005 we spoke with local Greenlanders and Danes within the Pituffik area that were subsistence hunters and/or had intimate knowledge of the area. When shown photographs of Gyrfalcons, individuals knew exactly what they were and could commonly point out multiple locations on a map where nests existed. However, when shown photographs of Peregrines, individuals were adamant they did not occur in the Pituffik area. Further, it appears that the Greenlandic and Danish words for Peregrine Falcon, *kiinaaleeraq* and *vandrefalk*, respectively, are not known in the Pituffik area.

While confusion could exist between species it seems highly unlikely, with over 99% ($n = >200$) of observed Gyrfalcons in the Pituffik area being white (Burnham 2008). Furthermore, reported Gyrfalcon nest sites were later checked and in almost all cases were either found to be occupied by Gyrfalcons or old nests were observed.

Literature review

Reports of Peregrine Falcons are extremely rare throughout the literature on the exploration of northwest Greenland. Reinhardt (1861), Salomonsen (1943), and Vaughan (1988) give perhaps the best reviews of literature on the birdlife of northwest Greenland. While we believe that almost all material in English was reviewed thoroughly, some information exists in Danish which we attempted to review as best as we could.

One of the first detailed accounts of birds in Greenland was presented by Sabine (1819), who visited the Pituffik area with John Ross in 1818. During this expedition one juvenile Peregrine was shot and three others were seen while at sea, at approximately 66° N, 58° W, off the coast of the Kangerlussuaq area. However, Peregrines were not reported farther north during the expedition. Walker (1860), on the ship "Fox" from 1857–59, visited the southern Pituffik area but made no mention of Peregrines in northwest Greenland, although he did mention seeing them in other areas much farther south. Later, in 1860, on board the schooner

“United States,” Hayes (1867) frequently wrote about collecting animals and birds in northwest Greenland, but made no mention of either Peregrine or Gyrfalcons. From 1871 to 1873, Davis (1876) regularly mentioned bird species seen and shot in the Pituffik area by individuals aboard the “Polaris,” but not Peregrines; however, “hawks” were referred to several times which were most likely Gyrfalcons. From the Peary expeditions of 1891 through 1896 no reference is made to Peregrine Falcons, either seen or shot, despite the expeditions spending several summers in northwest Greenland (Stone 1892, 1895, Chapman 1899, Gibson 1922). In his book *Etah and Beyond*, MacMillan (1927) included mention of Gyrfalcons, Snowy Owls *Nyctea scandiaca*, and “Gray Sea Eagles” *Haliaeetus albicilla* seen in northwest Greenland during the Crocker Land Expedition of 1914–17, however, again no mention was made of Peregrines. Rasmussen (1921), in the appendix on the “Flora and Fauna on the North Coast of Greenland on Dr. Wulff’s notes,” made no reference of Peregrines, despite commenting on Snowy Owls and mentioning that “Icelandic” falcons were not seen. At the Thule Station near Dundas Mountain, Freuchen (1921), who was the station manager and lived in the area for over eight years, published a description of the birds in the nearby area, only making reference to Gyrfalcons, with no mention of Peregrines. The ornithologist Dalgety (1936), on board the “Heimen” in 1934, spent weeks in southern Melville Bay, just south of the Pituffik area, and despite mentioning Peregrines further south in Greenland, made no reference of Peregrines in northwest Greenland, though he listed Gyrfalcons on multiple occasions (Wordie 1935).

In more recent times, Vibe (1938) reported a breeding pair of Peregrines seen on Dundas Mountain during The Natural History Expedition to Northwest Greenland 1936, led by Finn Salomonsen. Additionally, Salomonsen (1950) provided reports of Peregrines in the Pituffik area: “According to Rev. J. Olsen (*in litt.*) and Vibe it breeds at Thule settlement, at Uvdle (Ulli) (slightly more eastward), and on Appat.” The “Thule settlement” almost certainly referred to Dundas Mountain, which sits next to the settlement, and which was mentioned by Vibe (1938). However, in 1975 Gyrfalcons were reported for Dundas Mountain (C. White, pers. comm.), but no Peregrines were seen there. Further, from 13 May to 22 July, 1975, Thing (1976) traveled the Pituffik area with local Greenlanders and recorded observations made on birds in the area, of which Gyrfalcons, but not Peregrines, were seen. From 1978, Roby *et al.* (1981) make mention of “five potential Little Auk predators observed at two study areas” in the Pituffik area, of which Gyrfalcons were one of the predators observed, but not Peregrines. Vaughan (1988) presents results from a survey of the birds of the Pituffik area, including breeding season visits from 1983 to 1985 and late summer surveys from 1983 to 1986, with Gyrfalcons seen on multiple occasions but only one Peregrine observed, on 20 June 1985

near Thule Air Base. However, in 1987 Peregrines were seen on Dundas Mountain, very near Thule Air Base (K. Falk, pers. comm.). Most recently, in 1994, in a checklist of bird species found in Greenland, Boertmann described Peregrines as a “scarce breeder” in the Pituffik area (Boertmann 1994).

As Salomonsen (1950) referenced, Vibe (1938) reported Peregrine Falcons on a cliff near the former village of Ulli, which is about 14 km northeast of the “Thule settlement.” Vibe provided W. Mattox with a photograph of this site (W. Mattox pers. comm.) and it was determined that the photograph did not depict the small cliff above Ulli, but Dundas Mountain, which is the “Thule settlement” and so both reported sites appear to be one and the same.

Appat is located 14 km west of Dundas Mountain (Fig. 3). It is 391 m high and measures 16 km by 7 km with high cliffs around much of its perimeter. Up to several hundred thousand seabirds breed there, with the most numerous breeder being the Brünnich’s Guillemots, followed by Black-legged Kittiwakes *Rissa tri-dactyla* and Northern Fulmars *Fulmarus glacialis* (Boertmann 1994, Boertmann et al. 1996), and perhaps one or more pairs of Peregrines. Other than Salomonsen’s general reference to the Peregrines on Appat, there is no reference to any specific location, and it is difficult to know whether Peregrines actually bred there. None were found breeding there during this study, despite careful checks every year.

We were unable to find the reference to Peregrine Falcons by Rev. J. Olsen to which Salomonsen refers. The one reference we were able to find by Olsen concerning Greenland was in 1923, however, in the southwest (Olsen 1925). It thus seems probable that he would have also been in Pituffik sometime during this period, but we can not be certain. In conclusion, we were only able to document one historic location in the Pituffik area where Peregrines bred prior to the start of this research, Dundas Mountain, and from historic information this location was clearly not occupied on a regular basis.

Current surveys

The historical breeding site, at Dundas Mountain, was occupied by Peregrines in all 13 years. No breeding Peregrines were ever seen on Appat, the other location where Peregrines were reportedly seen in the past, although the island was surveyed annually and one Gyrfalcon nest was located. In 2002 an adult female Peregrine was observed flying and perched on a cliff within the seabird colonies. When approached, the Peregrine was not defensive, flew away, and did not return. There are, however, extensive high cliffs and it is still possible that Peregrine Falcons bred there but were missed.

At seven locations, including Dundas Mountain, Peregrines aggressively defended territories against humans and Gyrfalcons. Young were produced at six of these

locations in two or more years (Table 2). The single site with a territorial Peregrine where young were not discovered was at 77.58° N. There, an adult female Peregrine was observed aggressively driving away an adult male Gyrfalcon with multiple stoops, locking feet with it twice and tumbling hundreds of meters only to release moments before crashing into the sea. Because of fog blanketing cliffs and an approaching storm, it was not possible to search for a nest. The minimum inter-site distance of locations with territorial and nesting Peregrines had a median value of 24.4 km and mean of 36.1 km ($n = 6$, range 12.4–74.5) and median of 15.4 km and mean of 28.3 km ($n = 5$, range 12.4–67.4), respectively.

Table 2.

Site	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
1-D	3	4	F	4	4	≥ 2	2	4	4	4	≥ 3	4	4
2-Pi						U	3	4	3	F	F	3	2
3-Bo						U	2	F	F	3	F	F	F
4-Dr						U	F	Y?	≥ 2	≥ 2	Y?	2	4
5-In								U	4	Y?	Y?	3	2
6-Br	U	C	C	N	N	C	C	C	N	C	Gyr	4	4

Note: number = minimum young produced; U = never previously checked, unknown; Y? = occupied but reproduction unknown; C = checked but unoccupied; N = not checked; Gyr = occupied by breeding Gyrfalcons; F = failed, occupied by both adults.

Annual occupancy and reproduction of Peregrine nest sites in the Pituffik study area from 1993 to 2005.

Pairs, single adults, and single sub-adult Peregrines that were mildly defensive when approached or toward Northern Ravens *Corvus corax* and/or were seen multiple times at the same location were observed at nine other sites (including two sites provided by K. Kampp, pers. comm.). These sites were all generally in areas with high densities of nesting Little Auks and were not used in calculations of inter-site distances since the Peregrines were only mildly defensive.

Over the 13 years, 41 known breeding attempts produced young older than seven days of age (but not yet flying) at least 28 times, for a total of at least 89 nestlings. Some nests were not located/visited until the young were so old that climbing to the nest could have caused them to fly prematurely, so observations were made only from a distance. In that situation, most often the entire nest ledge was not visible and one or more young may have been missed, with the symbol “≥” used in Table 2 to indicate when this occurred. Based on the observed young, the mean production was ≥2.17 young/occupied site ($n = 41$) and ≥3.18 ($n = 28$) young/suc-

cessful site. Because inclement weather prevented boat travel, two of the known sites could not be visited/observed on two occasions each, but we know that one of those sites was occupied both years because the female carried an operating PTT. Results from these surveys were minima estimates, and some Peregrine nests had likely failed before they were checked the first time, resulting in a bias towards successful nests.

At five out of six locations where reproduction occurred, pairs were present each year they were surveyed, including the first time the nest sites were checked. Site 6–Br was the exception, being first checked in 1994 and subsequently checked five out of the next eight years and never found to be occupied (Table 2). In 2003 it was first occupied, by Gyrfalcons, but was subsequently occupied each year after by only Peregrines. Site 3–Bo was reported as having Gyrfalcons originally but when checked was found to be occupied by Peregrines. However, based on fecal material buildup and nest characteristics it seems likely to have been a Gyrfalcon nest in the past.

Marked adult females were replaced by new females the following breeding season at least four times in the Pituffik area. One marked female occupied the same site for four breeding seasons (2001–2004) and another two for two breeding seasons each (2001–2002 and 2003–2004). To the best of our knowledge no adult females changed territories between years. No adult males were marked in the Pituffik area.

Calculating backwards from the estimated average age of nestlings (ageing guide is in Cade *et al.* 1996) when each nest was visited, assuming a four-egg clutch and an egg laid every other day, incubation beginning on the third egg and a 34-day incubation period (Burnham 1983), the average date for the first egg laid by Peregrine Falcons in the Pituffik area (from 1993 to 2005) was 8 June ($n = 24$, $sd \pm 7$) (Table 3). The average date for incubation to begin was 12 June ($n = 24$, $sd \pm 7$) and for hatching 16 July ($n = 24$, $sd \pm 7$). Assuming a 42-day nestling period (Sherrod 1983), the average fledging, or nest-leaving date, was 27 August ($n = 24$, $sd \pm 7$). If young Peregrines in the Pituffik area depend on their parents for a further 21 days, as recorded elsewhere, the young would not reach independence until 17 September. Only then could they depart on migration. This estimated date fits well with information that is presented later on juvenile Peregrines for the Pituffik area, and with the known departure dates of breeding females.

Ring recoveries from Peregrines marked in the Pituffik area are limited to one bird captured and released on 13 October 1993 by W. Seegar (pers. comm.) on Assateague Island, Maryland. This bird was one of the three nestlings ringed on 30 July 1993. None of the other 19 nestlings or 12 flying Peregrines ringed in the Pituffik area prior to 2005 were recovered.

Table 3.

Date of:	South Greenland ^a median (min.–max.; n = nesting attempts) (Falk <i>et al.</i> 1986)	Kangerlussuaq ^b average (n = years) (Mattox 1997)	Pituffik ^c average (min.–max.; median; n = nesting attempts)
1st egg laid	26 May (15 May–9 June; n = 13)	2 June (n = 14)	8 June (28 May–25 June; 8 June; n = 24)
Start of incubation	30 May (19 May–13 June; n = 13)	6 June (n = 14)	12 June (1 June–29 June; 12 June; n = 24)
Hatch	4 July (23 June–19 July; n = 13)	10 July (n = 14)	16 July (5 July–2 Aug.; 15 July; n = 24)
Fledge	15 August (4–30 Aug.; n = 13)	21 August (n = 14)	27 Aug. (16 Aug.–13 Sept.; 27 Aug.; n = 24)

^a Data for South Greenland collected from 1979 to 1985, Falk *et al.* 1986.

^b Data for the Kangerlussuaq area collected from 1983 to 1997, W. Mattox, 1997 Field Report, Greenland Peregrine Falcon Survey.

^c Data for the Pituffik area collected from 1993 to 2005.

Nesting chronology of Peregrine Falcons in the South Greenland, Kangerlussuaq, and Pituffik study areas. Hatch dates are calculated from estimated age of young at ringing or in some cases pipping eggs or newly-hatched young. Average dates for first egg laid and start of incubation are calculated by subtracting 34 and 38 days from hatch date, respectively (see text). Average fledging date is calculated by adding 42 to hatch date (see text). Calculated dates are consistent with dates observed in the field.

Prey

Of 19 nests in the Pituffik area where prey remains were collected, Little Auk remains were found in 74% and Snow Bunting remains in 79%. This held despite all six nest cliffs being near wetlands with nesting shorebirds and the closest Little Auk colonies to any nest being more than 30 km distant. However, Little Auks regularly make long flights to feed and pass within less than 1 km of each nest. In the five nests where Little Auk remains were not found, Snow Buntings made up most of the diet, with additional limited prey remains from Lapland Longspur *Calcarius lapponicus* and shorebirds being found in three and one of those nests, respectively. Black-legged Kittiwake, Black Guillemot, and Rock Ptarmigan were found in 16%, 11%, and 6% of nests, respectively.

Little Auks and Snow Buntings thus appeared to make up the largest part of the Peregrine diet in the Pituffik area, with Little Auks being by far the most important prey by biomass. Despite remains from larger prey being collected at nests, including Black-legged Kittiwake, Rock Ptarmigan, and Black Guillemot, no more

than two of each of these species were found at the few nests where they were present and probably contributed little to the overall biomass needed to raise young. Quantification of the total number of items collected was difficult because only feathers remained for passerines, and in many cases remains fell out of the nest and could not be collected. Overall, prey remains were usually collected from Peregrine nests when chicks were small, and these data best represent the first 20–25 days of chick rearing. It seems likely that larger prey species, specifically guillemots and kittiwakes, may make up a larger part of the diet as Peregrine young get older and the adult female does more of the hunting.

Nest site characteristics

In the Pituffik area, breeding pairs of Peregrines were located at cliffs with a mean height of 59 m ($n = 33$, $sd \pm 25$, range = 25–137, median = 55) located less than 1 km from the sea in bays and fjords. Steep rock talus and/or more gradual gravel/sand slopes extended from the base of the cliffs to sea level. Nest ledges were on average located near the middle (0% = top, 100% = ground below cliff) of the cliff (average = 52, $n = 28$, $sd \pm 20$, range = 20–78, median = 52) and cliff aspect, on average, was 213° (southwest) when corrected to True North ($n = 30$, $sd \pm 75$, range = 225, median = 168) (Table 4).

All breeding attempts were on ledges, except one in a pothole previously used by breeding Gyrfalcons. Including the pothole nest, average nest length was 166 cm ($n = 21$, $sd \pm 98$, range = 50–500, median = 150) and depth 66 cm ($n = 21$, $sd \pm 30$, range = 50–150, median = 51). Very little protection existed from above except at the former Gyrfalcon nest site. The average of the vertical angle of exposure (mean of degrees of exposure at far left and right and in centre) for nine nesting attempts was 74° ($sd \pm 12$, range = 48–90, median = 78), including the pothole nest site. Average horizontal angle of exposure (falcon viewing angle) was 134° ($n = 19$, $sd \pm 41$, range = 70–180, median = 140). The average nest ledge aspect for each of 19 nests corrected to True North was 209° ($n = 19$, $sd \pm 59$, range = 210, median = 213). Thirteen of the 19 had a south to southwestern exposure (Fig. 5). However, further research is needed, by randomly selecting a range of cliffs for comparison, to determine whether Peregrines are actively “choosing” nests that face south to southwest or whether they are simply being forced to use what is available. But, based on the large number of cliffs available for use by Peregrines, it is probable that to some degree Peregrines are “choosing” specific nesting sites based on directional exposure.

Table 4.

	South Greenland (Falk <i>et al.</i> 1986)	Kangerlussuaq (Wightman & Fuller 2005)	Pituffik
	Mean \pm sd <i>n</i>	Mean \pm sd <i>n</i>	Mean \pm sd <i>n</i>
Cliff characteristics			
Elevation of cliff (m)	234 \pm 109 <i>n</i> = 15	288 \pm 115 <i>n</i> = 67	143 \pm 28 <i>n</i> = 22
Cliff height (m)	119 \pm 87 <i>n</i> = 15	99 \pm 66 <i>n</i> = 67	59 \pm 25 <i>n</i> = 33
Cliff aspect ($^{\circ}$)	na	188 \pm 6.5 <i>n</i> = 67	213 \pm 75 <i>n</i> = 30
Location on cliff (0% being top)	40 \pm 22 <i>n</i> = 15	na	52 \pm 20 <i>n</i> = 28
Height of ledge (m)	na	51 \pm 44 <i>n</i> = 65	27 \pm 16 <i>n</i> = 28
Nest ledge characteristics			
Length of nest ledge (cm)	na	686 \pm 1150 <i>n</i> = 57	166 \pm 98 <i>n</i> = 21
Depth of nest ledge (cm)	na	165 \pm 247 <i>n</i> = 57	66 \pm 30 <i>n</i> = 21
Nest ledge aspect ($^{\circ}$)	228 <i>n</i> = 15	189 \pm 7.4 <i>n</i> = 67	209 \pm 59 <i>n</i> = 19
Horizontal angle of exposure ($^{\circ}$)	159 \pm 38 <i>n</i> = 11	144 \pm 34 <i>n</i> = 49	134 \pm 31 <i>n</i> = 19
Vertical angle of exposure ($^{\circ}$)	83 \pm 14 <i>n</i> = 14	65 \pm 19 <i>n</i> = 48	74 \pm 12 <i>n</i> = 14

na = not applicable, information not collected.

Nest site characteristics from the South Greenland, Kangerlussuaq, and Pituffik study areas. Nest sites in the South Greenland (data from 1979 to 1985) and Pituffik (data from 1993 to 2005) areas were included more than once if used in multiple years while data in Kangerlussuaq were collected only once from each nest site with occupancy based on historical use from 1972 to 1999.

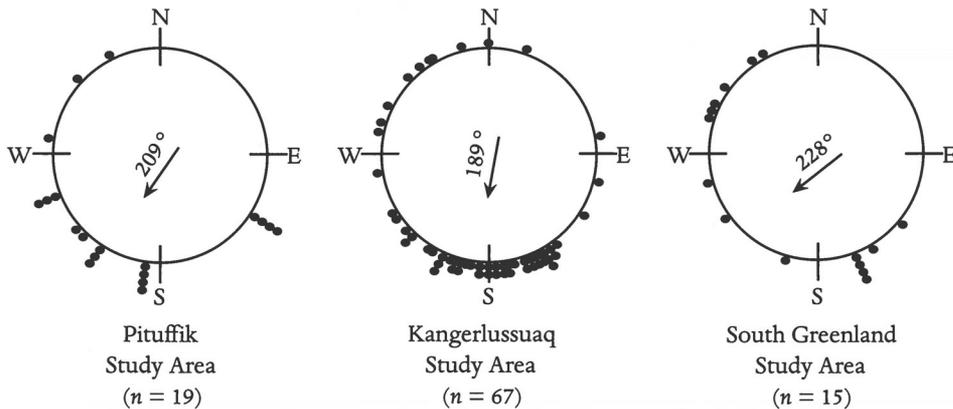


Figure 5

Nest ledge aspect of Peregrine Falcon nests in the Pituffik, Kangerlussuaq, and South Greenland study areas. The average vectors are indicated, but the range of variation was large. Stacked dots may indicate the same nest was used multiple years. Data for Kangerlussuaq from Wightman (2001) and Wightman & Fuller (2005) and for South Greenland from Falk et al. (1986).

Morphometrics

Adult female Peregrines from the Pituffik area had a significantly greater mass ($T = 2.53$, $p = 0.02$, $df = 17$) than females from the Kangerlussuaq area, but no significant difference in any linear measurements (Table 5). All five measurements taken on adult males in the Kangerlussuaq area were significantly smaller than those for females in the same area, as would be expected (Table 5).

The PCA yielded two components for adult females explaining 50% and 26%, respectively, of total variance (Table 6). The first principal component (PC1) described overall body size (bill, tarsus, wing, and tail length) with PC1 correlating positively and highly with all variables. The second principal component (PC2) described bill length and tarsus length, with PC2 having a high positive correlation with both. A PCA for adult male Peregrines from the Kangerlussuaq area presented two components that explained 87% of the total variance. Overall body size (mass, bill, tarsus, wing, and tail length) was described by PC1, but no variables were significantly correlated with PC1. PC2 described tail length and mass and again there were no correlations between PC2 and any variables. For male Peregrines, the lack of a significant correlation between measured morphometric variables and either PC1 or PC2 is most likely a product of small sample size. Some individuals, both male and female, did not have values recorded for all five meas-

urements and were excluded from the PCA analysis. Included in the PCA were 17 adult females (Pituffik area = 7, Kangerlussuaq area = 10) and four adult males from the Kangerlussuaq area (Table 6).

A two-sample t-test performed on PC1 showed no difference ($T = -0.06$, $p = 0.95$, $df = 10$) in overall body size between adult female Peregrines from the Kangerlussuaq and Pituffik areas. For adult females from both areas there was a significant relationship ($r^2 = 0.66$, $p < 0.001$) between PC1 and body mass (Fig. 6). Therefore, mass was a good predictor of overall body size for adult female Peregrines in the Kangerlussuaq and Pituffik areas; heavier birds were usually larger. Additionally, females from the Pituffik area were generally heavier for their overall body size than were females from the Kangerlussuaq area (see Fig. 6). Although it has been shown in other raptors that adult females are heaviest during the early laying period, with mass declining from incubation to the post-fledging period (Newton 1986, Village 1990), adult females in the Kangerlussuaq area were almost all captured during the early-to-mid incubation period while females in the Pituffik area were captured either during the young rearing period or prior to outward migration. Thus, based on timing of measurement and observations in other raptors, it seems likely that the difference in mass between females in the Kangerlussuaq and Pituffik areas is genuine, but likely under-estimated in these data.

Table 5.

Location Sex	Body mass	Bill length	Tarsus length	Wing chord	Tail length
Kangerlussuaq					
Female	932 ± 68 (12)	2.23 ± 0.09 (12)	6.49 ± 0.23 (11)	36.2 ± 0.8 (11)	17.1 ± 0.8 (12)
Male	607 ± 10 (7)	1.89 ± 0.07 (7)	5.82 ± 2.99 (5)	31.6 ± 0.6 (7)	14.4 ± 0.2 (6)
Pituffik					
Female	1010 ± 70 (9)	2.25 ± 0.7 (9)	6.51 ± 2.0 (7)	36.1 ± 2.1 (9)	17.1 ± 0.6 (9)
T-tests between: Females in Pituffik and Kangerlussuaq	T = 2.53 p = 0.02 df = 17	T = 0.55 p = 0.59 df = 18	T = -1.39 p = 0.19 df = 14	T = -0.24 p = 0.81 df = 12	T = 0.00 p = 1.00 df = 18
T-test between: Males & females in Kangerlussuaq	T = 16.30 p < 0.001 df = 11	T = -64.71 p < 0.001 df = 6	T = -38.45 p < 0.001 df = 4	T = 13.93 p < 0.001 df = 15	T = 10.57 p < 0.001 df = 14

Mean ± sd (n) for five measurements taken on adult and sub-adult Peregrine Falcons from the Kangerlussuaq and Pituffik areas. Measurements are in centimeters except for mass which is in grams.

Table 6.

Variable	Adult females (n = 17)		Adult males (n = 4)	
	PC1	PC2	PC1	PC2
Bill length	-0.373	-0.676	-0.375	0.516
Tarsus length	-0.463	-0.458	-0.476	0.471
Wing chord	-0.577	0.410	-0.516	0.010
Tail length	-0.560	0.406	-0.409	-0.589
Body mass	*	*	-0.447	-0.406
% Variance explained	50	26	56	31

*not included in PCA for adult females due to large variance, see methods.

Results of two separate principal component analyses (PCA): (1) adult female Peregrine Falcons from the Kangerlussuaq and Pituffik areas and (2) adult males from the Kangerlussuaq area. Component loadings on each significant axis and percent of total variance explained are shown.

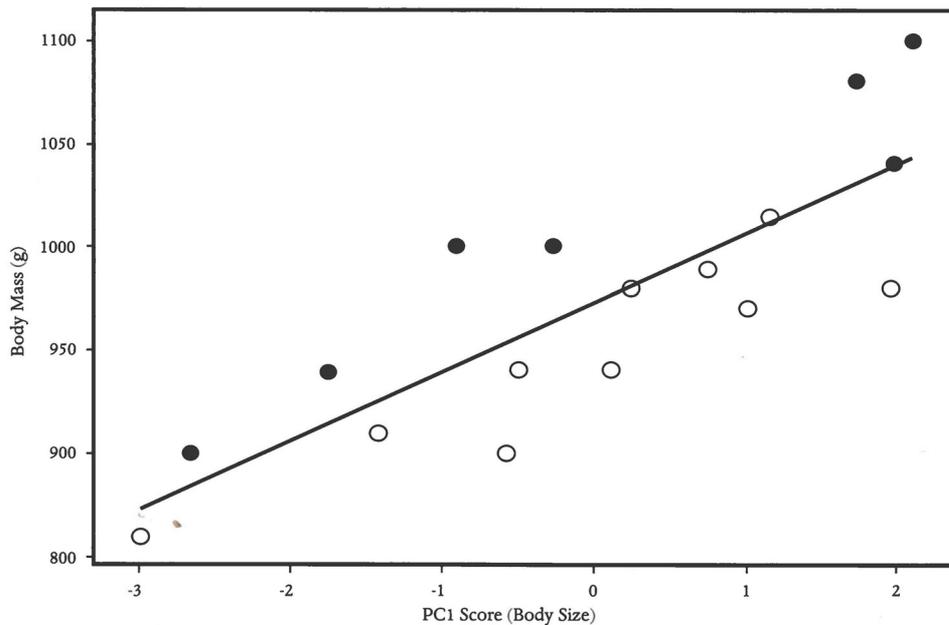


Figure 6 Significant linear relationship ($r^2 = 0.66$, $p < 0.001$) between PC1 (body size) and body mass (grams) in adult female Peregrines from the Kangerlussuaq and Pituffik areas, Greenland. Open circles represent birds from the Kangerlussuaq area and filled circles from the Pituffik area.

Genetics

Genetic diversity

All eight microsatellite loci were polymorphic among the sampling locations in the Kangerlussuaq, Pituffik, and Maniitsoq areas (Appendix B). After adjusting for multiple comparisons ($n = 16$), significant departures from Hardy-Weinberg equilibrium in the form of heterozygote deficiencies were observed at a single locus (fp79-4, Pituffik; $H_E = 0.853$, $H_O = 0.400$). In addition, five loci comparisons testing for linkage disequilibrium were significant after correcting for multiple comparisons ($n = 56$); however, in all cases, disequilibrium involved different pairs of loci. We therefore conclude that there was no evidence of significant linkage disequilibrium and that the loci could be appropriately treated as independent.

A maximum of 55 microsatellite alleles were observed among the surveyed Peregrine Falcon locations across eight loci, with a total of 52 alleles from the Kangerlussuaq area and 44 alleles from the Pituffik area (Appendix B). A number of alleles were unique to a sampling location; however, the majority of unique alleles were observed at low frequency (<5%). The average number of alleles per locus, allelic richness, and observed heterozygosity were not significantly different between birds from the Kangerlussuaq and Pituffik areas (Wilcoxon signed rank test, $Z = -1.36$, $p > 0.05$; $Z = -0.289$, $p > 0.05$; $Z = 0.00$, $p > 0.05$, respectively). Overall, based on measures of genetic diversity, the two populations, living 1,100 km apart, were indistinguishable.

Based on 1,540 bp of mtDNA cytb/control region sequence, 12 haplotypes were observed among Greenland Peregrine Falcons (Table 7), with two unique haplotypes observed in both the Kangerlussuaq and Pituffik areas. A third sampling location (Maniitsoq, $n = 3$), consisting of migrant Peregrines, was also included in this analysis, and each bird had a different haplotype, with one haplotype unique to this sampling location (Table 8, Fig. 7). However, despite unique haplotypes within sampling locations, a single haplotype, A, was observed at high frequency among the three locations (60%; Fig. 7). Of the 1,540 nucleotides scored, 32 nucleotides were variable among individuals: 26 sites were transition substitutions, five sites were transversions, and one site had a single nucleotide indel (Table 8). Polymorphism within each population was consistent with neutral expectations (Tajima's $D = -0.762$ to -0.662 , $p > 0.05$). Using a modified t-test (Nei 1987), haplotype diversity (h) was significantly lower ($p < 0.001$) in the Kangerlussuaq area, while nucleotide diversity (p) was similar across sampled populations (0.004; Table 7).

Table 7.

Sampling location	Sample size (micro/mtDNA)	Microsatellite DNA (8 loci)				Mitochondrial DNA (1,540 bp)			Tajima's D ^b
		Mean alleles/locus	Allelic richness ^a	H _o	H _E	Number of haplotypes	Haplotype diversity (<i>h</i>)	Nucleotide diversity (<i>p</i>)	
Pituffik	15/15	5.3 (0.7)	5.3 (0.7)	0.525 (0.104)	0.635 (0.080)	7	0.724 (0.031)	0.004 (0.000)	-0.662
Kanger.	27/24	6.1 (1.1)	5.4 (0.9)	0.532 (0.108)	0.593 (0.101)	6	0.554 (0.024)	0.004 (0.000)	-0.762
Maniitsoq	5/3	3.9 (0.5)	5.5 (0.9)	0.536 (0.093)	0.620 (0.091)	3	1.000 (0.157)	0.004 (0.001)	NA
Total	47/42	6.5 (1.1)	5.5 (0.9)	0.536 (0.093)	0.620 (0.091)	12	0.643 (0.013)	0.004 (0.000)	-0.653

H_o, observed heterozygosity

H_E, expected heterozygosity

^a Calculated based on minimum sample of 15 birds.

^b Tajima's *D* statistic, *p* > 0.05.

Genetic diversity measurements (microsatellite and mtDNA) among Peregrine Falcons sampled in three different locations in Greenland. Standard errors are given in parentheses unless indicated otherwise.

Table 8.

Maniitsoq	1	1	0	0	0	0	0	0
Kanger.	16	2	0	2	0	0	1	0
Pituffik	8	0	1	0	2	1	1	1
1525	C
1513	C	T
1477	C
1434	C	.	.	.	T	.	.	.
1346	G	.	.	A	.	.	A	.
1332	C	T	.	.
1256	A
854	A	G
820	A	.	.	G
805	A
802	A	G
796	T
795	C	T	T	T	T	T	T	T
731	A
681	T	A	A	A	A	A	A	A
638	C
634	C	T	T	.	.	T	.	T
551	A
549	T
546	C
530	T
471	A
469	T
450	T
400	T	C	C	C	C	C	C	C
386	T	.	.	.	C	.	.	.
209	C	T
144	G	A	A	A	A	A	A	A
113	T	C	.
77	T	C	C	C	C	C	C	C
68	T	C	C	C	C	C	C	C
65	G
Haplotype	A	B	C	D	E	F	G	H

Distribution of 12 observed mtDNA haplotypes from a sample of 42 Peregrine Falcons from three sample locations in Greenland. The vertical numbers indicate the positions of variable nucleotides within 1,540 bp of sequence. Dots indicate the same nucleotide is present as haplotype A and a double dash (see position 469) indicates a deletion. Totals at the end of each haplotype row indicate the number of individuals with that haplotype in each area.

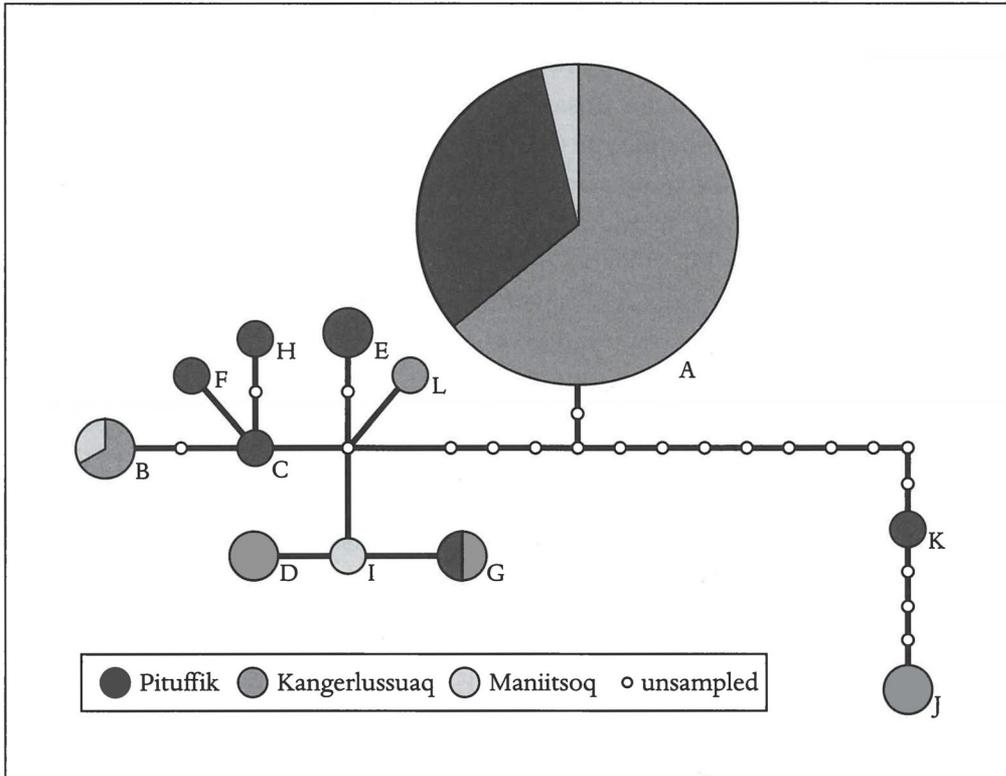


Figure 7

A minimum spanning cladogram inferred from maximum parsimony. Each circle represents a single haplotype where the size of the circle corresponds to the number of individuals observed with that particular haplotype. Solid lines represent parsimonious connections between haplotypes with a probability greater than 95%. Each connection between circles corresponds to a single point-mutation; open circles represent intermediate haplotypes that exist but were not sampled. See Table 7 for the exact number of individuals for each haplotype.

Population structure: F statistics, assignment test, and haplotype network

No significant pairwise differentiation (F_{ST}) was observed between the three sampling locations with either microsatellite or mitochondrial data ($F_{ST} = 0.007$, $p > 0.05$; $F_{ST} = -0.014$, $p > 0.05$, respectively). Furthermore, the program STRUCTURE using the microsatellite data from all three sample locations identified a single cluster (or population), with $K = 1$ having the highest log likelihood value. All other runs ($K = 2-4$) consisted of equal assignment probabilities (1:1, 1:1:1, etc.) for sampling location between clusters, indicative of unlikely scenarios consisting of multiple populations (Pritchard *et al.* 2000).

A number of mtDNA haplotypes were unique to a sampling location; however, geographic clustering was not observed (Fig. 7). The majority of haplotypes (B–I and L) formed a cluster with few unsampled haplotypes required to connect haplotypes. The most frequent haplotype (A), which was also observed in all three sampling locations, required a minimum of six unsampled haplotypes to connect to its closest sampled haplotype. In addition, two unique haplotypes (K and J) observed in the Kangerlussuaq or Pituffik area required a minimum of 12 point substitution steps to connect to their closest sampled haplotype (Fig. 7), and both haplotypes contained a single indel not observed in other haplotypes (Table 8).

In the Kangerlussuaq area an adult female Peregrine was captured on the nest early in the incubation period using nooses and artificial eggs in the scrape. Morphological measurements and a blood sample were taken in addition to a PTT being attached. Later in the season researchers revisited the nest and with the same female present, with the PTT being clearly visible, she defended the nest while four nestlings were ringed and bled. Using mtDNA it was later determined that the adult female was not the biological mother of the four chicks, with all four chicks having the same haplotype and the adult female a different haplotype. Presumably the original female that laid the eggs had been replaced.

In conclusion, no evidence exists, either using microsatellites or mtDNA, to suggest that population genetic differentiation exists between Peregrine sample locations in the Kangerlussuaq and Pituffik areas, and further suggests that gene flow exists between the two locations.

Satellite-received telemetry

Transmitters: number deployed, longevity, and location classes

The length of time data were received from PTTs on individual Peregrines varied greatly, ranging from three to 819 days, with a median of 88 days (average = 143, $sd \pm 189.9$) (Table 9). However, in multiple cases for unknown reasons PTTs stopped transmitting for extended periods of time, up to nine months, before resuming a regular pattern of transmission. For the 18 PTTs, on average, locations with LC 3–0 made up 59.1% ($sd \pm 6.0\%$, median = 58.1%) of all the data collected, while the most accurate location classes, LC 3 and 2, made up an average of only 1.8% ($sd \pm 2.2\%$, median = 1.0%). Locations with LC A, B, and Z made up an average of 40.9% ($sd \pm 6.0\%$, median = 41.9%) of all the data collected from each of the 18 PTTs. When locations with LC Z did not include a latitude and longitude they were excluded from all analyses. In total, 5,792 locations were received, with an average of 322 per individual Peregrine/PTT ($sd \pm 361$, range = 23–1,270, median

= 213). PTTs 12012 and 12017 had 1,240 and 1,270 locations, respectively. For further details regarding individual PTTs see Appendix C.

Table 9.

	<i>n</i>	Median	Mean	SD	Range
All Peregrines	18	88	143	± 189.9	3–819
Adults	13	104	197	± 215.84	35–819
Sub-adults	2	10.5	10.5	± 6.36	6–15
Juveniles	3	36	27	± 21.36	3–43

Number of days PTTs transmitted on female Peregrines.

Breeding home range

Breeding home ranges were estimated for 13 individual adult female Peregrines, seven in the Kangerlussuaq area and six in the Pituffik area, from 2001 to 2003. For two Peregrines in the Pituffik area, breeding home ranges were obtained for two seasons: 2001 and 2003 for Peregrine 10212, and 2001 and 2002 for Peregrine 10217. Data from both seasons were used in all calculations. Both females used the same respective nesting cliff that they were originally tagged at in subsequent years, with 10212 also being present at the original nesting cliff in 2002, but the PTT failed to record locations during the nesting period.

Home range size varied greatly depending upon which method was used to calculate area. The largest estimates of home range sizes for both study areas were calculated by using 90% MCP LC 3–0 and the smallest estimates from 50% kernels LC 3–1 (Table 10). For Peregrines in the Pituffik area, breeding home range areas that encompass glaciers and/or the Greenland Ice Sheet were included because prey species have been shown to cross the Greenland Ice Sheet both during migration and in the breeding season (Alerstam *et al.* 1986, R. Abbott pers. comm.), and could have been hunted there.

Using 90% MCP, adult female Peregrines in the Kangerlussuaq area had on average 99 ($n = 7$) locations with LC 3–0 (Table 11) and an average estimated breeding home range of 1,475 km², while females in the Pituffik area had an average of 97 ($n = 8$) locations with LC 3–0 and an average home range of 3,021 km². However, individual breeding home range sizes between populations in the two areas overlapped (Appendix D). No correlation was found between number of locations and breeding home range size (Spearman Rho = 0.17, $p > 0.05$) and the apparent dif-

ference between the average breeding home range sizes of adult female Peregrines in the Kangerlussuaq and Pituffik areas was significant only at the 10% level ($T = 1.89$, $p = 0.09$, $df = 9$, not equal variances).

When breeding home range size using locations with LC 3–1 were used to calculate 90% MCP, adult female Peregrines in the Kangerlussuaq area had an average breeding home range size of 72 km² ($n = 7$, average locations = 27), compared to 183 km² ($n = 7$, average locations = 34) for females in the Pituffik area. Breeding home range sizes between the two populations overlapped, with no significant difference between them ($T = 1.44$, $p = 0.18$, $df = 12$, equal variances). Number of PTT locations and home range sizes showed no correlation (Spearman Rho = 0.40, $p > 0.05$).

Table 10.

	Method and statistics	Kangerlussuaq home range in km ²	Pituffik home range in km ² ^a
90% MCP LC 3–0	Mean ± sd	1,475 ± 904	3,021 ± 2,106
	Median	1,720	3,529
	Range	175–2,709	305–5,451
	<i>n</i>	7	8
90% MCP LC 3–1	Mean ± sd	72 ± 41	183 ± 199
	Median	62	41
	Range	33–154	8–491
	<i>n</i>	7	7
95% Kernel LC 3–0	Mean ± sd	883 ± 770	2,007 ± 1,777
	Median	643	1562
	Range	158–2,524	427–1,659
	<i>n</i>	7	8
95% Kernel LC 3–1	Mean ± sd	144 ± 109	211 ± 259
	Median	82	123
	Range	52–337	15–719
	<i>n</i>	7	6
50% Kernel LC 3–0	Mean ± sd	181 ± 189	252 ± 140
	Median	123	243
	Range	26–590	52–483
	<i>n</i>	7	8
50% Kernel LC 3–1	Mean ± sd	23 ± 25	31 ± 37
	Median	11	21
	Range	7–72	1–103
	<i>n</i>	7	6

^a Breeding home ranges were recorded for two separate breeding seasons for two females in the Pituffik area, of which both have been included. Sample size in the Pituffik area varies as a result of some individuals having too few locations recorded to calculate viable breeding home range size when using only locations with LC 3–1.

Estimated home range size of adult female Peregrines in the Kangerlussuaq and Pituffik study areas, 2001–2003.

Table 11.

	Mean	Standard deviation	Median	Range
Kangerlussuaq home ranges LC 3-0 ($n = 7$)	99	± 40	88	50-169
Kangerlussuaq home ranges LC 3-1 ($n = 7$)	27	± 14	21	17-56
Pituffik home ranges LC 3-0 ($n = 8$)	97	± 77	62	31-236
Pituffik home ranges LC 3-1 ($n = 7$) ^a	34	± 25	25	6-84
Pituffik home ranges LC 3-1 ($n = 6$) ^a	38	± 24	33	18-84

^a Sample size drops from $n = 7$ to $n = 6$ in order to exclude one individual with only six locations, which were not sufficient for some tests in Table 10.

Mean, standard deviation, median, and range of locations used to calculate home range figures in Table 10. Values for n vary between tests in Table 10 because some PTTs did not have sufficient locations for specific tests.

Using fixed 95% kernels with locations with LC 3-0, the average breeding home range size of adult female Peregrines in the Kangerlussuaq area was 883 km² ($n = 7$, average locations = 99), and 1,562 km² ($n = 8$, average locations = 97) for Pituffik area females. Size of breeding home ranges overlapped slightly but in general, Pituffik area females had larger ranges than Kangerlussuaq area females; however, this difference was again not significant (Mann-Whitney U, $p = 0.18$). No correlation was found between number of PTT locations and the estimated size of home ranges (Spearman Rho = 0.06, $p > 0.05$).

When fixed 95% kernels were used in conjunction with locations with LC 3-1, average home range size for adult female Peregrines in the Kangerlussuaq area was 144 km² ($n = 7$, average locations = 27), and 211 km² ($n = 6$, average locations = 38) for females from the Pituffik area. Individual range sizes between geographical areas greatly overlapped, and again no difference was found between the Kangerlussuaq and Pituffik areas (Mann-Whitney U, $p = 0.94$). Home range size and the number of PTT locations used were not correlated (Spearman Rho = 0.11, $p > 0.05$).

Home range size was calculated using fixed 50% kernels with LC 3-0. Average size of breeding home range was 181 km² ($n = 7$, average locations = 99) in the Kangerlussuaq area and 243 km² ($n = 8$, average locations = 97) in the Pituffik area, with range sizes between study areas overlapping and not significantly different

(Mann-Whitney U, $p = 0.22$). Number of PTT locations used and range size were not correlated (Spearman Rho = 0.12, $p > 0.05$).

Fixed 50% kernel locations with LC 3–1 produced an average breeding home range size of 23 km² ($n = 7$, average locations = 27) for the Kangerlussuaq area and 31 km² ($n = 6$, average locations = 38) for the Pituffik area. No significant difference was found between the two geographical populations (Mann-Whitney U, $p = 0.89$) or between number of PTT locations used and range size (Spearman Rho = 0.18, $p > 0.05$).

Overall, when using 90% MCP to calculate home range size, each individual home range was on average 39.6 ($n = 14$, $sd \pm 51.0$, range = 1.5–159.0, median = 16.0) times larger when using locations with LC 3–0 compared to locations with only LC 3–1. Furthermore, on average the number of locations used to calculate breeding home range size decreased 68.5% ($n = 14$, $sd \pm 13.4$, median = 71.9) when excluding locations with LC 0. To determine whether the reduction in breeding home range size was simply an effect of reduced number of locations for each individual, we took the total number of locations used to calculate the size of the 90% MCP LC 3–1 (Appendix D) and randomly selected that number of locations five hundred times from the total number of locations used to calculate the 90% MCP LC 3–0 (Appendix D). For each of the five hundred groups of randomly selected locations, a 90% MCP was calculated along with an average size for all five hundred 90% MCP (Appendix E). Using a paired t-test, the average of the five hundred 90% MCP for each individual was compared to the actual breeding home range sizes calculated using 90% MCP LC 3–1. These range sizes were found to be significantly different ($T = 2.54$, $p = 0.05$), in all 14 cases much higher, despite using the same number of locations to calculate both range sizes, and reduction in range size from 90% MCP LC 3–0 to 90% MCP LC 3–1 is thus not an effect of fewer locations used to calculate range size on MCP LC 3–1.

Results from the stationary PTT (see Appendix A for specific results) support excluding locations with LC 0, with “home range sizes” calculated from the stationary PTT using LC 3–0 being between 5.5 and 8.6 times larger than those calculated using locations with LC 3–1. Locations with LC 0 were on average 11 km from the actual position of the PTT while locations with LC 3–1 were more accurate, with LC 1 being on average 2.3 km off and LC 3 and 2 even more accurate. Based on this, home range sizes for Peregrines should be viewed as maximum sizes, with the actual size likely being smaller than reported.

Despite no significant differences being found, 11 of 12 measures of range size indicated larger ranges for females in the Pituffik area than in the Kangerlussuaq area. Larger sample size may help to confirm this difference statistically.

Outward migration

From 2001 to 2003, adult female Peregrines with PTTs departed on outward migration from the Kangerlussuaq area between 25 August and 5 October (average = 20 Sept., $n = 3$, median = 2 Oct.) and from the Pituffik area from 8 to 23 September (average = 16 Sept., $n = 8$, median = 16 Sept.). In the Pituffik area PTT 10212 operated for three years and 10217 for two years, with departure dates for each individual relatively consistent and departure dates for each year included. All tagged females appeared likely to have bred. In the Pituffik area a juvenile female Peregrine departed on migration on 23 September 2001. Pre-migration areas were used as departure dates and departure locations for 10217 from the Pituffik area, with the pre-migration area approximately 58 km from the nest, and in the Kangerlussuaq area for Peregrines 35238 and 41438, with pre-migration areas approximately 122 and 136 km from the nest, respectively. Peregrine 10217 used Kitsissut (Fig. 3) as a pre-migration area while the two Peregrines from the Kangerlussuaq area traveled from their inland breeding areas directly west until reaching pre-migration areas on the coast.

For the Pituffik area, five complete outward migrations were obtained from four adult female Peregrines, with 10212 having complete outward migrations in 2002 and 2003 (Table 12). In the Kangerlussuaq area only one complete outward migration was obtained, from Peregrine 35238. For the Pituffik area, in 2002, PTT 10212 stopped functioning for most of the migration, but locations were received for the days prior to migration and one duty cycle after departing the area, as well as for one duty cycle before reaching the winter home range, with normal functioning resuming after that.

The average distance for outward migrations of Peregrines from the Pituffik area was 10,794 km ($n = 4$, $sd \pm 2,297$ km), with a median value of 11,603 km. Peregrine 10212 wintered in the same location both years so only the distance from 2003 was used, having the greater number of days with locations received during migration (Table 12). The overall distance falcons traveled varied widely from 7,532 to 12,438 km, with 36015 traveling the greatest distance and latitudinal shift ($>100^\circ$), and 36017 the largest range of longitudinal shift ($>41^\circ$). The single adult female (35238) from the Kangerlussuaq area that completed the outward migration traveled 3,235 km while covering approximately 23.6° of latitude.

Of the four individuals that completed the outward migration from the Pituffik area, two (10212 and 10217) used the Central Flyway, including 10212 in consecutive years, while 36017 used the Eastern Flyway (Fig. 8). Female 36014 from the Pituffik area used a combination of the two flyways, crossing diagonally from the southwest corner of Hudson Bay east into Florida. Peregrine 35238 from the Kangerlussuaq area stopped while traveling along the Eastern Flyway (Fig. 8).

Table 12.

Location tagged and PTT ID	Start and end date of migration	Total distance (km)	Speed of travel (km/day)	Number of days	Number of days with locations (%)	Range of distances travelled per day ^a (km)	Location classes used for daily locations ^b (LC 3,2,1,0)
Kanger. 35238	5 Oct 03–6 Nov 03	3,235	98	33	11 (33.3)	3–332	0, 1, 5, 3
Pituffik 10212	8 Sep 02–13 Oct 02 ^c	7,231	201	36	4 (11.1)	Insufficient data	0, 0, 1, 1
	17 Sep 03–15 Oct 03	7,532	269	28	22 (78.6)	58–530	0, 1, 5, 14
Pituffik 10217	15 Sep 01–10 Nov 01	10,836	190	57	49 (86.0)	13–1,349	0, 3, 10, 34
Pituffik 36015	10 Sep 03–14 Nov 03	12,438	188	66	15 (22.7)	81–588	0, 3, 4, 6
Pituffik 36017	17 Sep 03–25 Nov 03	12,370	177	70	16 (22.9)	108–482	0, 1, 7, 6

^a Range of distances travelled per day, see methods section for further description.

^b Location for start and end date of migration not included.

^c Estimated start date based on 2001 and 2003 data for same Peregrine.

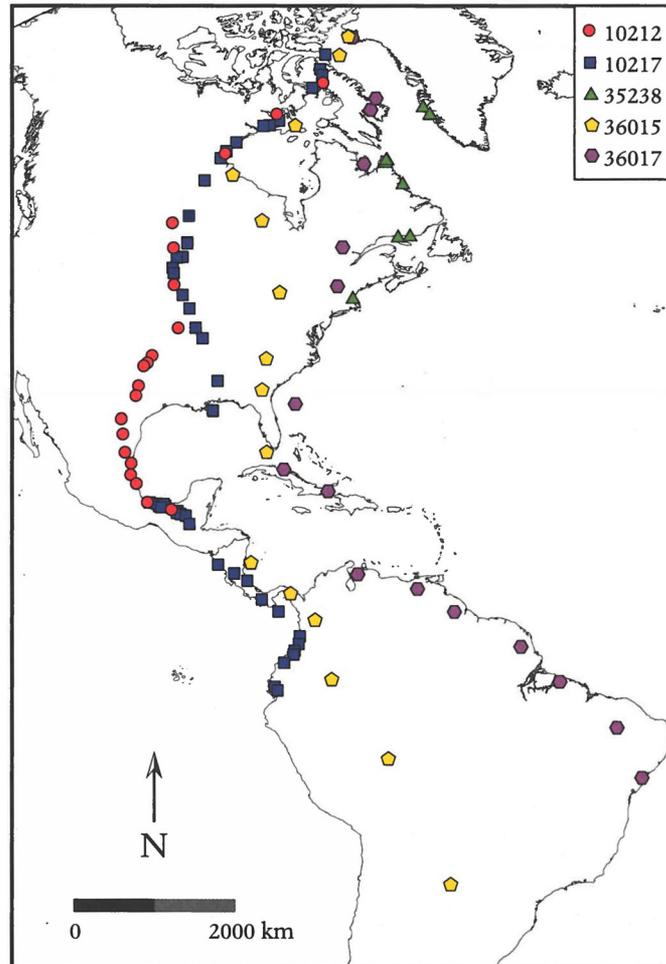
Complete outward migrations of female Peregrine Falcons from the Kangerlussuaq and Pituffik study areas (distances given as Great Circle Distances).

The calculated average speed of migration for birds from the Pituffik area was 205 km/day ($n = 5$, $sd \pm 37$, range = 177–269, median = 190) (Table 12). For calculating the speed of migration, individual 10212 was included twice because the speed was substantially different between 2002 and 2003: 201 versus 269 km/day, respectively. The fastest overall speed from the Pituffik area was 269 km/day (10212), and the slowest 177 km/day (36017). From the Kangerlussuaq area, falcon 35238 traveled at 98 km/day.

The individual measured speed of migration per day by Pituffik area Peregrines ranged from more than 1,349 km, when 10217 crossed the Gulf of Mexico in a single day, to less than 13 km, again 10217 shortly after arriving in Mexico (Fig. 8). Peregrine 36017 showed the least variation between the shortest and furthest distance traveled on any given day, less than 320 km, and 10217 showed the most fluctuation.

Figure 8

Complete outward migration routes for five adult female Peregrine Falcons tagged with PTTs in the Kangerlussuaq areas ($n = 1$) and Pituffik ($n = 4$) areas, from 2001 to 2003. Only days with locations with LC 3–0 are included and only a single location has been included for each day.



tuation, more than 1,336 km (Table 12). Kangerlussuaq area Peregrine 35238 had a minimum range from 3 to 332 km traveled per day. Considering the inaccuracy of satellite-based tracking using the Argos system (see above in methods), these daily distances should be treated with caution; however, all data were visually inspected and locations used were in concordance with other locations received based on distance, time, and date.

The time spent on outward migration by Pituffik area Peregrines ranged from 28 to 70 days and had a significant positive relationship with total migration distance ($r^2 = 0.72$, $p = 0.02$) (Fig. 9). Overall, Peregrines from the Pituffik area seemed to travel on a near daily basis. However, shortly after crossing the Gulf of Mexico, 10217 spent eight days in a coastal area in southern Mexico showing no southern movement. Additionally, 35238 from the Kangerlussuaq area had multiple stops

while on outward migration, ranging from 3 to 10 days in different areas. Stops by 36015 and 36017 may have been missed because locations were only received for 22.7% and 22.9% of the migration days, respectively, as a result of long duty cycles. Differences in distance traveled by 10212 in 2002 and 2003 on outward migration are likely a cause of locations being received for 11% versus 79% of the days spent on migration, with 2003 providing a more complete description of the flight path and distances.

Peregrines from the Pituffik area all departed in a generally southern direction, with three individuals traveling southwest along the west coast of Hudson Bay before turning due south, and one individual departing south through eastern Canada and then along the East Coast (Fig. 8). From there, one individual crossed the Gulf of Mexico while two others crossed the Caribbean Sea, with both of those individuals probably using islands along the way. The fourth individual completed its migration in northwest Mexico. From the Kangerlussuaq area, Peregrine 35238 immediately crossed the Davis Strait to northeast Labrador before going south.

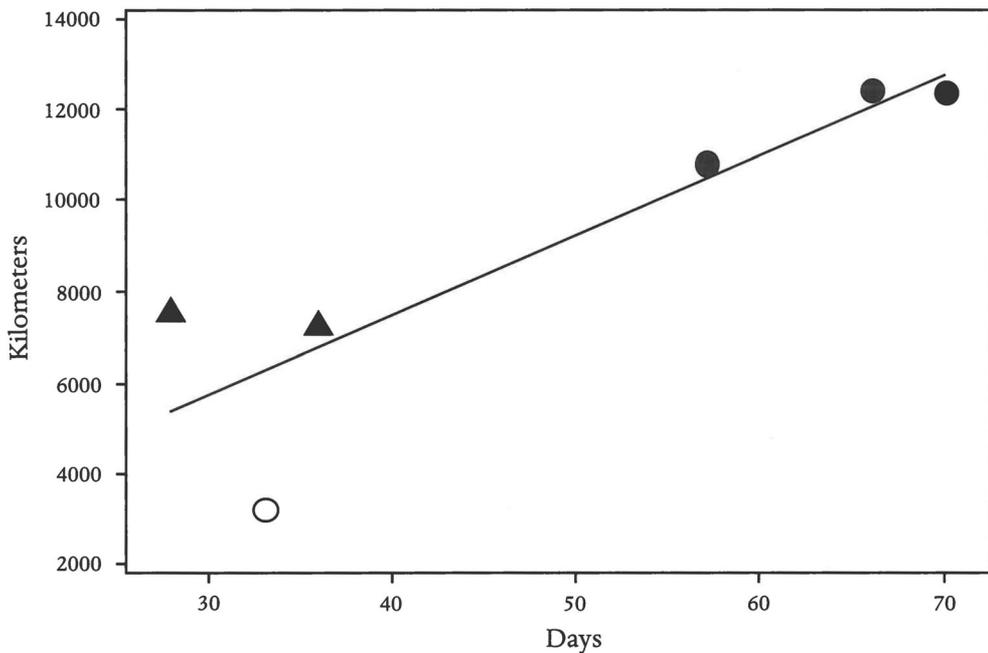


Figure 9 Positive significant relationship between overall outward migration distance and days spent on migration for adult female Peregrines from Greenland ($r^2 = 0.72$, $p = 0.02$). Filled circles are Peregrines from the Pituffik area, open circle from the Kangerlussuaq area. Individual 10212 (filled triangles) completed outward migration in 2002 and 2003 and each year is included.

Peregrines 10212 and 36015 traveled closest to the most direct route possible from the breeding to winter range, the Great Circle Distance (GCD), traveling only 11.9% and 11.2% farther than the GCD, respectively. Peregrines 10217 and 36017 traveled 23.1% and 24.1% farther than the GCD, respectively. Peregrine 35238 from the Kangerlussuaq area traveled 13.7% farther than the GCD. Clearly, these Peregrines were greatly influenced in their migration routes by the disposition of land area, especially in the Central American–Caribbean region.

Arrival date at winter home ranges for adult female Peregrines from the Pituffik area varied from 13 October to 25 November. Median arrival date was 12 November ($n = 4$). Peregrine 10212 is shown twice in Table 12 (2002 = 13 Oct., 2003 = 15 Oct.). However, only the average of 2002 and 2003, 14 October, was used to calculate the median arrival date for Peregrines from the Pituffik area. Peregrines 36015 and 36017 traveled the furthest distance from the Pituffik area and had the latest arrival dates, 14 and 25 November, respectively. Female 10212 had the earliest arrival dates while traveling the shortest distance. The arrival date for 35238 from the Kangerlussuaq area was on 6 November.

Table 13.

Location tagged and PTT ID	Start date of migration to date of last transmission	Total distance (km)	Speed of travel (km/day)	Number of days	Number of days with locations (%)	Range of distances travelled per day ^a (km)	Location classes used for daily locations ^b (LC 3, 2, 1, 0)
Kanger. 35236	25 Aug 02–21 Sep 02	1,409	50	28	18 (64.3)	3–804	2, 4, 10, 1
Kanger. 41438	2 Oct 03–15 Oct 03	2,905	208	14	4 (28.6)	165–259	0, 0, 2, 1
Pituffik 10212	14 Sep 01–6 Oct 01	4,156	181	23	22 (95.7)	7–913	1, 2, 10, 8
Pituffik 10292 ^c	24 Sep 01–3 Oct 01	2,826	283	10	8 (80.0)	61–526	0, 2, 3, 2

^a Range of distances travelled per day, see methods section for further description.

^b Location for start date of migration is either a harmonic mean from pre-migration area or GPS from nest location.

^c Juvenile Peregrine from Thule.

Incomplete outward migrations from 2001 to 2003 of female Peregrine Falcons from the Pituffik and Kangerlussuaq areas encompassing 10 or more days of travel (distances as Great Circle Distances).

Incomplete data on outward migrations were collected from three other adult female Peregrines, two from the Kangerlussuaq area and one from the Pituffik area, and one juvenile female Peregrine from the Pituffik area (Table 13). Peregrines 35236 and 41438 from the Kangerlussuaq area traveled at speeds of 50 and 208 km/day, respectively. Peregrine 10212 from the Pituffik area traveled at 181 km/day, while the juvenile Peregrine from the Pituffik area, 10292, showed the fastest speed at 282 km/day. However, locations were collected only for a period of 10 days for 10292 and probably the speed would have slowed later in the journey.

All incomplete outward migration routes had a minimum of 10 days of locations collected, providing an accurate description of the initial migration route taken (Fig. 10). The route for 10212 follows the same initial path as taken in 2003 when a complete migration was collected for the same bird (see Figs. 8 & 10). The juvenile female Peregrine from the Pituffik area, 10292, took a route not used by other Pituffik area Peregrines, traveling farther west into Canada before turning south, almost as if disoriented. Peregrine 35236 traveled the first 27 days of migration (605 km, 22 km/day) in Greenland before crossing the Davis Strait to Canada on day

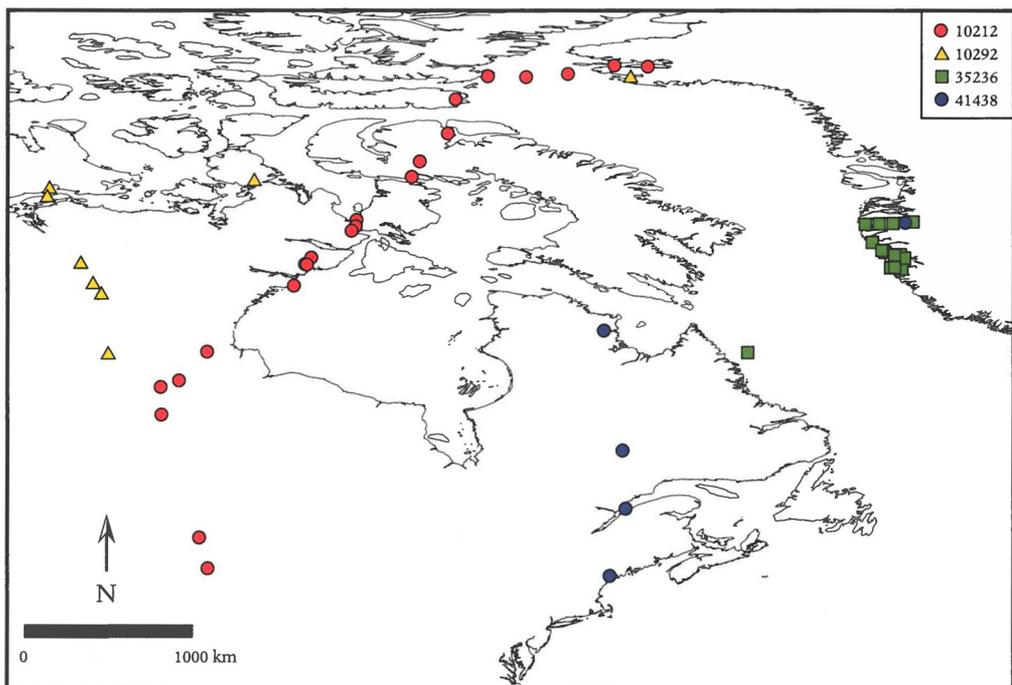


Figure 10 Incomplete outward migration routes used by three adult female Peregrines and one juvenile female Peregrine from the Kangerlussuaq and Pituffik areas, from 2001 to 2003. Only locations with LC 3–0 were used and only a single location was included per day.

28, covering 804 km in one day. Adult female 41438 from the Kangerlussuaq area crossed directly into Canada and went south.

Winter range

Adult females from the Pituffik area wintered in southern Mexico, Ecuador, Brazil, and Paraguay, with the lone individual from the Kangerlussuaq area wintering in the northeast United States (Fig. 8, Table 14). Winter ranges were obtained from all five of these individuals from 2001 to 2004, with bird 10212 providing data on winter range in both 2002/2003 and 2003/2004 (Table 15). On average, 43 (sd \pm 28) locations were received per individual Peregrine, with 10217 and 35238 only providing nine and eight locations, respectively. Additionally, locations for bird 35238 were received for only one month after it had reached the winter range and, although a winter range area is given in Table 15, it will be excluded from further analysis because the bird may have moved further south at a later date.

All winter range locations were in areas with human disturbance, with two birds wintering in areas that were residential with scattered forests (Table 14). Four of the five individuals wintered near water, including coasts, rivers, and wetland areas (Table 14). Generally speaking, all five Peregrines wintered in areas with large open spaces to hunt, including water, agricultural fields, and grasslands.

Winter range sizes were similar between individual Peregrines, with 95% fixed kernels LC 3–0 providing the largest estimate of winter range size and 50% fixed kernels LC 3–0 the smallest. No unit had more than 11 locations with LC 3–1, and range sizes were not calculated for locations with LC 3–1 based on the limited number of locations. Overall, 83% of the data used to calculate winter range sizes were locations with LC 0. With the previously demonstrated inaccuracy using locations with LC 0, most likely all of these winter range sizes are overestimated. Despite the long period of time spent on winter ranges by each individual (163 day average, $n = 4$, sd \pm 31), few locations were received. Potential causes of this could include individuals perched on trees, buildings, large cliff faces, or other sites causing the PTT to be blocked from direct line from the sky.

Peregrine 36017, which spent the most time on outward migration (70 days), spent the shortest period of time (132 days), on the winter range. In 2002 female 10212 spent the shortest time on outward migration (36 days), while spending the longest period on winter range (205 days). The correlation between the number of days spent on outward migration and the number of days spent on winter range was not quite significant ($Z = -1.826$, $p = 0.068$, $n = 4$, Wilcoxon paired sign rank test), but additional samples may strengthen the relationship.

Table 14.

PTT ID	Country	Comments on wintering area ^a :
10212	Mexico	40 km west of Villahermosa, wetlands area w/numerous islands, bordered by small plot agriculture w/orchards and grasslands, minimal farms and small communities
10217	Ecuador	on west side of Guayaquil on Guayas River, some residential and commercial w/scattered forest, large island in middle of river which appears uninhabited w/forest and some minor grasslands
35238	United States	multiple bays and estuaries, scattered forest and residential, on coast
36015	Paraguay	scattered forest w/large open pastureland for grazing, two large wetlands in addition to scattered man-made ponds, scattered farms
36017	Brazil	small plot agriculture with interspersed forest, minimal farms and small communities

^a Information on wintering areas obtained by using Google Earth.

Countries where Peregrines marked with PTTs established winter ranges and comments on each specific location.

Table 15.

Location tagged and PTT ID	Year	90% MCP LC 3-0	95% Kernel LC 3-0, LC 3-1	50% Kernel LC 3-0, LC 3-1	Number of LC 3-0 used, respectively
Kanger. 35238	2003/2004	4,147	12,541, *	2,587, *	0, 1, 3, 4
Pituffik 10212	2002/2003	961	1,230, *	286, *	0, 1, 9, 50
	2003/2004	779	1,070, *	134, *	1, 0, 5, 48
Pituffik 10217	2001/2002	511	1,724, *	216, *	0, 2, 0, 7
Pituffik 36015	2003/2004	907	907, *	178, *	0, 2, 9, 63
Pituffik 36017	2003/2004	1,659	2,193, *	512, *	1, 1, 9, 41

*not enough data to establish a meaningful value.

Winter range in square kilometers for adult female Peregrine Falcons from the Kangerlussuaq and Pituffik study areas.

Return migration

Peregrines marked in the Pituffik area with PTTs left wintering areas and began return migration from 10 April to 7 May ($n = 4$). Peregrines 10212 and 10217 completed the return migration in 2003 and 2002, respectively (Table 16, Fig. 11). Peregrines 36015 and 36017 began return migration on 30 April and 7 April, respectively, but data were received for only a limited number of days after departure from their respective winter ranges. In general, birds wintering further south, or further from the breeding area, departed earlier on return migration.

The average speed of return migration for 10212 and 10217 was 276 and 201 km/day, respectively. Both these speeds are faster than those recorded on southern migration for the same individuals. Interestingly, bird 10212 spent 36 days on outward migration in the autumn of 2002, 28 days on return migration in spring 2003, and 28 days on outward migration in the autumn of 2003, traveling thus 75 km/day faster on return migration in 2003 than on outward migration the previous autumn; yet only 7 km/day faster than the outward migration in 2003. Peregrine 10217 spent 57 days on outward migration and 55 on return migration, traveling at a speed of 190 versus 201 km/day, respectively.

Peregrine 10212 traveled 7,715 km on return migration compared to 7,532 km on outward migration (183 km difference) and 10217 traveled 11,071 km going north versus 10,836 km south (235 km difference). The difference between the actual distance traveled and the GCD increased for both Peregrines from outward to return migration. However, 10217 began outward migration from a pre-migration territory 58 km from the nest it departed from and returned to, explaining part of the difference.

Table 16.

Location tagged and PTT ID	Start and end date of migration	Total distance (km)	Speed of travel (km/day)	Number of days	Number of days with locations (%)	Range of speed of travel ^a (km)	Location classes used for daily locations ^b (LC 3, 2, 1, 0)
Pituffik 10212	7 May 03– 3 June 03	7,715	276	28	20 (71.4)	28–550	0, 0, 3, 15
Pituffik 10217	10 Apr 02– 3 June 02	11,071	201	55	37 (67.3)	32–613	1, 6, 8, 20

^a Range of distances travelled per day, see methods section for further description.

^b Location for start and end date of migration not included since they were not Argos locations.

Complete return migrations of female Peregrine Falcons from the Pituffik area (distances as Great Circle Distances).

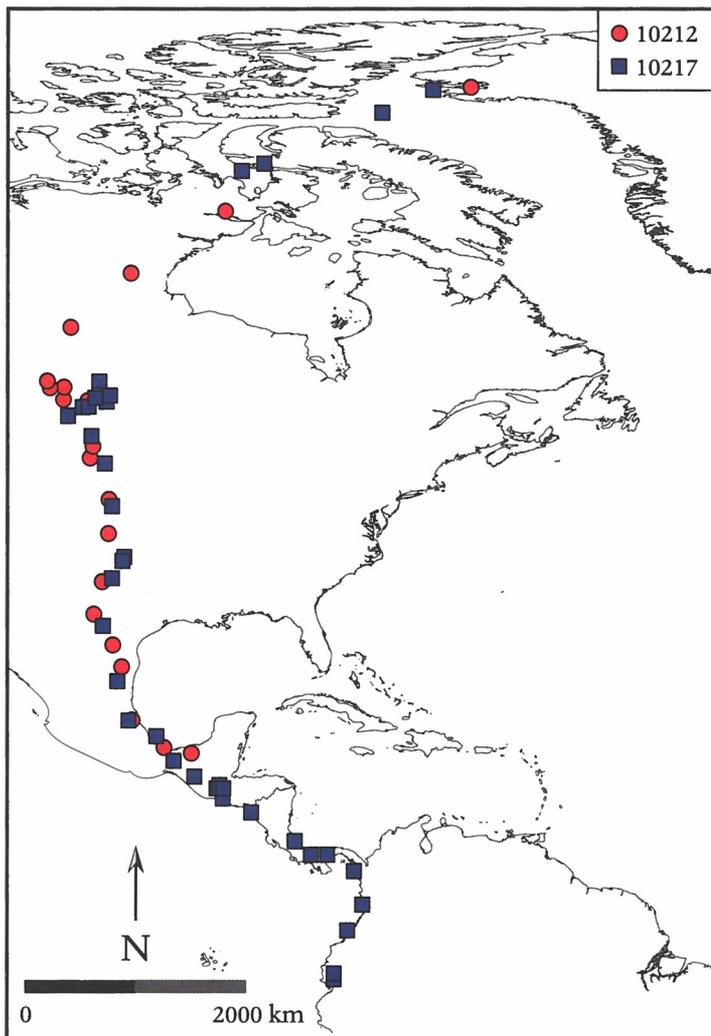


Figure 11
Return migration routes used by two adult female Peregrine Falcons fitted with PTTs in the Pituffik area. All days when locations with LC 3–0 were received were included a single time.

Climatic trends

Analyses of the 27-year period of weather data from Thule Air Base for May through September showed temperatures generally increased. Mean, minimum, and maximum monthly temperatures increased 1.107 °C, 0.540 °C, and 1.566 °C, respectively, for each five month period (Fig. 12, Appendix F). Of the 18 regression analyses, 13 showed an increase in temperatures, with both May and September having large increases for mean (1.809 °C/1.377 °C), minimum (5.346 °C/1.620 °C), and maximum (1.863 °C/1.161 °C) monthly temperatures. The minimum monthly temperatures for August showed the greatest decline, -2.079 °C, with July also having slight declines for each temperature category.

In the general context of global warming, it is now accepted that the high latitude regions of the Arctic and Antarctic have experienced more rapid temperature rises than many other regions. Although none of the 13 positive regression analyses are statistically significant (p value tested using Holm's Sequential Bonferroni corrections), using a one tail binomial test and an equal chance of having a positive or negative slope, the probability of having 13 or more of the 18 be positive was less than 5%, clearly supporting a warming trend. This warming trend, particularly in May and September, could have had the effect of lengthening the favorable summer season in the Pituffik area over the years covered.

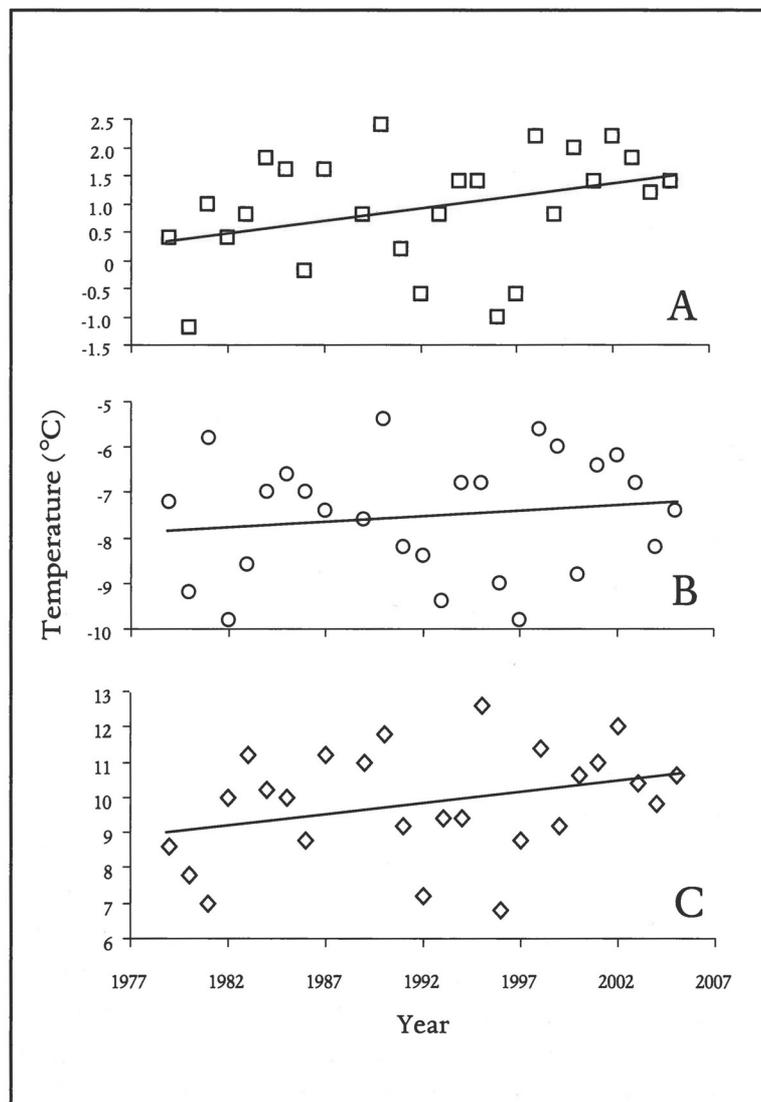


Figure 12
Changes from 1979 to 2005 in the mean (A), minimum (B), and maximum (C) daily temperatures for the months of May through September recorded at Thule Air Base, Greenland.

Discussion

It is difficult to determine where the world's northernmost nesting population of Peregrine Falcons is, but in the western hemisphere, the Pituffik area population (nest furthest north: 77.2° N) must be near the northern limit. For the Alaskan/Canadian Arctic, Peregrines have been reported nesting only as far north as Cape Sparbo on Devon Island (75.8° N, Fig. 2), but two birds were reported on Axel Heiberg Island at 79.7° N, although no evidence of breeding was found (Ross 1974). In the Eastern Hemisphere, Dement'ev & Gladkov (1951) reported Peregrine breeding sites generally "in Novaya Zemlya to Matochkin Shar Strait" (to 73.4° N, Fig. 2) and on "Markham Land" (Markham Island, 75.3° N, Fig. 2) and the "Stalinets Island around Cape Tillo" (actually should be Stalinets (now Leningrad) Strait near Tillo Islands, 74.7 to 74.5° N, Fig. 2, E. Potopov pers. comm.). Studying Peregrines breeding in the extreme environments of the far northern latitudes, near the northern limits of their range, helps us to detect any change which may be occurring and to better understand some of the factors influencing populations. The wealth of long-term information on Peregrines gathered in the Kangerlussuaq and South Greenland areas allows for latitudinal comparisons within what is potentially an almost continuous breeding population.

DDT/DDE impacts

The use of DDT starting in the late 1940s marked the beginning of a dramatic decline in Peregrine Falcon populations throughout North America, Europe, and elsewhere (Ratcliffe 1993, Cade & Burnham 2003). Although the use of DDT was finally restricted in 1972 in the United States and in 1969 in Canada, the effects were long lasting as Peregrine populations were greatly reduced, and in some cases extirpated, from huge areas across North America (for in-depth reading see Hickey 1969, Cade *et al.* 1988, Cade & Burnham 2003). In 1974 the first captive-produced Peregrine chicks were released into the wild by The Peregrine Fund in New York and Colorado, USA (Cade & Burnham 2003, Enderson 2003). These exploratory actions began an effort that lasted over 30 years, in which approximately 7,000 young, captive-produced Peregrines were released back into the wild in the United States and southern Canada. Currently, Peregrine Falcon populations in North America are in almost all regions at breeding densities equal to, or greater than, before the use of DDT (Cade & Burnham 2003).

Peregrine populations in the Arctic, specifically Alaska and Canada, were some of the first to be studied and to show eggshell thinning and a subsequent decline in numbers, both of which were correlated with DDE levels in eggs (Cade *et al.* 1968, 1971, Berger *et al.* 1970, Fyfe *et al.* 1976). While no decline in the Kangerlussuaq area Peregrine population was ever recorded, DDE was detected in eggs during the 1970s by Walker *et al.* (1973) and Burnham & Mattox (1984), with the latter collecting eight addled Peregrine eggs from 1972–78, with eggshells being 16% thinner than pre-1940s eggshells. Both studies agreed that DDE levels observed were at a “near critical” level, with a small increase likely to cause serious population decline. Additionally, Mattox & Seegar (1988), in a review of pollutants and eggshell thinning in Peregrines in the Kangerlussuaq area, reported that “some thin-shelled eggs did not hatch.”

Current research on DDE in Peregrines in Greenland, from plasma samples collected from adult females in 1985 in southern Greenland and 1983–89 in the Kangerlussuaq area, shows a decline in DDE levels beginning around 1980, to levels well below those associated with any reproductive impact (Jarman *et al.* 1994). Vorkamp *et al.* (2009) showed similar results, with DDT levels in egg shells collected from 1986–2003 in South Greenland showing a slight decrease over time. Additionally, based on eggshell fragments and whole eggs collected between 1972 and 2003 in the Kangerlussuaq area and South Greenland, Falk *et al.* (2006) found that eggshells over that period increased in thickness by an average of 0.19% per year. These findings correspond well with what has been reported as a “stable” Kangerlussuaq Peregrine population from 1972 to 1982 by Burnham & Mattox (1984) and later an increasing population, reported by Mattox & Seegar (1988), Restani & Mattox (2000), and Wightman (2001). Increases in Peregrine populations have also occurred in other parts of the western Arctic, some exponentially, with doubling times of five to seven years (Shank *et al.* 1993).

The actual effect that DDT and DDE had on the Peregrine population in the Kangerlussuaq area before the early 1970s is unknown. However, as mentioned above, both Walker *et al.* (1973) and Burnham & Mattox (1984) concluded that even a “comparatively small increase in the DDE levels these birds are exposed to would endanger the population.” It therefore seems possible, if not probable, that DDT and DDE did have an effect on Peregrine population levels in the Kangerlussuaq area. The increase in density observed from the mid-1980s to the late 1990s could be partially, if not completely, a result of the reduced use of DDT in the United States and Canada from the early 1970s on, with the lower levels observed by Jarman *et al.* (1994) in the mid-to-late 1980s largely a result of continuing DDT use in Central and South America where these birds winter, as discussed by Henny *et al.* (1996). What effect, if any, releases of captive-bred Peregrines in the contigu-

ous United States and southern Canada have had on the increased sizes of arctic Peregrine populations is unknown. However, evidence from Fig. 7, specifically haplotypes J and K, suggest that potential new haplotypes have recently entered the Greenland populations. Further research is warranted.

Density

The density of Peregrines in the Pituffik area appears to be much lower than those found by Restani & Mattox (2000) and Falk & Møller (1988, 2005) for Kangerlussuaq and South Greenland areas, respectively. Even if an occasional nest was missed, this still represents a relatively low density of breeding Peregrines. Additionally, when compared to other Peregrine populations in the Queen Charlotte Islands and Aleutian Islands, both areas with large seabird colonies much like those found in the Pituffik area, these populations had much greater densities than in the Pituffik area (Beebe 1960, White 1975). However, the Pituffik area population is distributed more linearly along the coastline, much like Peregrines along Alaskan and Canadian rivers (Cade 1960, Fyfe 1969), and an area-based density value is of limited use with Peregrines hunting primarily over the ocean.

Based on the virtual absence of breeding records for Peregrines in the Pituffik area pre-DDT, it seems probable that Peregrines have slowly colonized the Pituffik area in recent decades, perhaps helped by a general increase in Peregrine populations to the south and by a warming climate which is turning previously unsuitable breeding areas into suitable areas. Furthermore, based on the current spacing of nest sites it seems likely that the Pituffik area population is still increasing and not yet at capacity.

Nest site characteristics

Nest site characteristics in the Pituffik area differ from those in Kangerlussuaq and South Greenland areas in that nesting cliffs are generally at lower elevations and smaller in height; however, this is likely a reflection of the cliffs in the area and not something Peregrines are actively selecting for. Nevertheless, considering the harsh High Arctic environment in northwest Greenland, with snow banks and glaciers regularly occurring at elevations above 300–400 m, this is not surprising. Nesting cliffs used in the Pituffik, Kangerlussuaq, and South Greenland areas commonly face south. In general, in all three areas cliffs and ledges are present that face in all directions. Nesting ledges have a southwest directional exposure/aspect in the Pituffik area and South Greenland while they are oriented more to the south in the Kangerlussuaq area. However, Wightman (2001) reports for the

Kangerlussuaq area that traditionally occupied nesting cliffs and nest ledges were significantly oriented to the southwest, while recently occupied cliffs were significantly oriented to the south. This suggests the most desirable sites are oriented southwest and newer occupied, and probably less desirable sites, face more south. This change may be a result of the increased breeding density, and an increased shortage of cliffs with the most desirable orientation.

In the Pituffik area, severe winds of 185–240 km/h occur during each breeding season, causing driving precipitation and potential chilling temperatures, or even small chicks blowing off nesting ledges. Nest size (nest ledge depth and length) along with horizontal angle of exposure are likely key components to nest ledges that successfully produce young in the Pituffik area. When compared to the Kangerlussuaq area, nest ledges in the Pituffik area are much smaller, being on average 520 cm shorter in length and 99 cm shorter in depth. Furthermore, the horizontal angle of exposure in the Pituffik area is 25° and 10° less than in the South Greenland and Kangerlussuaq areas, respectively, providing the nest ledge more protection from high winds. This combination of a lesser horizontal angle of exposure and smaller overall nest ledge size provides the Pituffik nests with more protection from the wind and driving rain and snow, and is probably the reason behind reproduction rates being similar between the study areas despite the harsher environmental conditions found in the High Arctic of the Pituffik area. However, these differences could also be a reflection of the average nest ledge characteristics in each area; further research is needed.

Carrying capacity

In the Kangerlussuaq area, most cliffs which appear suitable for nesting are now regularly occupied by falcons. From 1983 to 1996, of 259 adult females marked, 196 were at the same nest in the following year and 12 were at different nests (Mattox & Seegar 1996). Considering these facts, and increased population density and high reproductive rate, Peregrine reproduction likely exceeds mortality (Mattox & Seegar 1988, Restani & Mattox 2000). While placing PTTs on seven adult females at the nest, in all cases during the 50–75 minute period required, extra females were seen at each nesting cliff. Additionally, as determined by using mtDNA, in one instance an incubating adult female was shown not to be the genetic mother of young later raised. While carrying capacity of this area for breeding falcons is unknown, it must be nearing or already have reached its upper limit, with non-breeders (floaters) potentially equaling or even outnumbering breeders, as suggested by Newton (1988) for Peregrine populations with high reproductive rates and survival. If true, for excess Peregrines (floaters) to breed, they must either

displace established breeders or move to areas where unoccupied habitat exists (Newton 1979, 2003a). Vacant habitat with an abundance of cliffs and prey exists to the north.

Range expansion

Despite a long history of human exploration in North Greenland, including observations on birds, sightings of Peregrines were unusual and notable. Even as recently as 1983–86, Vaughan (1988) surveyed birds in northwest Greenland, including exact locales where we found both territorial pairs and single Peregrines, but he reported only once sighting a single Peregrine, which was near Thule Air Base and likely from Dundas Mountain. Additionally, Hall spent time from 1871 to 1873 in multiple localities where current nests and Peregrines were observed, with precise written instructions from Prof. Baird, 9 June 1871, National Academy of Sciences, Washington D.C., USA, that “The Arctic falcons should be collected in all their varieties, to ascertain whether there are two forms, a brown and a white, distinct through life, or whether one changes with age into the other” (Davis 1876). However, no Peregrines or Gyrfalcons were collected or seen. Peary, from 1891 to 1896, spent many months in the Pituffik area, with large camps in areas where currently nesting Peregrines or lone individuals were observed. However, no Peregrines were reported or collected, but Gyrfalcons in these areas were clearly noted, in some cases collected, and still breed at the same exact localities. Freuchen (1921), while living approximately 1 km from Dundas Mountain in the mid-1910s, kept a record of bird life in the area, reporting that Gyrfalcons bred on Dundas Mountain for eight consecutive years, giving detailed descriptions of their battles with ravens. However, he never once mentions Peregrines in his description of bird species in the area. Local Inuit hunters provide further evidence that Peregrines are only recently colonizing the Pituffik area, as they are still unfamiliar with them.

We have located both breeding and non-breeding Peregrines over a large area. Although we cannot definitively prove Peregrines are expanding their range northward in Greenland, there is certainly strong circumstantial evidence. The fact that single adults and sub-adults are being regularly observed in association with certain sites during the breeding season is suggestive of an increasing (or decreasing) population (Newton 1979). The continual occupancy of all known breeding sites and annual replacement of lost marked females is evidence of a robust population, with birds (floaters) looking for mates and/or breeding sites. If Peregrine populations are indeed increasing and expanding their range northward, why is this occurring now, while it was not evident during the pre-DDT era?

The Pituffik (76.5° N) and Kangerlussuaq (67° N) study areas and the Pituffik and the South Greenland (60.5–61.0° N) study areas are separated by approximately 1,100 km and 9° of latitude, and by 1,700 km and 16° of latitude, respectively. In the Kangerlussuaq area, the longest recorded natal dispersal for a female was 690 km, to the southern study area (Restani & Mattox 2000). In Alaska a male dispersed 370 km (Abrose & Riddle 1988) and, from captive-bred and released Peregrines in the Midwestern United States, one male dispersed 1,520 km and a female 1,760 km (Tordoff & Redig 1997). These are extreme values, but the approximate 1,100 km distance between the Pituffik and Kangerlussuaq study areas could clearly be covered by first year birds when dispersing, especially considering that Peregrines occur in-between, albeit likely at much lower densities.

The temporal breeding window for Peregrines, and other bird species, must narrow moving northward within Greenland. Avian species breeding at high latitudes are said to be restricted by two major environmental constraints (O'Reilly & Wingfield 1995). First, they must arrive in breeding areas, establish a territory, attract a mate, and successfully breed as early as possible because the arctic summer is so brief. Particularly for species with prolonged incubation and parental care (including Peregrines), departure from the breeding areas must occur before winter sets in and environmental conditions deteriorate (weather and food availability), reducing survivorship of breeders and progeny. Secondly, the earlier the arrival the more unpredictable the weather, and Peregrines run the risk of arriving before their prey. Emphasizing the importance of breeding early, Restani & Mattox (2000) found that broods producing recruits in the Kangerlussuaq Peregrine population tended to fledge earlier (median = 16 August) than other broods (median = 18 August). A similar tendency has also been found in other bird species (including raptors) nesting at lower latitudes (Newton 1986, Village 1990).

Latitudinal summary of breeding

In South Greenland, using the estimated average age of young at ringing, the median (only median given in literature) hatch date for 13 Peregrine clutches over seven years (1979–1985) was 4 July and the median fledging date 15 August (Falk *et al.* 1986). Peregrines in the Kangerlussuaq area usually arrive at nests in mid-to-late May (W. Mattox & W. Burnham pers. comm.). Using the annual estimated average age of Peregrine young ringed from 1983 to 1997 (Mattox 1997), we calculated a 14-year average hatch date of 10 July and a 42-day-of-age average fledging date of 21 August (Table 3). For the Pituffik area, hatching occurred on 15 July and fledging, or nest leaving, on 27 August, with the median and average date being the same. Nesting chronology for Peregrines in the study areas of South Greenland,

Kangerlussuaq, and Pituffik are about six to seven days later for each location from south to north, or 12–13 days for the whole $\sim 17^\circ$ latitudinal span.

Based on information from Kangerlussuaq, we estimated the usual time required for Peregrines to arrive at the nesting site, breed, and for their young to become independent of parental care and capable of migration to be approximately 117 days. That is two weeks from arrival to first egg, a four-egg clutch with one egg laid every other day with incubation begun on the third egg, 34-day incubation period, 42-days fledging for young, and 21 days after fledging until young are independent of parental care and capable of migration. This fits well with known arrival dates of Peregrines in the Kangerlussuaq area and the dispersal of young from nest sites (Sherrod 1983), but less well for the Pituffik area (see below).

Home range size

While breeding home range and winter range sizes were calculated for adult female Peregrines from the Kangerlussuaq and Pituffik areas by using PTTs, this information must be considered cautiously. Data from the stationary PTT at Thule Air Base (Appendix A, Tables 2, 3, and 4) clearly shows that using locations with LC 0 to calculate home range sizes greatly increases error. While it may be necessary to use locations with LC 0 to increase sample sizes, these range sizes should be considered maximum likely home range sizes and be viewed skeptically. Furthermore, while home range sizes and the numbers of PTT locations used in calculations showed no significant relationship for any of the methods of calculation in this study, a relationship may exist with fewer locations, as home range size tends to increase up to a point with the number of locations used. Girard *et al.* (2002) show that between 30 and 100 locations are needed to reach an asymptote, based on GPS-equipped satellite-received telemetry which is much more accurate. A better procedure is to calculate home range sizes using multiple methods and to include data on the number and class of locations used for calculations (e.g., see Tables 10, 11, and Appendix D). This procedure allows readers to draw their own conclusions based on the data, since the actual breeding and winter home range sizes most likely lie somewhere between the largest and smallest sizes calculated.

The average breeding home range size of adult female Peregrines in the Pituffik area emerged as larger than in the Kangerlussuaq area (Table 11) based on 11 of 12 methods used for calculation, but on the samples available, the difference was not significant. This possible difference may be influenced by Peregrine nesting density in the Kangerlussuaq area being higher than in the Pituffik study area, possibly resulting in more territorial conflicts that may compress home ranges, while in contrast, the Pituffik area population may be well below capacity level,

facilitating larger range sizes. In addition, based on the long distances between Little Auk colonies and Peregrine nest sites and visual inspection of PTT locations, Peregrines are likely hunting passing Little Auks over large expanses of ocean, while Kangerlussuaq Peregrines prey upon what appear to be fairly dense populations of passerines.

Breeding home range sizes calculated using 90% MCP LC 3–0 for females in the Kangerlussuaq (1,475 km², $n = 7$) and Pituffik (3,021 km², $n = 8$) areas were both larger than those found by Ganusevich *et al.* (2004) (1,175 km², $n = 4$), who used PTTs and the same method of calculation for female Peregrines breeding in the Arctic on the Kola Peninsula, Russia. However, these differences in apparent range sizes may be a result of differences in the average number of locations used for calculations, 99 and 97 in Greenland compared to 47 in Russia, respectively. These home range sizes were calculated using locations with LC 0 and should, therefore, be considered maximum likely home range sizes.

McGrady *et al.* (2002) calculated the winter home range size for Peregrines with PTTs using 90% MCP LC 3–1. They found an average size of 169 km² for 13 adult females and one adult male wintering along the coast of the Gulf of Mexico. Using 90% MCP LC 3–0, we calculated an average winter range size of 1,077 km², based on four winter range sizes with more than 10 locations (Table 15). We had too few locations with LC 3–1 to calculate the equivalent range size and our results do not allow for a meaningful comparison of winter range sizes between the two studies.

Timing of breeding and migration

PTTs show that two adult female Peregrines arrived in the Pituffik area on 3 June (Table 18), one each in 2002 and 2003. Egg laying in Pituffik area Peregrines begins about 7 June. Observations in the Kangerlussuaq area show Peregrines arriving at nest sites in mid-to-late May with an average laying date of 2 June. Peregrines breeding in the High Arctic may therefore be able to compress the breeding cycle by laying eggs sooner after arrival. Thus, the earlier-mentioned 117-day minimum time to breed may be shortened in the Pituffik area by about one week.

In the Pituffik area, Peregrine young are probably not independent of parental care until mid-September or later. This coincides with the single juvenile nestling marked with a PTT in 2001, which departed the area and began outward migration on 23 September. However, in 2002, a juvenile male was caught near the nest on 26 September and a juvenile female was caught at a capture and ringing station on 30 September. The average departure date from nest sites (1994, 1996, and 1997) for adult female Peregrines with PTTs from the Kangerlussuaq area was 12 September ($n = 14$; M. Fuller pers. comm.) with Peregrines showing similar depar-

ture patterns as observed during this study, including the immediate crossing of the Davis Strait after departing the nest, the use of pre-migration coastal areas, and individuals moving south along the coast before crossing the Davis Strait (M. Fuller & B. Seegar pers. comm.). In 1994, an adult female Peregrine at Dundas Mountain was tagged with a PTT by W. Burnham and departed on 21 September ($n = 1$; M. Fuller pers. comm.). During 2001–2003 the average departure date for adult female Peregrines in the Pituffik area was 16 September ($n = 8$). Of the four adult females that completed the outward migration from the Pituffik area, two used the Central Flyway (one female in consecutive years), one the Eastern Flyway, and one a combination of the two. Based on the average fledging date of nestlings given above, 27 August, and the average departure date for adult females, 16 September, this leaves a 19-day post fledging period when adult females are present to care for young. This contrasts to what Sherrod (1983) found for two family groups in the Kangerlussuaq area, where in each case both adults along with their chicks stayed at the nesting cliff as a family unit for five and just over six weeks before departing on migration. However, we do not have same nest information on fledging date and departure date of adult females, and the 19-day post fledging period we give for the Pituffik area is a rough estimate, and may be off by up to several weeks. Given the much shorter breeding window in the Pituffik area it seems likely the post fledging period is shorter than in the Kangerlussuaq area.

Ring recovery from Peregrines in all three study areas show long seasonal movements (Mattox & Seegar 1988, Fuller *et al.* 1998, Restani & Mattox 2000, Falk & Møller 1988, Lyngs 2003). Fuller *et al.* (1998), using PTTs, found that on average 22 adult female Peregrines from the Kangerlussuaq study area, Quebec, and the Northwest Territories traveled 8,624 km at a speed of 172 km/day during outward migration. Pituffik area females tagged during this study traveled an average of 10,794 km ($n = 4$) at a speed of 205 km/day ($n = 5$) during outward migration (Table 15), over 2,000 km farther and 30 km/day faster. This difference may be expected as the Peregrines in the Pituffik area nest much further north than the birds marked by Fuller *et al.* (1998), and winter further south. Of specific interest is Peregrine 10212, which during outward migration in 2002 traveled at a speed of 201 km/day compared to 269 km/day in 2003, while both years wintering in the same location (Table 13). These results within Greenland extend the leapfrog migration pattern of Peregrines previously described by Newton (2003b).

As stated by O'Reilly & Wingfield (1995), to establish territories successfully and obtain mates it is important for birds to arrive at breeding sites as early as possible. Fuller *et al.* (1998) found Peregrines in the western hemisphere traveled at an average speed of 198 km/day ($n = 7$) going north. This contrasts with an average speed of 239 km/day ($n = 2$) for females from the Pituffik area. Considering the separa-

tion between study areas in Greenland and the distances that Peregrines must fly to reach more northern latitudes, distance and prey availability, both affected by weather, may be the primary factors that influence arrival dates for Peregrines in North Greenland.

Butler (2003) examined arrival dates from 1903 to 1950 and from 1951 to 1993 for 103 species of migrant birds in New York and Massachusetts. He found that during the more recent interval, birds wintering in the southern United States (short-distance migrants) arrived on average 13 days earlier, and those wintering in South America arrived only four days earlier (long-distance migrants). As an explanation for the differences, he hypothesized that the short-distance migrants are able to take advantage of moderating climate by gradually moving northward in the spring (and south in the autumn/winter), sensing and taking advantage of favourable conditions, while long-distant migrants cannot judge climatic conditions in the breeding grounds and are less plastic in their ability to respond. Additionally, Murphy-Klassen *et al.* (2005) examined dates of first arrival at Delta Marsh, Manitoba, for a 63-year data set for 96 species of migrant birds in association with increasing mean monthly spring temperatures. They found that climate warming has influenced the spring arrival date of a number of species, with waterfowl species that breed at Delta Marsh and other short-distance migrants more frequently arriving earlier than other groups of birds, such as long-distance migrants. Further, Gilyazov & Sparks (2002) found that from 1931 to 1999 at the Lapland Nature Reserve, Kola Peninsula, Russia, most avian species increased their period of stay on the breeding grounds, while environmental conditions in general also improved during the same period.

Survival, particularly in juveniles, may be increased from having more time after fledging until outward migration, allowing a longer period to learn to hunt and increase body reserves.

Weather impacts

Bradley *et al.* (2007) showed that weather can have a significant effect on the breeding success of Peregrines in the Arctic. Despite the harsh High Arctic conditions, Peregrine reproductive rates in the Pituffik area compare very favorably with those in the South Greenland and Kangerlussuaq area. In South Greenland between 1981 and 2005, the average number of young produced per year per occupied site was 1.8 and per successful site was 2.9 ($n = 23$ years, Falk & Møller 1999, 2005). For the Kangerlussuaq area, from 1972 to 1998, the mean number of young per year per occupied site was 2.30, and per successful site 2.93 ($n = 27$ years; successful pairs, $n = 702$; Mattox 1997). This compares with an average of ≥ 2.17 young per year

per occupied site and ≥ 3.18 per successful site in the Pituffik area from 1993 to 2005. Bradley *et al.* (1997) found a linear relationship between chick mortality and precipitation during lengthy storms, and suggested that severe weather could be survived, as long as it was broken by periods of good weather, when hunting could occur. Also, nest failure was most likely to occur when chicks were small. In the Pituffik area, although weather can be severe, long periods of precipitation were unusual in recent years. Weather-caused nest failures in the Pituffik area may now be no more frequent than for more southern West Greenland Peregrine populations, especially considering the greater protection afforded by nests in the Pituffik area. However, the reported differences in productivity between the three study areas may also simply be a function of sample size.

Effects of weather, and particularly climatic trends, on prey species could significantly influence Peregrine populations. In the Kangerlussuaq area and South Greenland, passerine species form the largest component of Peregrine prey by numbers and biomass (Burnham & Mattox 1984, Rosenfield *et al.* 1995, Falk *et al.* 1986). Rock Ptarmigan are next in importance, but because of their population fluctuations and low densities they are a less dependable food source. In these more southern West Greenland areas, the other more common passerine prey species and wetland species do not arrive until mid-May, about the same time as Peregrines, except for Snow Buntings which occur at low densities (Salomonsen 1950, Falk *et al.* 1986). Falk *et al.* (1986) also points out that fledging dates of Peregrines and passerines are similar for South Greenland and the Kangerlussuaq area. Salomonsen (1967) reports that Little Auks arrive in the first half of May in North Greenland, probably prior to Peregrines. Even when Peregrines do arrive, the locations where Little Auks may occur and be available as prey are influenced by sea ice, as Little Auks need open water to feed. Passerines arrive in June and are mostly gone by early September. Little Auks depart from nesting sites by mid-to-late August, and along with most other potential prey are gone from North Greenland by early September (Salomonsen 1950). Breeding Peregrines may have difficulty finding food for their fledged young before they migrate, with larger prey species such as Black Guillemots and Black-legged Kittiwakes, which fledge in mid-to-late August and depart in September, being probable prey species in September (Salomonsen 1950). Salomonsen (1950) says that the Black Guillemot is "extremely hardy and ... the last bird in the autumn to yield to the ice."

Given the age of Salomonsen's (1950) information, now over 55 years old, it is likely that arrival and departure dates that he gives have changed, as even then he noted in kittiwakes that "[t]he departure has been delayed in recent years, owing to the amelioration of the climate." Additionally, from our own experience from 1993 to 2005 in the Pituffik area, in late-August through late-September we would

agree that Black-legged Kittiwakes and Black Guillemots make up the majority of the prey species available to Peregrines. However, passerines, specifically Snow Buntings, also appear to stay well into September now. Falcon populations probably benefit from any shift in climate that increases prey densities at the start and end of the season and, more importantly for North Greenland where Little Auks provide an unlimited prey base when present, allowing for earlier arrivals and later departures of prey in breeding areas.

Ecological impacts of climate change

Hussell (2003) found spring temperatures to be strongly correlated with timing of laying in Tree Swallows *Tachycineta bicolor* and estimated that a climate warming of 5 °C in May could result in an average advance of about seven days in the median date of laying. He speculated that greater insect abundance during the pre-laying period was a possible reason that swallows were breeding earlier, at least in some locations. In North Greenland prior to 2000, mosquitoes were virtually unknown by the northern Inuit and Thule Air Base residents, and had not been seen at Thule Air Base for at least 30 years (longest resident at Thule Air Base). In 2001 the first mosquitoes were seen, and by 2003 mosquito density in wetland areas appeared similar to that in southwest Greenland. Snow Buntings were observed carrying beaks full of mosquitoes back to their nests. Mosquitoes provide a new and potentially important food source for passerines and may indirectly increase density and prey availability for falcons. Since Snow Buntings are one of the later species to leave the High Arctic (Salomonsen 1967), an increase in their numbers could importantly benefit Peregrines. However, while ringing nestling Peregrines we now have observed young plagued by mosquitoes. This sudden addition of mosquitoes, along with changing climatic conditions, could lead to problems, such as was found in Brünnich's Guillemots in Hudson Bay in 1997–1999, when high maximum daily temperatures and large numbers of mosquitoes led to both breeding failures and adult mortality (Gaston *et al.* 2002).

There is an increasing body of evidence documenting that a warming trend in climate is occurring in the Arctic, as in many other regions (Overpeck *et al.* 1997, Morison *et al.* 2000, Arctic Climate Impact Assessment 2004). Within Greenland, Burnham & Burnham (2011) recently showed that from 1994 to 2010 the lay date of Gyrfalcons in the Pituffik area significantly advanced, likely as a result of warmer and earlier springs. Similarly, favorable ecological conditions would seem to be promoting the expansion of the Peregrine population in the Pituffik area. This may be occurring as a range extension from further south in West Greenland by increasing numbers of falcons which are moving northward and breeding, made

possible by the long dispersal abilities of Peregrines (see above), and/or by allowing a small local population of Peregrines further north in Greenland to have an increased reproductive rate.

From historical information, at least one nest site has been irregularly occupied by Peregrines for over 75 years in the Pituffik area. How frequently the nest was occupied is unknown, but from historical records presented earlier, it appears likely that the nest was not occupied on a regular basis until the 1980s. One possible explanation for the past reported sporadic use of this lone nest, on Dundas Mountain, could be that it is what Hickey (1942) referred to as an "ecological magnet," a site that is so desirable that it is re-used time after time, despite the fact that the current birds have no former familiarity with the location. In the same way, following the extirpation of Peregrines in much of Europe and North America, captive-bred and released birds reoccupied former nests first, in some cases even using the exact nesting ledge (Ratcliffe 1993, Oakleaf 2003). Additionally, Kleinstäuber & Kirmse (1988) found that cliffs were reoccupied in the reverse order that they were deserted, with Peregrines obviously showing a preference for certain cliffs. Based on this idea, it seems plausible that over the past 75 years, a limited number of Peregrines have immigrated into the Pituffik area, possibly only a bird every few years or small invasions of several birds at once, and in each case attempted to breed on Dundas Mountain when both sexes were present. However, the breeding attempts likely would have been unsuccessful due to cooling climatic trends that were found throughout the Arctic from ca. mid-1930s to ca. 1960s (Kelly *et al.* 1982), and a local population would have never been established, with adults dying off over time and only being replaced by new breeders when new immigration took place. Only in recent times (ca. early 1980s to present; Serreze *et al.* 2000, Mountain *et al.* 2001, Whitfield 2004) have environmental conditions improved, enabling successful reproduction on a regular basis, with a local population becoming established. This explanation seems even more likely given the long-term high level of nest site fidelity in Peregrines (Newton 1979). Since 1993, all six Peregrine nests in the Pituffik area have been occupied every year after the nest was initially found (Table 2), including Peregrines on Dundas Mountain each year for the past 13 years. Furthermore, based on the current distribution and close proximity of nests, and that Vaughan (1988) found no falcons at several of these current locations in the mid-1980s, it seems likely that the population in the Pituffik area is expanding out from immigrants from further south which first bred at Dundas. This same pattern of expansion from a central location has also been observed with other raptor populations (Newton *et al.* 1994, Lensink 1997).

It is, of course, impossible to rule out the alternative that a small local population of Peregrines has always existed in North Greenland, albeit at a low density. In

this case reproduction was probably successful only in a limited number of years, keeping the population small. With better and changing climatic conditions, productivity may have increased or mortality decreased, with the population currently expanding. However, our research does not support this conclusion.

Overall body size of Peregrines, measured as PC1, is not significantly different between female Peregrines in the Kangerlussuaq and Pituffik areas. However, the average mass of females between the two areas is significantly different; with Pituffik area females weighing more than Kangerlussuaq area individuals of the same body size (Fig. 6). Genetic evidence based on both microsatellites and mtDNA show that there is clearly no difference between the populations. Despite this, the possibility exists that, while the populations have always been linked, historically gene flow was much reduced and only in the recent past (say 10–20 years) has gene flow increased. Unfortunately, not a single historical specimen was ever collected from the Pituffik area so it will never be possible to compare current genetic structure to that of the past. Whether the cause was local population growth, immigration of birds from the south, or a combination of the two, Peregrine density appears to have increased and the breeding range expanded northward. Climate change seems the most plausible facilitating factor.

Bradley & England (1978) concluded that a major climate change occurred in the Canadian High Arctic and northwest Greenland in approximately 1963–64. Mean freezing level height (elevation) dropped up to 500m in July and mean July maximum surface temperatures decreased up to 2.7 °C, with levels staying low throughout the study which ended around 1976 (Bradley & England 1978). Temperatures appear to have only begun to increase in the late 1970s to early 1980s in the Pituffik region. Whitfield *et al.* (2004) compiled circumpolar weather data from 1976 to 1995 for 247 temperature and 555 precipitation climate stations. In the cluster of stations that included the Pituffik area (and all of North Greenland), they reported with moderate to strong confidence that warming has occurred from the beginning of April through mid-August. This is further supported by Mountain *et al.* (2001) who, using High Arctic weather stations at Thule Air Base, Alert, Eureka, and Resolute, concluded that from 1994 to 2000 temperatures have increased during spring months, leading to “the onset of an earlier spring for the region,” and an overall continual warming trend in the area. Additionally, Serreze *et al.* (2000), showed an increase in the annual surface air temperature for northwest Greenland from 1966 to 1995, with spring showing the greatest seasonal increase and autumn being second.

Our analysis of the Thule Air Base weather data from 1979 to 2005 was based solely on the five-month period, May through September, which would have the greatest potential effects on Peregrines. Although the long-term trends in none of

these individual months were statistically significant, this was likely due in part to the large fluctuations in temperatures from year to year. However, the general trend is extremely clear, showing that over the past 27-year period (1979–2005) that the mean monthly temperature, minimum monthly temperature, and maximum monthly temperature have increased for almost all months, with only July having a negative trend for all three temperature variables and May and September having a positive trend for all three (Appendix F).

Even though the above-mentioned temperature changes are relatively small, they could have an important impact on the climate in the Pituffik area, specifically the Greenland Ice Sheet and sea ice cover (Chapman & Walsh 1993, Paterson & Reeh 2001, Walsh & Chapman 2001, Weller *et al.* 2005), which could significantly impact Peregrines and their ability to reproduce successfully and survive. With the warming trend during the spring and autumn months, sea ice break-up is occurring earlier and freeze-up is occurring later (Weller *et al.* 2005). That, combined with a decrease in snow accumulation as demonstrated for northwest Greenland by Hanna *et al.* (2001) from 1979 to 1998, potentially allows Little Auks and other birds earlier access to breeding and foraging areas, both of which previously would have been covered by snow and sea ice, respectively, until some later date. However, and perhaps most importantly, warmer autumns, specifically the month of September, may allow prey species for Peregrines to remain in the Pituffik area longer and to begin migration later, providing an increased late season prey base for Peregrines. Furthermore, in the past, the periodic extreme low minimum temperatures each month may have played an important role in causing failure of breeding Peregrines, with a more stable climate enabling better reproduction.

The cooling period from the 1930s through the late 1970s likely made for a climate in the Pituffik area too cold, with a breeding window too short, for Peregrines to reproduce successfully on an annual basis. Probably the length of the potential breeding window in the Pituffik area has continued to expand since the mid-to-late 1980s, with breeding conditions having improved as a result of earlier and warmer springs and longer and warmer autumns. On this basis, species breeding at the periphery of their range would be expected to increase in density and the more southern nesting species to expand their ranges northward (Burton 1995, Newton 2003a). An example may be the Canada Goose *Branta canadensis*, which Salomonsen (1981) described as a rare and irregular breeder in the Disko Bay region, west Greenland. However, since the early 1990s, Canada Geese have greatly expanded their range and density throughout west Greenland (Boertmann 1994, Fox *et al.* 1996), and have bred successfully in the Pituffik area since 1998.

Overall, the most probable benefits for Peregrines from climate change would be enhanced prey availability early and/or late during their breeding cycle, effec-

tively expanding the breeding window, and better conditions for incubation and rearing of young, allowing for successful reproduction more often than in the past. Even if pre-DDT Peregrine density, productivity, and mortality rates for West Greenland were as they are at present, Peregrines may have had only limited success exploiting North Greenland's huge food supply and nesting sites because of a narrow breeding window and a colder climate from the mid-1930s into the late 1970s.

Conclusion

Falcon surveys from 1993 through 2005 in the Pituffik region, northwest Greenland, located a previously unknown breeding population of Peregrine Falcons. Previous sightings of Peregrines were unusual, and the species was unknown to the northern Inuit and arctic explorers. Only a single nesting location has ever previously been reported for the Pituffik area. This population may compose the most northern nesting Peregrines in the world. Well-studied Peregrine populations exist over much of Low Arctic Greenland, particularly in the central-west (Kangerlussuaq) and South Greenland, and previous long-term research was accomplished on these populations. Differences and similarities in ecological strategies between these populations are evident.

The Peregrines in the Pituffik area nest on coastal cliffs, primarily feeding on Little Auks that occur there in the tens of millions. Peregrines breeding in the Kangerlussuaq area nest on cliffs in a large ice-free inland area and feed primarily on small passerines. The Pituffik area Peregrines are ecologically functioning like the North American maritime race, *F. p. pealei*, but have the migratory behavior of the arctic race, *F. p. tundrius*, in which Peregrines in Greenland are included.

Morphological comparisons of adult female Peregrines from the Kangerlussuaq and Pituffik area populations show no significant differences except in body mass, which is significantly greater for the more northern female Peregrines. The difference in body mass may reflect better physical condition because of the large available prey population and less density-dependent stress on Pituffik area Peregrines than those in the Kangerlussuaq area. The Peregrine population in the Kangerlussuaq area may be at carrying capacity for the habitat because almost all cliffs that appear suitable are regularly occupied. Genetically, Peregrines from both the Kangerlussuaq and Pituffik area populations are essentially the same. Because of the significant lack of morphological and genetic differences, we conclude that the newly-discovered Pituffik area population probably represents a northern extension for Peregrines in Greenland rather than an increase in a previously unknown existing population.

Information from PTTs on adult female Peregrines show that Pituffik area females arrive at nest cliffs in the spring about two weeks later and depart from sites two weeks earlier than the Peregrines breeding in the Kangerlussuaq area. The difference in arrival dates probably results from a combination of wintering

areas being further south, the migration distance being longer, and prey not being available earlier. Interestingly, although Pituffik area Peregrines arrive two weeks later at nest sites they are only about one week later to lay eggs. Peregrines must have the ability to compress to some extent the time between arrival and reproduction if necessary. For egg laying to begin within one week of arrival in the Pituffik area, females must immediately find a mate and territory and begin copulation to breed successfully. Additionally, adult females depart on migration approximately three weeks after their young fledge from the nest, between two and three weeks earlier than females in the Kangerlussuaq area. Young Peregrines are thus either fed by the adult male for a longer period of time or must learn to hunt much faster and earlier.

PTT data show breeding home range size is not significantly different between Peregrines in the Kangerlussuaq and Pituffik areas. However, results from the stationary PTT at Thule Air Base clearly show that using locations with LC 0 when calculating home range size artificially inflates the overall range size. Additionally, range size should be calculated using both MCP and fixed kernels, providing a range of estimated sizes from smallest to largest based on the method of calculation. Information should also be given on the number of locations used to calculate range sizes, as well as their location classes, allowing the reader to compare more easily between papers and to judge for themselves the validity of the calculated range sizes. In general, the best overall use of PTTs is for tracking birds on migration where the scale of the area being covered is much greater and the effects of location inaccuracies relatively less.

During migration, Peregrines from the Kangerlussuaq area use the Eastern Flyway while Peregrines from the Pituffik area use both the Eastern and Central Flyways and areas in-between. Peregrines from the Pituffik area flew southwest, passing to the east and west of Hudson Bay, then fanning out and traveling either over Mexico and Central America or across the Gulf of Mexico or Caribbean Sea. Pituffik area Peregrines migrated at a more rapid speed than Peregrines from the Kangerlussuaq area (see discussion above), the possible advantage being to reach prime wintering areas before other falcons. Pituffik area Peregrines carrying PTTs wintered in Central and South America, including Mexico, Ecuador, Brazil, and Paraguay, making theirs some of the longest migrations known for any raptor. This may result because by the time the more northern nesting falcons reach potential optimum wintering areas they are already occupied by territorial Peregrines from elsewhere.

Peregrines can probably regularly reproduce and survive in the High Arctic now, due to a warming trend over the past 20–25 years, resulting in earlier and warmer springs and warmer autumns. This warming trend, particularly during

the months when Peregrines are on nesting territories, has probably widened the breeding window, making successful nesting possible much more often than in the past. Nesting chronology between South Greenland, Kangerlussuaq, and Pituffik area Peregrines show they breed about six to seven days later for each location south to north, or 12 to 13 days later over the whole $\sim 17^\circ$ latitudinal range. Soon after climate moderation, it is unlikely that Peregrines wintering far to the south can sense or evolve and take advantage of increased minimum temperatures by arriving earlier on breeding territories, unless during the last part of their journey they accompany their prey northward. Instead, the greatest benefits are probably during the post-fledging to migration period, possibly by increasing prey abundance and availability and reducing mortality, particularly of immature Peregrines.

Peregrines probably were able to quickly take advantage of the temperature change because they were already present further south. As the nesting density and related density dependent factors increased to the south, in particular, non-breeding sub-adult Peregrines probably annually moved further north, eventually reaching northwest Greenland where territorial adults were few or absent and the summer abundance of prey was great. Some of these falcons may even occasionally have attempted, or even succeeded in, breeding. Once reproduction/immigration exceeded mortality/emigration, breeding density could increase and will probably continue to do so, unless environmental temperatures change to their disadvantage.

Considering the Peregrine's adaptable nature – emphasized by its predatory behavior; its almost global distribution and existence in both arctic, temperate, and tropical environments; and the variation in its migratory patterns, from being a long-distance migrant to having no seasonal movements at all – it should not be surprising that the species can extend its range northward into the High Arctic with an abundance of prey, providing environmental conditions allow. By comparing regional populations of Peregrines along Greenland's west coast, we can begin to understand the probable dynamic short-term and more slowly evolving long-term environmental influences and ecological processes allowing this to happen. If the apparent High Arctic climate amelioration continues, the Peregrine Falcon breeding range may eventually extend into Peary Land, the most northern land mass in the world.

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Appendix A

The stationary PTT at Thule Air Base, 36321, operated from 30 September 2002 to 20 November 2003. During this period 2,284 locations were received, with locations with LC 3-1 and LC 3-0 making up 44.0% and 66.2%, respectively (Table 1). These percentages are much greater, specifically for LC 3-0, than for PTTs we attached to Peregrines during this study and probably reflect the unit being stationary and in the open, a near-optimal setting. Despite the PTT being in a fixed position and having a constant duty cycle, the numbers of receptions per month varied, with summer months generally having more receptions than winter months. Differences most likely were caused by snow cover during winter months when during some periods colleagues were unable to check the unit due to winds exceeding 275 km/h and ambient temperatures below -40 °C. During the period late May through early October 2003, the PTT was checked frequently and no snow cover or other problems were found.

“Home range size” for the stationary PTT was calculated using locations collected from 3 June to 23 September 2003, a period of time when Peregrines have been shown to be in the Pituffik area. Despite this unit being stationary, estimated range size varied depending upon method of calculation from 104 km² using 90% MCP LC 3-0 to 0.8 km² using a 50% kernel with LC 3-1 (Table 2). Range sizes calculated for PTT 36321 were much larger when using locations with LC 3-0 than those calculated using locations with LC 3-1, and generally kernel methods were much closer to reality (i.e., smaller, since the PTT is stationary) than MCP.

To verify the accuracy of individual location classes, home range sizes and the average distance of error were calculated for the entire life of the stationary PTT using each location class, LC 3, 2, 1, and 0 (Tables 3 & 4). Results were as expected, with subsequent reductions in range size and distance error from LC 0 to 3. Error was greatest when using locations with LC 0, with range size varying from 30 to 1,607 km², and each location being on average 11 km from the centre. Centres were calculated as the harmonic mean of all locations for each location class. Despite there being fewer locations, 506 versus 611, range sizes using locations with LC 0 were on average 17.3 times larger than range sizes calculated using locations with LC 1 (sd ± 4.7). The majority of locations with LC 3 and 2 were located within 1 km of the calculated centre (Fig. 1 & 2) while locations with LC 1 were generally within two km of the calculated centre (Fig. 3). Locations with LC 0

were most commonly within 10 km of the calculated centre, although a number were off from 10 to 50 km (Fig. 4).

Appendix A, Table 1.

	Total number of locations	LC3 (%)	LC2 (%)	LC1 (%)	LC0 (%)
3 June– 23 September 2003 ^a	774	36 (4.7)	98 (12.7)	181 (23.4)	209 (27.0)
30 September 2002 – 20 November 2003 ^b	2284	91 (4.0)	303 (13.3)	611 (26.8)	506 (22.2)

^a Time period when adult female Peregrines are in Thule.

^b Locations for entire battery life of PTT.

Number of locations, location classes, and percent of total LC 3–0 receptions received from stationary 30 gram battery-powered PTT at Thule Air Base, Greenland.

Appendix A, Table 2.

	90% MCP LC 3–0	90% MCP LC 3–1	95% Kernel LC 3–0	95% Kernel LC 3–1	50% Kernel LC 3–0	50% Kernel LC 3–1
Area in km ²	104	19	43	5	5	0.8

“Home range sizes” for the stationary PTT at Thule Air Base calculated using the same methods as for Peregrines in Table 10 of the main text. Locations from 3 June to 23 September 2003, a time period when Peregrines have been shown to be in Thule.

Appendix A, Table 3.

	LC 3 area in km ² (n = 91 loca- tions)	LC 2 area in km ² (n = 303 loca- tions)	LC 1 area in km ² (n = 611 loca- tions)	LC 0 area in km ² (n = 506 locations)
95% MCP	3.5	14	69	1,607
90% MCP	2.6	8.6	50	599
95% Kernel	2.6	4.9	12	193
50% Kernel	0.4	0.7	1.7	30

Home range sizes calculated using locations with LC 3, 2, 1, and 0 from a stationary PTT at Thule Air Base that operated from 30 September 2002 to 20 November 2003.

Appendix A, Table 4.

	LC 3 (n = 91 locations)	LC 2 (n = 303 locations)	LC 1 (n = 611 locations)	LC 0 (n = 506 locations)
Average distance from centre (km)	0.967	1.344	2.346	11.028
Maximum distance from centre (km)	7.000	10.369	14.556	116.628
Minimum distance from centre (km)	0.052	0.122	0.052	0.113

Average distance (km) each location varied from the centre based on locations with LC 3, 2, 1, and 0 for the stationary PTT at Thule Air Base. Centre was calculated as harmonic mean of all locations for each location class. Locations are from 30 September 2002 to 20 November 2003.

Appendix C.

ID	Attachment location (year)	Total life of unit in days	Total locations LC 3–Z	Total LC 3–0 (%)	Total LC 3 (%)	Total LC 2 (%)	Total LC 1 (%)
10212	Pituffik (01)	819	1,240	879 (70.9)	4 (0.32)	19 (1.53)	105 (8.47)
10217	Pituffik (01)	407	1,270	784 (61.7)	12 (0.95)	5 (3.94)	131 (10.3)
10292	Pituffik (01)	43	238	151 (63.4)	2 (0.84)	4 (1.68)	22 (9.24)
35234	Pituffik (02)	6	23	15 (65.2)	0	1 (4.35)	1 (4.35)
35240	Pituffik (02)	35	107	71 (66.4)	1 (0.94)	5 (4.67)	13 (12.1)
35255	Pituffik (02)	3	41	27 (65.9)	1 (2.44)	6 (14.6)	5 (12.2)
36014	Pituffik (03)	48	161	101 (62.7)	2 (1.24)	6 (3.73)	27 (16.8)
36015	Pituffik (03)	283	406	201 (49.5)	2 (0.49)	5 (1.23)	26 (6.40)
36016	Pituffik (03)	15	40	22 (55.0)	0	0	1 (2.50)
36017	Pituffik (03)	242	322	164 (50.9)	1 (0.31)	4 (1.24)	19 (5.90)
10219	Kanger. (01)	36	144	82 (56.9)	2 (1.39)	6 (4.17)	22 (15.3)
32948	Kanger. (03)	83	139	80 (57.6)	1 (0.72)	1 (0.72)	19 (13.7)
35235	Kanger. (02)	104	373	217 (58.2)	2 (0.54)	11 (2.95)	36 (9.65)
35236	Kanger. (02)	99	439	252 (57.4)	4 (0.91)	16 (3.64)	69 (15.7)
35237	Kanger. (02)	53	131	67 (51.1)	2 (1.53)	1 (0.76)	14 (10.7)
35238	Kanger. (03)	175	271	143 (52.8)	3 (1.10)	11 (4.16)	38 (14.0)
41437	Kanger. (03)	93	188	109 (58.0)	0	5 (2.66)	26 (13.8)
41438	Kanger. (03)	114	259	154 (59.5)	1 (0.39)	5 (1.93)	37 (14.3)

Longevity, amount, and location class of data for female Peregrine Falcons tagged with PTTs in the Kangerlussuaq and Pituffik areas, Greenland.

Appendix D.

ID	Yr	Location	90% MCP LC3-0, LC3-1	95% Kernel LC3-0, LC3-1	Number of LC 3-0, respectively (Total 3-1, 3-0)
10212	01	Pituffik	3,297, 491	1,620, 719	0, 9, 34, 156 (43, 199)
	03	Pituffik	403, 271	427, 224	2, 5, 27, 24 (34, 58)
10217	01	Pituffik	305, 39	531, 88	1, 5, 12, 13 (18, 31)
	02	Pituffik	4,296, 393	1,659, 157	8, 14, 62, 152 (84, 236)
35240	02	Pituffik	3,760, 40	1,504, 64	1, 5, 12, 47 (18, 65)
36014	03	Pituffik	1,272, 8	774, 15	1, 5, 26, 60 (32, 92)
36015	03	Pituffik	5,386, 41	4,531, *	2, 0, 4, 47 (6, 53)
36107	03	Pituffik	5,451, *	5,010, *	0, 1, 0, 40 (1, 41)
32948	03	Kanger.	2,709, 92	2,524, 255	1, 1, 19, 59 (21, 80)
35235	02	Kanger	1,720, 68	968, 82	1, 5, 21, 100 (27, 127)
35236	02	Kanger.	1,931, 47	423, 78	2, 10, 44, 113 (56, 169)
35237	02	Kanger.	2,187, 154	838, 337	2, 1, 14, 50 (17, 67)
35238	03	Kanger.	175, 33	158, 52	2, 6, 11, 31 (19, 50)
41437	03	Kanger.	752, 62	643, 124	0, 5, 26, 78 (31, 109)
41438	03	Kanger.	848, 50	629, 80	1, 1, 16, 70 (18, 88)

*not enough locations for a meaningful calculation.

Breeding home range size (in km²) for adult female Peregrine Falcons tagged with PTTs in the Kangerlussuaq and Pituffik areas, Greenland, based on multiple methods of calculation.

Appendix E.

ID	$t = \text{total LC } 3-0$	$n = \text{total LC } 3-1$	90% MCP	SD	SE
10212	199	43	2,168	± 557	85
	58	34	329	± 49	8
10217	31	18	231	± 69	16
	236	84	3,874	± 538	59
35240	65	18	2,406	± 1062	250
36014	92	32	943	± 331	58
36015	53	6	965	± 603	246
36017	41	1	*	*	*
32948	80	21	2,148	± 856	187
35235	127	27	1,059	± 266	51
35236	169	56	1,932	± 443	59
35237	67	17	993	± 872	212
35238	50	19	140	± 25	6
41437	109	31	599	± 116	21
41438	88	18	391	± 159	37

*not enough locations for a meaningful calculation.

Averages of five hundred 90% MCP calculated for each individual by randomly selecting n locations from t locations.

Temperature	Months	Regression equation ^b	SE of slope (° C)	t	p	r ²	T ^c (° C)
Mean monthly	May - Sept. ^a	$y = 0.041x - 80.30$	0.024	1.69	0.104	0.107	1.107
	May	$y = 0.067x - 138.66$	0.044	1.53	0.140	0.085	1.809
	June	$y = 0.022x - 41.30$	0.038	0.58	0.564	0.013	0.594
	July	$y = -0.005x + 15.21$	0.033	-0.15	0.884	0.000	-0.135
	August	$y = 0.046x - 88.68$	0.038	1.22	0.236	0.056	1.242
	September ^a	$y = 0.051x - 103.30$	0.043	1.20	0.243	0.056	1.377
Min. monthly	May - Sept. ^a	$y = 0.020x - 47.89$	0.033	0.61	0.544	0.015	0.540
	May	$y = 0.198x - 412.68$	0.076	2.60	0.015	0.213	5.346
	June	$y = -0.001x - 1.60$	0.043	-0.03	0.976	0.000	-0.027
	July	$y = -0.015x + 28.22$	0.041	-0.36	0.723	0.005	-0.405
	August	$y = -0.077x + 150.27$	0.051	-1.50	0.145	0.083	-2.079
	September ^a	$y = 0.060x - 131.68$	0.060	0.99	0.333	0.039	1.62
Max. monthly	May - Sept. ^a	$y = 0.058x - 106.65$	0.037	1.56	0.131	0.092	1.566
	May	$y = 0.069x - 131.64$	0.084	0.82	0.421	0.026	1.863
	June	$y = 0.029x - 45.60$	0.074	0.40	0.695	0.006	0.783
	July	$y = -0.035x + 84.61$	0.053	-0.67	0.512	0.017	-0.945
	August	$y = 0.071x - 130.69$	0.073	0.98	0.337	0.037	1.917
	September ^a	$y = 0.043x - 80.01$	0.055	0.78	0.443	0.025	1.161

^a No data for September 1988. 1988 was also excluded when calculating mean minimum temperatures from May to September.

^b Regression equation is in the format $y = mx + b$ where y is the temperature, m is the slope of the line, x is the year, and b is the y intercept.

^c Change in temperature over the period analyzed.

Changes in average, minimum, and maximum temperature for the five-month period May to September from 1979 to 2005. Data from Thule Air Base weather station.



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KURT BURNHAM has worked throughout Greenland studying Peregrine Falcons and Gyrfalcons for the past 22 years. He is currently the President and CEO of the High Arctic Institute.

WILLIAM A. BURNHAM was President of The Peregrine Fund, an international conservation and research organization focused on rare and endangered birds of prey, from 1986 until his death in 2006.

IAN NEWTON is a British ornithologist who has worked on many different aspects of avian ecology.

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